ENERGY BUDGETS FOR THE CARIBBEAN REEF CORAL *PORITES PORITES* (PALLAS)

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ABSTRACT

The aim of this study was to extend the contemporary energy budget methodology for algal-cnidarian symbioses and apply it to the tropical reef coral Porites porites growing in two different environments. It was hoped that the measured energy inputs to P. porites would be equalled by the measured energy requiring processes, without a surplus or deficit of energy being determined by subtraction, and that P. porites would show a differential derivation, allocation and utilisation of energy in the two environments.

Porites porites was studied at 10 m depth at both the West Fore Reef (WFR) and Columbus Park (CP) regions of Discovery Bay, Jamaica. The transmission of surface photosynthetically active radiation (PAR) to 10 m depth, the temperature, sedimentation rates and nutrient levels were recorded at both sites. The CP site received less PAR, had a greater sedimentation rate and slightly enhanced nitrate concentrations compared to the WFR site.

The energy budgets were calculated from measurements of photosynthesis, zooxanthellae and host respiration, zooxanthellae and host growth, colony reproduction and mucus loss. These budgets show that P. porites at both sites can be autotrophic in terms of energy on an 'ideal' day. No evidence was obtained for habitual zooplankton capture at either site. Photoadaptation at the CP site ensured that the input of photosynthetically fixed energy (PFE) was greater than at the WFR site. On an 'ideal' day at both sites 21% of the PFE was used for zooxanthellae respiration and less than 0.5% for colony reproduction whilst 26.3% (WFR site) or 6.6% (CP site) was used for host respiration and 7.1% (WFR site) or 4.3% (CP site) for zooxanthellae and host tissue growth. The loss of soluble or particulate macromolecular mucus did not account for significant

amounts of energy. More than 45% of the PFE remained unaccounted for at both sites on an ideal day. A similar autotrophic status and an apparent surplus of PFE can be maintained on nearly every day of the year at both sites.

In order to account for the apparent surplus energy from P. porites the colony respiration rate was compared during the day and night, the formation and energy content of mucus tunics were measured and lipid reserves determined. The colony respiration rate (representing the colony energy expenditure) increased after exposure to light and this was a function of the host tissue alone. The effect was greater at the CP site. Calcification and nutrient uptake mechanisms, and in particular the active transport of ions involved in these processes may account for the increased energy expenditure. The between-site differences in the magnitude of the elevated daytime respiration rate may represent a hitherto unrecognised cost of inhabiting the CP site.

Lipid accounted for more than 18% of the dry tissue content of P. porites at both sites and supported the concept of a lipid based energy economy in corals. The daily surplus of energy can be stored as lipid in P. porites, although lipid was not metabolised during 5 days of darkness. It is suggested that lipid reserves may be important at the CP site where they could be lost as mucus during sediment shedding. Circumstantial evidence suggests that P. porites can utilise heterotrophic sources of nutrition (< 50 μm in size).

The hypothesis that energy was periodically lost as mucus tunics was shown to be incorrect. Although tunics have a low energy content they may have an important effect in decreasing the autotrophic input by decreasing colony photosynthesis. It is suggested that the loss of low molecular weight compounds may be an alternative route for surplus energy instead of mucus.

The initial objectives of the study were only partly fulfilled. Although the energy budgets showed some between site differences they were still balanced by subtraction. However, studies of lipid reserves, the daytime respiration rate and mucus tunics show that these can partially account for the apparent surplus of energy. Further studies of the significance and mechanisms of an elevated daytime respiration rate and the role of heterotrophic nutrition in scleractinian corals will probably make a major contribution to our further understanding of the nutritional relationships in algal-cnidarian symbioses.

CHAPTER 1: INTRODUCTION

1.1 General introduction.

Present day living coral reefs occur to a depth of 100 m (Goreau et al., 1979) in tropical seas where the annual temperature generally remains above 18°C (Wells, 1957). They represent the integrated action of plants, invertebrates and vertebrates through thousands of years of secretion, accretion and solution of $CaCO_3$. The single most important group in the development of tropical reefs are the hermatypic scleractinian corals. Corals secreting massive robust skeletons are the main reef builders (Goreau, 1959a) and provide the primary framework which is colonised by a secondary growth (Goreau and Goreau, 1973), including encrusting algae (Dahl, 1974), sponges (Wulff and Buss, 1979) and corals. The latter corals are often branching, fragile forms which readily break off (Tunnicliffe, 1982) and fill the spaces between the massive corals.

Scleractinian corals can be divided into reef-building (hermatypic) containing zooxanthellae and non reef-building (ahermatypic) without zooxanthellae (but see Sheppard, 1982 for exceptions). Zooxanthellae are photosynthetically active dinoflagellates endosymbiotic in representatives from five phyla. Originally described as Symbiodinium microadriaticum (Freudenthal, 1962) and then monospecific Gymnodinium microadriaticum amongst benthic marine invertebrates (Taylor, 1974), it now appears that host-specific strains of Symbiodinium (=Gymnodinium) microadriaticum occur (Schoenberg and Trench, 1980 a,c) which may be genetically different (Blank and Trench, 1985).

Coral zooxanthellae are intracellular in the gastrodermis and are surrounded by a host vacuole. Each zooxanthella is about 10-14 µm in diameter (Muscatine, 1980a), contains a chloroplast, pyrenoid, "assimilation product" (Trench, 1971a) and lipid droplets (Patton and Burris, 1983). Zooxanthellae and host cells divide in harmony (Trench, 1980), but zooxanthellae *in situ* have lower specific growth rates than some free living dinoflagellates (Wilkerson *et al.*, 1983) and show morphological changes including the development of a motile phase when isolated and cultured (Freudenthal, 1962; Schoenberg and Trench, 1980b). Under normal conditions, either an active or passive mechanism must act between the host and algae to control both reproduction and development of the zooxanthallae.

1.2. Advantages of the symbiosis

The nature of the association between host and zooxanthellae has been widely discussed since the start of coral physiological work (Yonge, 1930; Yonge and Nicholls, 1931a,b; Yonge, 1934; Goreau *et al.*, 1971; Muscatine, 1973) and hermatypic corals are now considered as mutualistic symbioses (Muscatine and Porter, 1977; Trench, 1980). Benefits of the symbiosis are expressed in the calcification and nutrition of the hermatypic coral colony, but are the direct result of algal-animal interactions.

Hermatypic corals with zooxanthellae calcify faster in the light than they do in darkness (Goreau and Goreau, 1959; Kawaguti and Sakumoto, 1948; Pearse and Muscatine, 1971), whilst aposymbiotic and ahermatypic corals without zooxanthellae calcify more slowly (Goreau, 1959b; Goreau and Goreau, 1959; Jacques *et al.*, 1983). Three mechanisms have been proposed to explain this enhancement:

1. Goreau (1963) suggested that the photosynthetic fixation of CO_2 by the zooxanthellae promotes the calcification reaction:

$$Ca^{++} + 2HCO_3^- \leftrightarrow Ca(HCO_3) \leftrightarrow CaCO_3 + H_2CO_3$$

to deposit $CaCO_3$ at the calcifying surface.

2. Simkiss (1964) showed that <u>in vitro</u> $CaCO_3$ deposition could be inhibited by the presence of PO_4^{3-}, and suggested that zooxanthellae enhance calcification by taking up mineral PO_4^{3-}.

3. Zooxanthellae may indirectly enhance calcification by providing metabolites (Pearse and Muscatine, 1971), for the organic matrix (Wainwright, 1963), free energy for the calcification process (Goreau <u>et al.</u>, 1979), or by a non-specific enhancement of host metabolism (Rinkevich and Loya, 1984).

Colony morphology and skeletal architecture are important for protection (Yonge, 1968), in optimising light or zooplankton capturing ability (Porter, 1976), resisting wave damage (Schuhmacher and Plewka, 1982) and in sediment shedding ability (Hubbard and Pocock, 1972). Rapid growth and calcifation are advantageous in overgrowth (Connell, 1973), in combating digestive aggression (Lang, 1973) and also in aiding recovery after fragmentation (Highsmith, 1982). The ecological importance of rapid calcification in corals cannot be over emphasised in its contribution to their success.

Studies of coral nutrition have focused on determining the proportional significance of autotrophy or heterotrophy. Early researchers considered corals to feed entirely on zooplankton (Murray, 1889; Duerden, 1902), or that corals fed entirely "by" their zooxanthellae (Gardiner, 1901; 1904) or that they digested their zooxanthellae (Boschma, 1925). During the Great Barrier Reef

Expedition of 1928-29, Yonge (1930) and Yonge and Nicholls (1931 a,b) studied coral nutrition and found that neither tentacles nor mesenterial filaments reacted to the presence of plant material and that some corals fed with zooplankton could survive without atrophy in total darkness for up to 228 days. They concluded that corals were carnivores and obtained no nourishment from their zooxanthellae. Although evidence of host digestion of zooxanthellae has been found in the giant clam Tridacna (Frankboner, 1971), the alcyonarian Heteroxenia fuscescens (Schlichter, 1982) and the ahermatypic coral Astrangia danae (Szmant-Froelich and Pilson, 1980), conclusive evidence for digestion of zooxanthellae in hermatypic corals is lacking (Cook, 1983). As corals may be unable to digest plant cells if they lack cellulase as in some anemones (Elyakova, 1972), it is therefore unlikely that they obtain nutrients by digesting their zooxanthellae if these algae also contain cellulose in their cell walls.

Corals can also obtain nutrients from their zooxanthellae if the algae have a surplus of photosynthetically fixed carbon (PFC) which is available to the host. According to Yonge et al. (1932) photosynthetically produced carbohydrate is used solely for zooxanthellae requirements. These authors also showed that photosynthetic oxygen production could exceed the respiratory demands of the coral colony. However, the stoichiometry between carbon and photosynthetic oxygen evolution and respiratory oxygen consumption was not fully understood until the late 1940's and they were therefore unable to relate oxygen flux to carbon fixation. Similar results were later found for whole coral reefs (Sargent and Austin, 1949; Kohn and Helfrich, 1957; Barnes, 1983) and individual colonies (Kawaguti, 1937; Roffman, 1968). These authors were able to show that corals with a net

oxygen evolution (that is corals with a ratio of oxygen production: respiratory oxygen consumption (P:R) exceeding one) were photosynthetically fixing more carbon than they were respiring, and were therefore potentially autotrophic.

Muscatine and Hand (1958) provided the first proof that PFC was translocated from zooxanthellae to the host in the symbiotic anemone Anthopleura elegantissima. Isolated zooxanthellae from various cnidarian hosts have since been shown to release a variety of low molecular weight compounds including glycerol, glucose, aspartate, alanine, mannose, leucine, and succinate (Muscatine and Cernichiari, 1969; Smith et al., 1969; Trench, 1971b; Trench, 1974; Schmitz and Kremer, 1977), and that the in vitro release is enhanced by the presence of host extract (Muscatine, 1967; Trench, 1971c). Zooxanthellae release similar compounds in vivo (Trench, 1971a; Lewis and Smith, 1971).

As late as 1968 Yonge still maintained that "Scleractinia are specialised carnivores" even though he accepted that the interchange of metabolites occurred between zooxanthellae and the host. The fed in darkness experiment of Yonge and Nicholls (1931b) was repeated under slightly different conditions by Franzisket (1970). He maintained 4 species of Pacific hermatypic corals in darkness in unfiltered seawater containing the natural zooplankton population. All the corals atrophied or died within 60 days suggesting that zooplankton could not supply all their nutritional requirements. Atrophied corals fully regenerated if returned to filtered water in the light, and Franzisket (1970) concluded that some hermatypic corals were able to live from the photosynthetic products of their zooxanthellae. It is now beyond doubt that corals obtain nutritional benefits from their zooxanthellae.

Symbiotic zooxanthellae require PFC for their own growth and reproduction and only the surplus is available for translocation. Early experiments suggested that less than 50% of the PFC was translocated *in vivo* (Muscatine and Cernichiari, 1969; Trench, 1971a), but more recent work shows that greater than 90% can be translocated to the host (Davies, 1984; Muscatine *et al.*, 1984). Although Steele (1977) described the extrusion of zooxanthellae containing pellets in a variety of tropical anemones and the coral *Porites* spp., they have not been found in a wide variety of corals and probably do not represent a significant loss of PFC.

Glycerol was consistently found to be a major component of translocated carbon and was thought to be converted to lipid within the host using host derived fatty acyl and/or fatty alcohol chains (Muscatine and Cernichiari, 1969; Trench, 1971a), since more than 50% of photosynthetically fixed $^{14}CO_2$ was recovered from coral lipid (Schmitz and Kremer, 1977; von Holt and von Holt, 1968). A source of acyl moieties required by this mechanism was not found, and an alternative pathway was sought to explain the origin of lipids which can constitute more than 33% of the dry tissue of tropical anemones (Bergmann *et al.*, 1956) and corals (Patton *et al.*, 1977). Patton *et al.* (1977) found that the majority of coral lipogenesis in *Pocillopora capitata* occurred in the zooxanthellae whilst most lipid was stored in the host tissue. Zooxanthellae in intact *Stylophora pistillata* used $^{14}CO_2$ and acetate-1-^{14}C in the light to synthesise lipid which contained labelled acyl moieties (Patton *et al.*, 1983), whilst zooxanthellae released discrete lipid droplets in *S. pistillata* (Patton and Burris, 1983) and *Acropora acuminata* (Crossland *et al.*, 1980). It now seems likely that coral zooxanthellae use photosynthetically fixed carbon to synthesise lipid and translocate discrete lipid droplets to the host in addition to glycerol. Glycerol

may be used as an immediate respiratory substrate by the host, whilst lipids provide a longer term energy store (Battey and Patton, 1984). The lipid based energy economy of Pocillopora capitata (Patton et al., 1977) may be a common feature among hermatypic corals.

Zooplankton capture by corals has been observed by Yonge and Nicholls (1931b), Johannes et al. (1970) and Johannes and Tepley (1974), whilst Porter (1974) found zooplankters representing 8 phyla in gut samples from the coral Montastrea cavernosa. Coral feeding responses are initiated by chemical (Mariscal and Lenhoff, 1968) and tactile (Lewis and Price, 1975) stimuli leading to ingestion and digestion. Digestion is initially extracellular within the coelenteron involving the mesenterial filaments and protease enzymes, followed by phagocytosis and intracellular digestion (Yonge and Nicholls, 1930). Mesenterial filaments are mobile structures and can also creep through the mouth or body wall to engage in extracoelenteric detritus feeding (Goreau et al., 1971).

Yonge (1968) noted that expanded corals have a "feeding surface in relation to the actual volume of living tissue unparalleled in the animal kingdom" and suggested that this was one of the main reasons for the success of the group. Although zooplanktivory is intuitively consistent with a tentacular morphology it accounted for less than 11% of the daily energy requirements of Montastrea cavernosa (Porter, 1974) and Porites lobata (Johannes and Tepley, 1974). However corals have a suite of mechanisms for obtaining heterotrophic nutrition including 4 methods of suspension feeding (Yonge, 1930; Muscatine, 1973; Lewis and Price, 1975):

1. Tentacular feeding with the epidermal cilia concerned with cleansing.
2. Ciliary-mucoid feeding alone.

3. Ciliary-mucoid feeding with a variable role of the tentacles.

4. Extrusion of mesenterial filaments.

The epidermal cilia of corals are arranged into directionally coordinated tracts which carry materials either into the mouth or off the colony. Together with a mucus coating, the epidermis provides a sticky trap for food particles including protozoa and nanoplankton (Muscatine, 1973), and perhaps bacteria. Corals can take up labelled bacteria from sea water (DiSalvo, 1971; Sorokin, 1973), but suggestions of digestion and assimilation of these bacteria by the host (Sorokin, 1973) are confounded by the external mucus layer which harbours a natural bacterial population (Ducklow and Mitchell, 1979a), and which would also be able to adsorb and support an active labelled bacterial population. Bacteria may alternatively be "farmed" by corals within their coelenterons as appears to occur in the tropical anemone Stoichactis giganteum (Hernal and Velimirov, 1985).

The uptake of dissolved organic matter (DOM) is a potential but controversial source of nutrition for corals. Corals are pre-adapted for DOM uptake with numerous epidermal microvilli (Goreau and Philpott, 1956; Mariscal, 1974) providing a high surface area for uptake. A variety of corals take up low molecular weight organic compounds from solution (Lewis and Smith, 1971; Stephens, 1962), and may metabolise them (Lewis and Smith, 1971). However, the experiments on corals may be confounded by the presence of bacteria in the epidermal mucus layer. These may account for a major portion of the observed uptake of low molecular weight organic compounds by corals even if antibiotics are included in the incubation medium since many antibiotics are not 100% effective against bacteria (Dalla Via, 1983). Nevertheless a wide range of marine invertebrates can utilise DOM (Ferguson, 1982) and corals are unlikely to be exceptional.

As corals survive extremely well in tropical seas depleted of mineral nutrients (Muscatine, 1980b; Thomas, 1970) they must have mechanisms for obtaining and retaining them. Various intact symbioses have an uptake or reduced excretion of phosphorous (D'Elia, 1977), ammonium (Muscatine and D'Elia, 1978) and nitrate (Webb and Wiebe, 1978). Similar uptakes are shown by freshly isolated zooxanthellae (D'Elia et al., 1983; Muscatine et al., 1979). Light enhances coral uptake of PO_4^{3-} and NH_4^+, but probably not NO_3^- (Webb and Wiebe, 1978; but see Muscatine, 1980b). As zooxanthellae have been shown to translocate nitrogen- and phosphorous-containing compounds in vitro and in vivo (see Cook, 1983 for a review), it seems certain that corals retain, recycle and absorb mineral nutrients through the action of their zooxanthellae. Zooplankton ingestion may also be important in supplying essential nutrients (Johannes et al., 1970) but this idea remains unproven.

Using morphological evidence alone, Porter (1976) suggested that Caribbean reef corals could be located on a continuous scale between a totally autotrophic nutritional strategy and a totally heterotrophic nutritional strategy. More autotrophic species have a high surface area to volume ratio (S:V) to optimise light capture, with small diameter polyps, whilst more heterotrophic species have a low S:V ratio and large diameter polyps to optimise zooplankton capture. He suggested that individual families occupy discrete and non-overlapping niches based on resource partitioning of limiting nutrients.

Within the last decade attempts have been made to accurately quantify the contribution of zooxanthellae to the hosts nutrition. Muscatine, Porter and co-researchers have looked at the contribution of translocated zooxanthellae carbon to the animal daily respiratory carbon requirements (CZAR) (Muscatine et al., 1981; Muscatine and Porter, 1977). They argued that the importance of translocated carbon

lies in its use by the host for respiration, and they determined the percentage translocation by direct measurement. When CZAR is greater than 100% the coral is potentially fully autotrophic in terms of respiratory carbon demand. CZAR for Pocillopora damicornis and Fungia scutaria growing in "shallow water" was 63% (40% PFC translocation) and 69% (25% PFC translocation) respectively (Muscatine et al., 1981).

Davies (1984) took a different approach and assumed that all PFC unrequired by the zooxanthellae was translocated to the host for use in a variety of processes in addition to animal respiration. Considering PFC in terms of energy, Davies (1984) predicted a daily surplus of 48% of photosynthetically fixed energy for Pocillopora eydouxi at 5m depth. Muscatine et al. (1984) subsequently broadened their CZAR methodology to include daily carbon budgets for Stylophora pistillata growing at 2 m depth in the light or shade. They showed that more than 95% of the PFC was translocated to the host in both the light and shade specimens, and that CZAR was 143% and 58% respectively. Their budgets show that there was a daily surplus of carbon only in the light specimens.

Hermatypic corals have a wide variety of sources and uses of nutrients and energy, and because many of these remain unquantified the full proportional significance of autotrophy or heterotrophy in the nutrition of corals remains unresolved.

1.3 The research topic

Models of carbon or energy flow through algal-cnidarian symbioses have been constructed by Davies (1984), Muscatine et al. (1984) and Tytler (1982). These have been based on the concept of equating energy inputs with energy uses in the form of an energy budget. The energy

budgets as defined by Tytler (1982) and Davies (1984) are extended and applied to a tropical reef coral in the present study as shown in Figure 1.

The previous energy or carbon budgets have incorporated measurements of respiration, photosynthesis and growth (although Muscatine et al. (1984) measured host tissue growth by subtraction). Tytler (1982) went slightly further by including the heterotrophic input as squid rations and the energy expended in specific dynamic action into his energy budget for Anemonia sulcata, whilst Muscatine et al. (1984) included the loss of particulate and dissolved organic carbon into their carbon budgets for Stylophora pistillata. In all of these studies the energy inputs and the energy uses could not be balanced from the measurements alone and at least one energy source or use was determined by subtraction.

Davies (1984) calculated the energy budget for Pocillopora eydouxi on a cloudless day in Guam by making measurements of colony growth, photosynthesis and respiration. The energy content of zooxanthellae and coral tissue were obtained from other cnidarians. As Crossland et al. (1980) had shown that 40% of the net carbon fixed by Acropora acuminata was lost as mucus, Davies (1984) speculated that the surplus of energy in P. eydouxi might follow the same route.

None of these previous studies incorporated an in situ estimate of heterotrophic nutrition which has been shown to be important in some corals. The zooxanthellae respiration rate is a crucial quantity in determining the magnitude of the PFC available for translocation, but has only been indirectly estimated (Muscatine et al., 1984) or extrapolated from another coral (Davies, 1984; Tytler, 1982). With an increasing awareness of the potential importance of coral mucus in the reef environment (Gottfried and Roman, 1983; Richman et al., 1975), only Muscatine et al. (1984) have made an attempt to quantify the loss

Figure 1. The bioenergetic model used for a tropical reef coral in the present study. The energy of the photosynthetically fixed carbon is used to supply the energy demands of zooxanthellae respiration and growth. Energy surplus to these requirements is assumed to be translocated to the animal host. The host obtains energy from translocates, zooplankton and other heterotrophic sources (bacteria, DOM etc.) which supply the energy demands of host respiration, growth, reproduction and mucus secretion. Surplus energy is presumed to be lost from the colony by various routes.

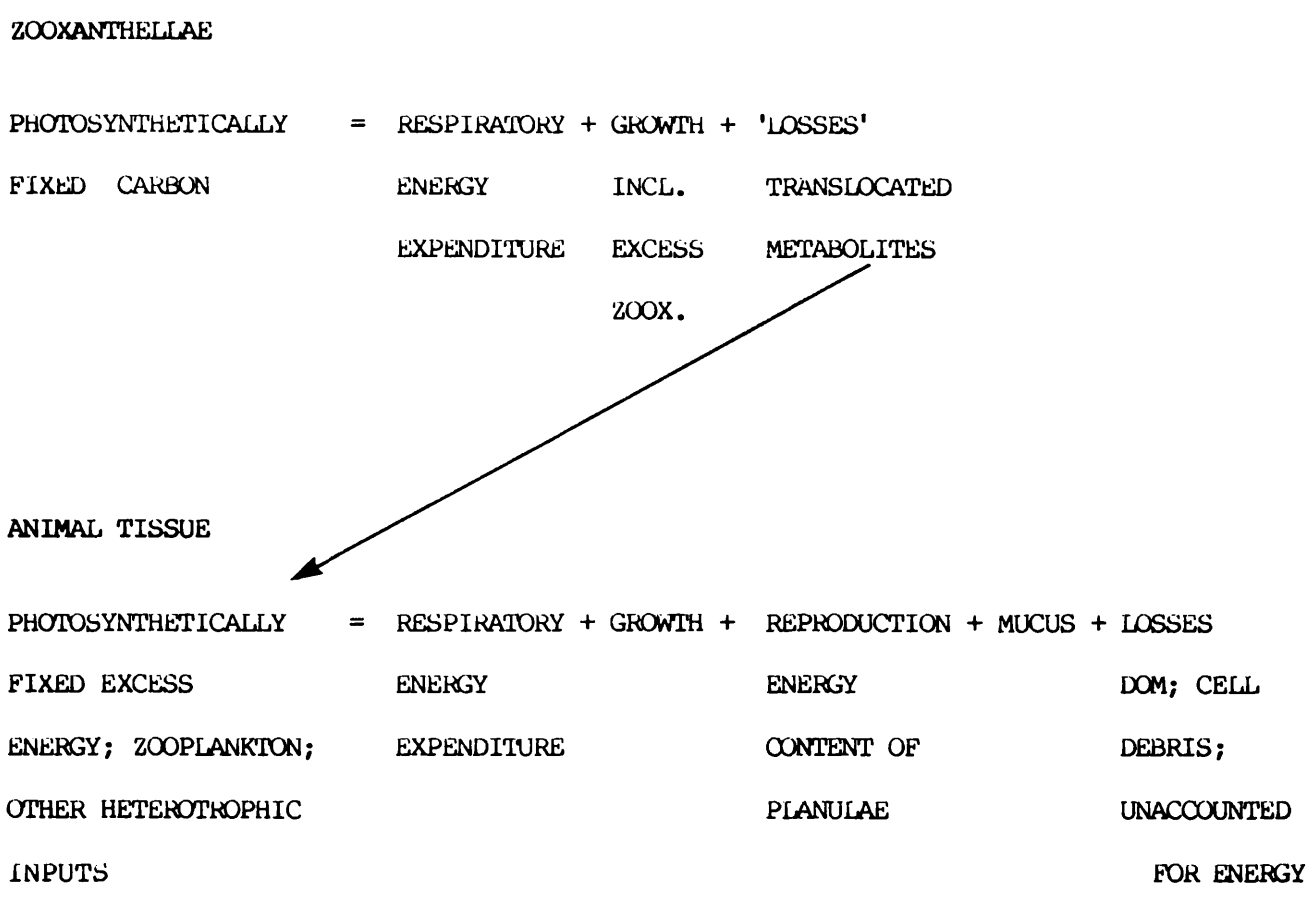

ZOOXANTHELLAE
PHOTOSYNTHETICALLY FIXED CARBON
=
RESPIRATORY ENERGY EXPENDITURE
+
GROWTH INCL. EXCESS ZOOX.
+
'LOSSES' TRANSLOCATED METABOLITES
ANIMAL TISSUE
PHOTOSYNTHETICALLY FIXED EXCESS ENERGY; ZOOPLANKTON; OTHER HETEROTROPHIC INPUTS
=
RESPIRATORY ENERGY EXPENDITURE
+
GROWTH
+
REPRODUCTION ENERGY CONTENT OF PLANULAE
+
MUCUS
+
LOSSES DOM; CELL DEBRIS; UNACCOUNTED FOR ENERGY

FIGURE 1.

of particulate/dissolved organic carbon in relation to an overall carbon budget for Stylophora pistillata. Finally, all previous budgets have been calculated on 'sunny days' and data have not been available to extend the budgets over a longer period.

In the present study energy budgets were constructed for the tropical reef coral Porites porites (Figure 1). The first aim of the study was to replace some of the estimates in the earlier studies with accurate measurements so that the energy inputs would be equalled by the measured energy uses. Frequent inspections of P. porites for the presence of zooplankters were used to answer the controversial question of the importance of heterotrophy in corals. For the first time measurements of the energy expended by zooxanthellae were used instead of estimated or extrapolated values. The concept that significant quantities of energy or carbon are lost from corals was challenged by in situ measurements of mucus release. Measurements of planulae release together with their energy content were used to quantify the previously undetermined energy expenditure on coral reproduction. Finally, growth rates over at least 9 weeks were converted to energy units using the predetermined energy content of zooxanthellae and host tissue.

The second aim of the study was to further extend the energy budget methodology by attempting comparisons of Porites porites from both a 'favourable' and an 'unfavourable' environment. It was hoped that different environmental conditions would result in differences in the derivation, allocation and use of energy within the colony and that these would be shown by the energy budgets. An additional aim was then to extrapolate the daily energy budgets at each site to a whole year using frequent measurements of the transmission of surface light to the study depth together with annual light data to estimate the annual autotrophic input to P. porites.

Finally, it was hoped that the study would propose new areas of research to increase the accuracy of the energy budgets in representing the flow of energy through algal-cnidarian symbioses. To this end data on lipid storage, mucus tunics and the variability of colony respiration rate were collected. These were compared between study sites and were used to suggest future modifications to the energy budgets.

CHAPTER 2: THE STUDY SITES

2.1 Introduction

There are abundant data in the literature which show that coral growth and development can be detrimentally effected by environmental conditions. Both hypersaline and hyposaline conditions (Marcus and Thorhaug, 1982; Goreau, 1964), elevated or reduced temperatures (Jokiel and Coles, 1974; 1977), eutrophication (Pastorok and Bilyard, 1985), high sedimentation (Dodge *et al.*, 1974) and increased turbidity (Johannes, 1975), whilst hard substrate is essential for planula settlement (Fadlallah, 1983).

Other studies show more directly that the energy sources and uses in corals are effected by environmental conditions. Corals have an increased respiratory energy expenditure whilst shedding sediments (Dallmeyer *et al.*, 1982), which involves the use of mucus (Hubbard and Pocock, 1972) containing photosynthetically fixed carbon (Crossland *et al.*, 1980). Whilst shedding sediments polyps may be unable to simultaneously capture particulate food to replace the energy loss (Pastorok and Bilyard, 1985). Increases in temperature may decrease production:respiration ratios in corals (Coles and Jokiel, 1977), whilst both photosynthesis and respiration increase with temperature in the coral *Astrangia danae* (Jacques *et al.*, 1983). High temperatures may also prevent normal feeding behaviour in corals (Edmondson, 1928).

In order to document and compare the differences in energy derivation and allocation within *Porites porites* under different environmental conditions, energy budgets were calculated for this coral growing in both an 'ideal' and a 'less than ideal' environment. It was presupposed that these two environments were sufficiently different to result in measurable changes in the energy sources and uses within *P. porites* growing at each site.

2.2 The research sites

The study was carried out on the reefs at Discovery Bay on the north coast of Jamaica. Discovery Bay (Figure 2) is a semi-enclosed basin with a fringing reef across the mouth bisected by a 12 m deep ship channel. The fringing reef forms a partial barrier between the bay and the fore reef environment. The bay has a 50 m deep central depression, a shallow lagoonal shelf (to 8 m depth) occupying the eastern third of the bay, and areas of shallow lagoonal water interspersed with narrow, steeply sloping reefs along the western shore. The Discovery Bay Marine Laboratory (DBML) is situated on the north western shore of the bay.

The fore reef at Discovery Bay is generally less than 500 m wide and has major submarine reef breaks parallel to the shore at about 25 m and 60 m depth, where the reef gradient increases and the biota changes (Goreau and Wells, 1967). Most reef growth occurs above the 25 m break and can be separated into three zones seaward from the shore, each with a characteristic species composition: backreef (0.5 - 15 m depth), reef crest including the buttress zone (1 - 10 m depth) and the fore reef (7 - 15 m depth) (Goreau, 1959a). The buttress zone is characteristic of Jamaican fringing reefs and consists of elongated buttresses projecting into the prevailing seas and normal to the reef front. These can be up to 10 m high and 20 m - 30 m in length and are separated by sand channels.

A study site was chosen on the West Fore Reef at 10 m depth on the horizontal surface of a coral buttress close to 'Mooring 1' (WFR site), and also at 10 m depth on the western shore of Discovery Bay at 'Columbus Park' (CP site). These sites are shown in Figure 2.

Figure 2. Location of Discovery Bay in Jamaica and the Discovery Bay Marine Laboratory (DBML). The two study sites are marked as CP (Columbus Park) and WFR (West Fore Reef) and the ship channel is shown in dashed lines.

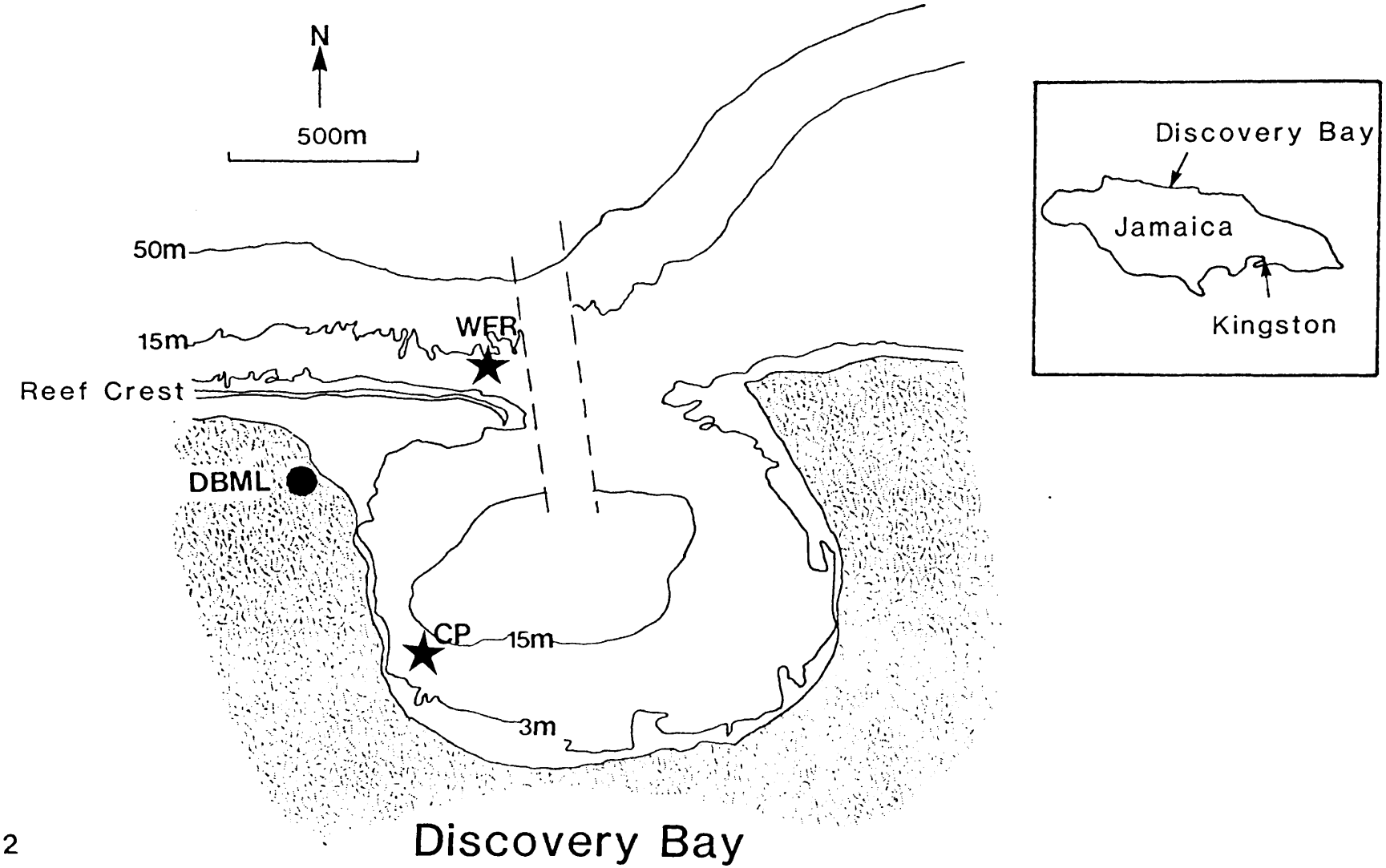

N
500m
50m
15m
Reef Crest
WER
DBML
CP
15m
3m
Discovery Bay
Jamaica
Kingston

Figure 2

The WFR site approximated an 'ideal' reef environment with a solid substrate, clear water and an apparent low sedimentation rate. Summer swells generally had little effect at 10 m depth, but winter storms and hurricanes created considerable turbulence. Hurricane Allen in 1980 severely damaged the scleractinian fauna on Discovery Bay reefs to 50 m depth (Woodley et al., 1980) and the coral cover was reduced from about 53% to about 11% at 10 m depth (Porter et al., 1981). Pre-hurricane coral fauna had not been replaced when the present study was carried out (May 1984 - April 1986), but the corals Porites porites, P. furcata, P. astreoides, Montastrea annularis, M. cavernosa, Madracis mirabilis, Agaricia agaricites and Acropora cervicornis were present at the WFR site, although colonies were small and the percentage cover appeared low.

The CP site was 'less than ideal' for coral growth and provided a contrast to the fore reef. A shallow lagoon less than 1 m deep extended approximately 30 m from a limestone cliff into the bay, and was marked by extensive growths of Millepora spp. at the start of the reef slope. The reef sloped downward at about 70° to the CP site at 10m depth and then to 30 m depth where an extensive Spondylus spp. (Mytiloida) reef developed and continued into the central depression at 50 m depth. In many places freshwater percolated through the reef to provide a significant enrichment of nitrogen to the bay (D'Elia et al., 1981). Much of the substrate on the reef slope below 3 m depth was loose, unconsolidated sediments which were readily resuspended. Particulate matter in the water column kept underwater visibility less than 5 m at 10 m depth. Strong north-easterly daily Trade Winds and storms had a 1.5 km fetch across the bay and resulted in choppy water and resuspended sediments at the western shore. Corals at the CP site grew on solid substrate protruding through the sediments and the coral cover appeared lower than at the WFR site, although quantitative

comparisons were not made. Porites porites, P.furcata, Madracis mirabilis, Eusmilia fastigiata, Siderastrea siderea and Montastrea annularis were found at the CP site.

Measurements of light transmission to 10 m depth, temperature, sediment deposition, and nitrogen concentration present as ammonium, nitrite and nitrate were made at these two sites. It was anticipated that P. porites would have different energy budgets at each site and that these differences could be related to a limited number of quantified environmental characteristics.

2.3 Light measurements

2.3.1 Methods

Light measurements were made nearly every day between 27 May 1985 and 21 July 1985 and also 21 December 1985 and 23 January 1986 at both sites, using a LiCor LI 185B meter with a LI 192SB sensor. The sensor measures photosynthetically active radiation (PAR) between 400 nm and 700 nm wavelength. PAR was measured at various times of the day (most frequently between 11.30 and 12.30 hrs.) from the sunward side of a small moored boat. Readings with the LI 192SB sensor were affected by gyration along the vertical axis of the sensor relative to the light source. As this was pronounced in a small boat, light readings were made immediately below the water surface in lieu of a surface reading. The sensor was clamped vertically upward and was lowered into the water to take readings below the surface (2 - 3 cm depth) and at 10 m depth in quick succession. Boat movement altered the depth and attitude of the sensor and caused fluctuations in the readings. All readings were taken as the mean of the two extremes of the fluctuation. PAR at 10 m depth was expressed as a percentage of the PAR immediately below the surface to give the percentage transmission.

In order to determine whether the transmission of surface PAR to 10 m depth varied throughout the day, the surface PAR was measured continuously on 24 June 1985 using a LI 185A meter and a LI 192S sensor placed on the roof of the marine laboratory. PAR was also measured at 10 m depth on the fore reef throughout the same day using the LI 185B meter and LI 192SB sensor. Underwater measurements were made every 15 minutes during the early morning and late afternoon when PAR changes rapidly, but were made approximately every 30 minutes during the midday period when PAR changes more slowly. Percentage transmissions to 10 m depth throughout a whole day were calculated from these data.

In order to compare the total PAR received on a cloudless day with that received on a heavily overcast day, PAR was also measured on the roof of the marine laboratory on 16 June 1985 and 13 January 1986 using the LI 192SB sensor and LI 185B meter. PAR vs time curves were divided into 15 minute increments and the PAR was interpolated from the curve at the median time for each increment. These instantaneous values in units of $\mu E.m^{-2}.s^{-1}$ were converted to absolute values (in units of $\mu E.m^{-2}.15\ min^{-1}$) over each 15 minute period and summed over the whole day to give the integrated daily PAR.

2.3.2 Results

Light transmission data are shown in Table 1 and Figure 3. Mean values, confidence intervals and statistics were carried out on arcsine transformed data (Sokal and Rohlf, 1969). The bulked data for May/July and Dec./Jan. for each site are normally distributed for a class interval of 1.9% (Kolmogorov-Smirnov Test: WFR site, D = 0.0337, n = 16; CP site, D = 0.0744, n = 16: both not significantly different

Condition		WFR	CP	t	df
May/July	Mean	26.2 (30)	20.4 (38)	6.5159 ***	66
	95% range	[24.9 - 27.4]	[19.1 - 21.7]		
	Total range	[18.3 - 32.1]	[12.8 - 34.0]		
Dec/Jan	Mean	27.8 (28)	17.9 (28)	7.2253 ***	54
	95% range	[26.2 -29.3]	[15.8 - 20.2]		
	Total range	[21.8 - 39.2]	[10.3 - 41.3]		
Bulked	Mean	26.9 (58)	19.4 (66)	9.5565 ***	122
	95% range	[25.9 - 27.9]	[18.2 - 20.6]		
	Total range	[18.3 - 39.2]	[10.3 - 41.3]		

Table 1. Transmission of photosynthetically active radiation to 10 m depth at the West Fore Reef (WFR) and Columbus Park (CP) study sites. All values are percentages of incident irradiance reaching to 10 m depth, sample size in parenthesis. The bulked data are all the data from May/July and Dec./Jan. Arcsine transformed data are used to calculate the 95% ranges and the Students t-test statistic significantly different at $P < 0.001$ (***).

Figure 3. Percentage transmission of surface photosynthetically active radiation to 10 m depth at the Columbus Park and West Fore Reef sites during May/July and Dec./Jan. ▼ = mean of two readings made on the same day.

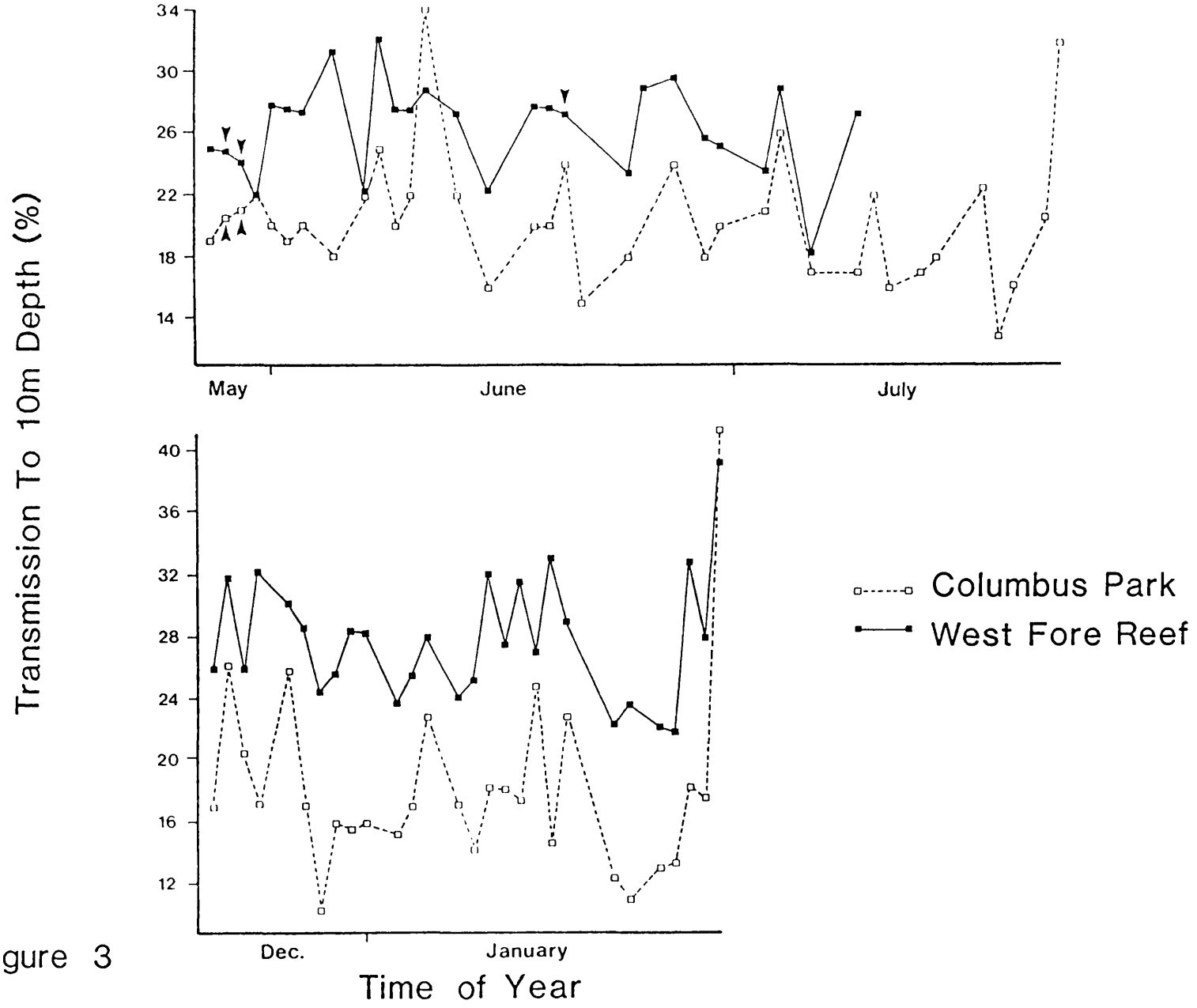

Transmission To 10m Depth (%)
34
30
26
22
18
14
May
June
July
40
36
32
28
24
20
16
12
Dec.
January
Time of Year
Columbus Park
West Fore Reef

Figure 3

from a normal distribution at P = 0.05). Between-site transmissions showed consistent fluctuations with high transmissions occurring on the same day at both sites, and similarly with low transmissions (Figure 3).

The mean May/July and the mean Dec./Jan. daily percentage transmissions were not significantly different at either the WFR or CP sites (t-test; t = 1.6685. d.f. = 56, P = 0.05 (WFR site); t = 1.9617, d.f. = 64, P = 0.05 (CP site)), but the mean transmissions between sites for the May/July, Dec./Jan. and bulked data were all significantly different (Students t-test, P < 0.001 for all groups, Table 1). The CP site received significantly less PAR than the WFR site.

Figure 4 shows the PAR at the surface and at 10 m depth on 24 June 1985, together with the percentage transmission to 10 m depth. 24 June was a sunny, clear and calm day with hazy clouds after 15.30 hrs. Surface PAR increased steadily during the morning to a maximum of 2120 $\mu E.m^{-2}.s^{-1}$ at 12.30 hrs, but decreased with peaks and troughs in the afternoon caused by clouds at 15.30 hrs and 15.45 hrs. PAR at 10 m depth paralleled surface PAR and reached a maximum of 605 $\mu E.m^{-2}.s^{-1}$ at 12.30 hrs. Transmission to 10 m depth was close to 27% between 08.00 and 15.15 hrs but varied between dawn and 08.00 hrs and 15.15 hrs and dusk. This was an artifact of low ambient PAR and fluctuations due to sensor orientation which increased the variance.

Figure 5 shows the surface PAR for a sunny and a heavily overcast day. 16 June 1985 was an "ideal" sunny day with no clouds and its PAR curve approximates a sine wave. A maximum irradiance of 2016 $\mu E.m^{-2}.s^{-1}$ was reached at 11.45 hrs and the integrated daily PAR was 56.3 $E.m^{-2}.d^{-1}$. 13 January 1986 was heavily overcast with reduced PAR, but a maximum irradiance of 2410 $\mu E.m^{-2}.s^{-1}$ occurred as a single spike at 11.15 hrs, and the integrated daily PAR was 13.4 $E.m^{-2}.d^{-1}$.

Figure 4. Simultaneous recordings of photosynthetically active radiation (PAR) made on land (A) and at 10 m depth (B) on the West Fore Reef throughout 24 June 1985. A was recorded continuously and B was produced from individual measurements shown as closed circles. The percentage transmission to 10 m depth is calculated from A and B and plotted as C. Note the different scales on the irradiance axis which are different for the A and B recordings.

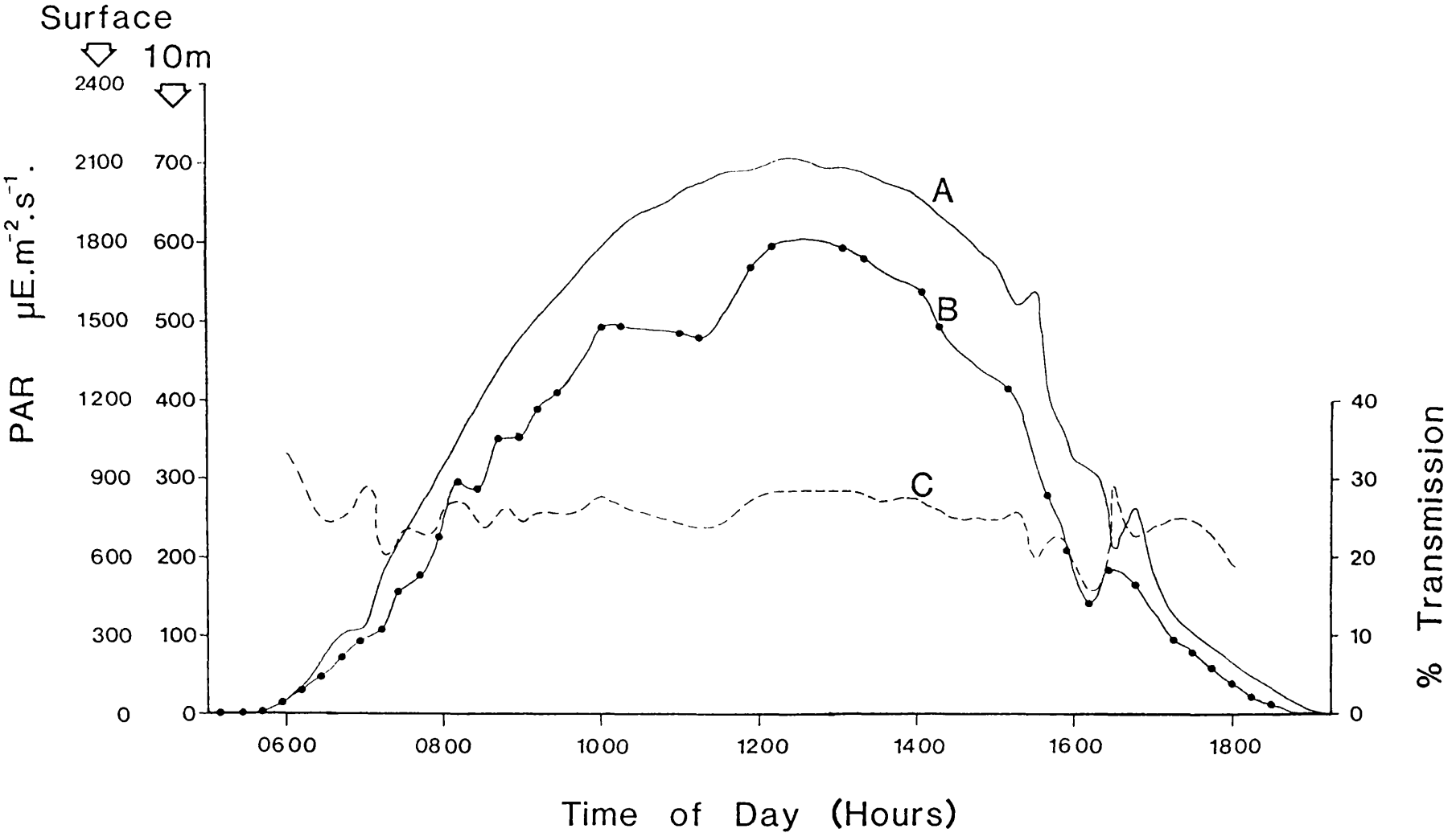

Surface
10m
2400
2100
700
1800
600
1500
500
1200
400
900
300
600
200
300
100
0
0
PAR µE.m-2.s-1.
A
B
C
40
30
20
10
0
% Transmission
0600
0800
1000
1200
1400
1600
1800
Time of Day (Hours)

Figure 4

Figure 5. Photosynthetically active radiation (PAR) at Discovery Bay recorded on the surface throughout 16 June 1985 (an "ideal" day) and 13 January 1986 (heavily overcast), and plotted on the same scale. The total PAR received on these days was 56.3 $E.m^{-2}.d^{-1}$ (16 June) and 13.4 $E.m^{-2}.d^{-1}$ (13 January).

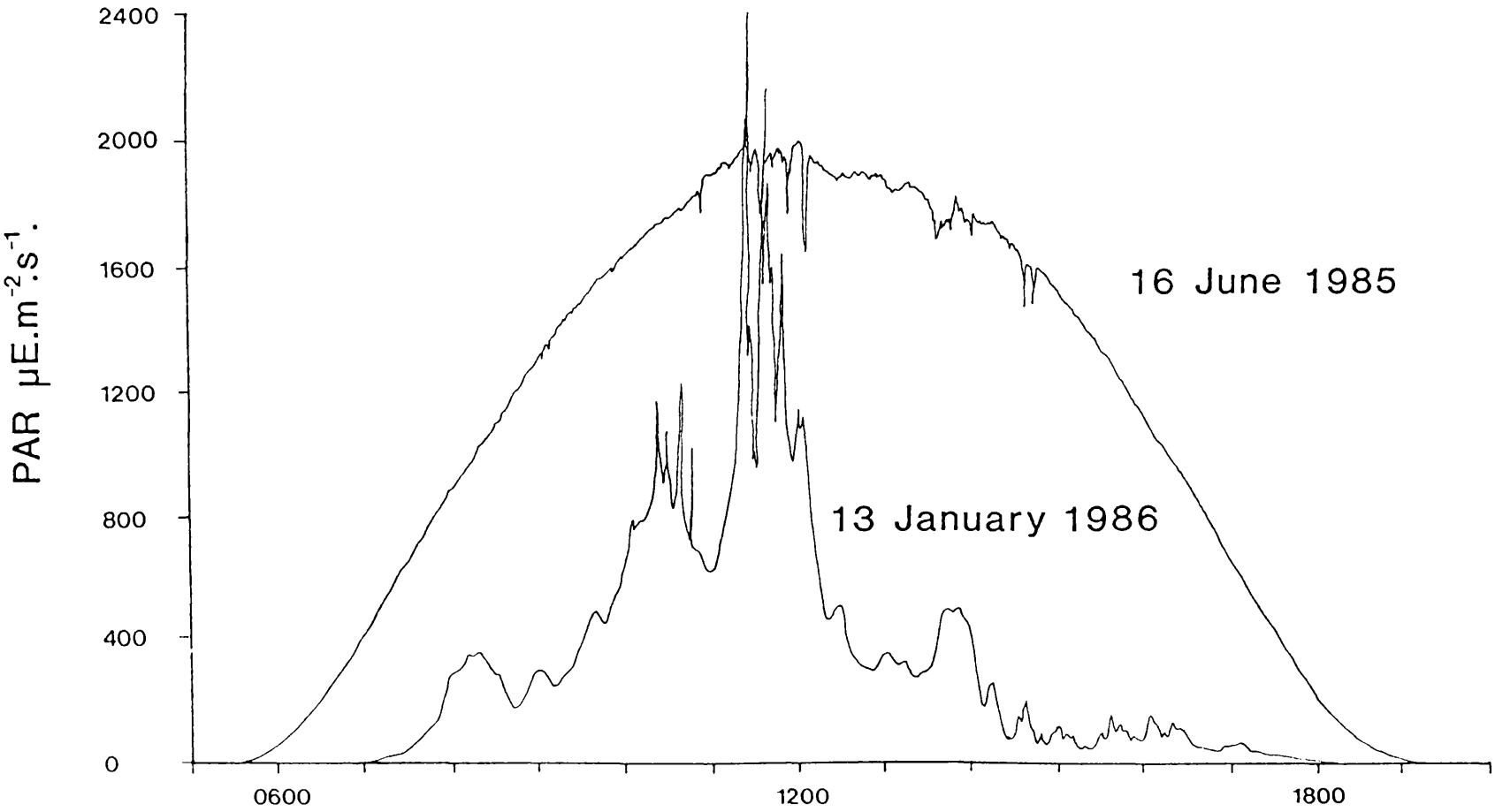

2400
2000
1600
1200
800
400
0
PAR µE.m-2.s-1.
16 June 1985
13 January 1986
0600
1200
1800
Time of Day

Figure 5

2.3.3 Discussion

The percentage transmission of surface PAR to 10 m depth at the WFR site remained constant throughout most of a calm day (Figure 4). Similar recordings of surface and 10 m depth PAR were not made at the CP site but transmissions to 10 m depth at 12.05 hrs and 17.59 hrs on a typical day at the CP site were identical. Diurnal wave and turbulence patterns were not investigated on the fore reef but turbidity regularly increases in some parts of Discovery Bay in the afternoon (Dodge *et al.*, 1974). Midday measurements of PAR transmission to 10 m depth are good estimates of the transmissions throughout most of the day on the fore reef, and probably also at the CP site where deeper water reduces the effect of waves in the resuspension of sediments.

Subsurface PAR was measured *in lieu* of surface PAR. Readings made in air and subsurface on calm days were very similar, whilst the transmissions calculated on 24 June 1985 (Figure 4) from PAR measured on land and at 10 m depth (ca. 27%) are similar to the values determined with subsurface PAR measurements on 23 and 26 June 1985 (29% and 31%). The use of subsurface PAR in calculating percentage transmissions accurately measures the light transmission through the water column but ignores the surface albido and therefore slightly over estimates the transmission of surface PAR to 10 m depth.

The depression of PAR at 10 m depth at the WFR site between 10.00 hrs and 12.00 hrs (Figure 4) cannot be explained by surface effects, and was probably caused by transitory water turbulance. The maximum irradiance of 605 $\mu E.m^{-2}.s^{-1}$ at 10 m depth is consistent with both the 58 measurements of transmission of surface PAR to 10 m depth at the same sites (Table 1, Figure 3) and the maximum surface irradiance recorded in the present study (Figure 4, 2120 $\mu E.m^{-2}.s^{-1}$).

The mean transmissions to 10 m depth for all the data at both sites (26.9% (WFR site) and 19.4% (CP sites)) are lower than equivalent published figures. Brakel's (1979) regression lines of path length through the water on percent surface irradiance for Discovery Bay give 36.6% and 27.4% transmission to 10 m depth for the fore reef and bay area respectively (LI 192S sensor, with the sun overhead). Dustan (1982) recorded a transmission of 31% to 10 m depth (cosine collector, 400 - 700 nm sensitivity) on the fore reef at Discovery Bay, Porter (1985) recorded a value of 40% transmission from 1 m to 10 m depth (LI 193S sensor) at the same location, whilst Oliver et al. (1983) recorded a transmission of 28% to 10 m depth (LI 192S sensor) on the Great Barrier Reef, Australia. Transmissions in the present study were measured in calm and in rough weather and subsurface PAR was always measured within 10 seconds of the 10 m depth PAR. These figures more accurately represent the mean percentage of surface PAR reaching 10 m depth.

Both the CP and the WFR sites had corresponding transmissions on the same days (Figure 3) showing that turbulance affected the bay and the fore reef areas simultaneously. Although bay waves were smaller than fore reef waves, sediments were more easily suspended resulting in high turbidity at the CP site at the same time as high turbidity on the fore reef. Similarly calm weather simultaneously affects both locations to increase PAR transmission to 10 m depth.

The lack of seasonality in transmission is surprising as winter months are marked by heavy seas and strong winds. The winter of 1985-86 was not different from this pattern. Winter transmissions show a greater range than summer values and high transmissions can occur which contribute to the lack of a significant seasonal difference.

The maximum surface PAR recorded on 16 June 1985 is similar to figures recorded by Steen and Muscatine (1984) at Bermuda (2500 $\mu E.m^{-2}.s^{-1}$) and Brakel (1979) at Discovery Bay (2525 $\mu E.m^{-2}s^{-1}$ with LI 192S sensor; pers. comm. from Dr. W.H. Brakel). The maximum intensity on a heavily overcast day briefly surpassed the clear day maximum and was probably a result of temporary cloud thinning together with downward reflectance from clouds.

The integrated daily PAR on an overcast day was less than 24% of that for an 'ideal' day. During 1983-84 Porter (1985) recorded 6 days duller than 13 January 1986, but none as bright as 16 June 1985 whilst using an equivalent sensor (LI 190SB). 16 June 1985 is therefore a good approximation of an 'ideal' day, and 13 January 1986 approaches the dullest expected day (4 $E.m^{-2}.d^{-1}$ on 2 March 1984; Porter, 1985). PAR recorded on 16 June 1985 will be used to calculate energy budgets under 'ideal' conditions (Chapter 4), and will be used together with PAR recordings from 13 January 1986 to compare energy budgets on 'ideal' and 'non-ideal' days in Chapter 5.

2.4 Temperature

2.4.1 Methods

Sea water temperature was measured at 10 m depth whilst SCUBA diving between April 1985 and April 1986 using a mercury thermometer which could be read to 0.1°C.

2.4.2.Results

Data are plotted in Figure 6. Fewer measurements were made at the CP site than at the WFR site but temperatures were always similar and differed by less than 0.5°C (mean = 0.1°C, s.d. = 0.1°C) on the 23 days that measurements were made at both sites. The water warms slowly through May to August, reaches a maximum in September/October and then decreases through November to January, reaching a minimum in February/March. The highest recorded temperature at the WFR site was 29.8°C (7 October 1985) and the lowest was 26.3°C (27 February 1986). The equivalent figures at the CP site were 29.7°C (17 September 1985) and 26.2°C (3 March 1986). The maximum rate of change in temperature at the WFR site was 0.4°C over 3 days between 8 and 11 January 1986 and 0.8°C over 7 days between 13 and 20 March 1986 at the CP site.

2.4.3 Discussion

Temperatures recorded in the present study are similar to recordings made on the Discovery Bay fore reef by Reiswig (1971), Dustan (1975) and Ohlhorst (1980) (for 1969-70, 1972-73 and 1976-77 respectively). Mixing of fore reef and bay waters occurs over the eastern reef crest and through the ship channel to help maintain a uniform temperature. Localised warming of bay water does not occur at 10 m depth and the temperatures at both sites are similar throughout the year. Any temperature effects therefore probably act simultaneously at each site.

Figure 6. Sea water temperatures at 10 m depth throughout 1985-1986 at both the West Fore Reef and at the Columbus Park sites.

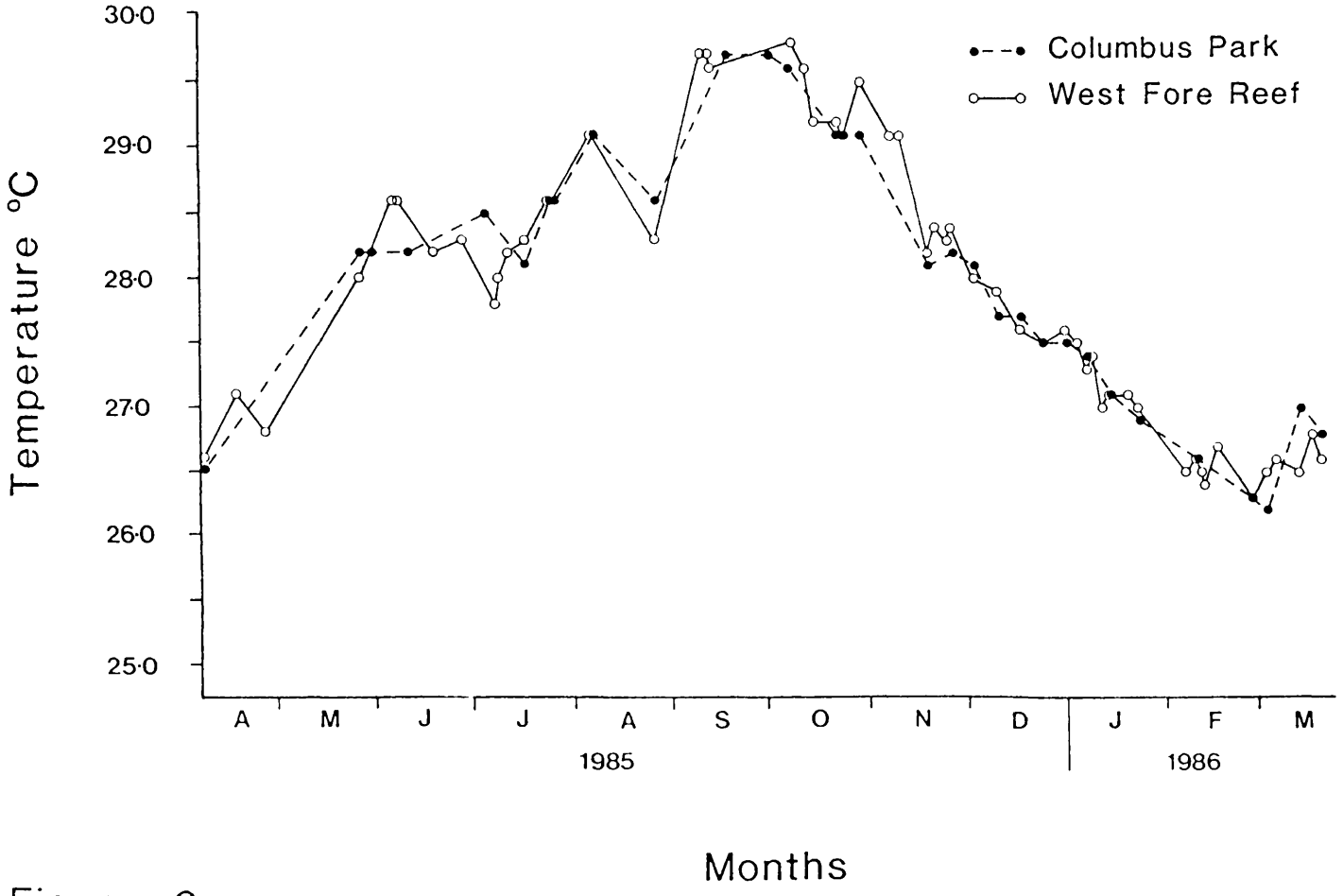

30·0
29·0
28·0
27·0
26·0
25·0
Temperature °C
Columbus Park
West Fore Reef
A
M
J
J
A
S
O
N
D
J
F
M
1985
1986
Months

Figure 6

The annual range of seawater temperature at 10 m depth is 3.5°C but the rate of change can be more than 3% of the range per day, suggesting that large volumes of seawater of different temperatures can be rapidly exchanged over the reefs at Discovery Bay. Both daily changes and seasonal fluctuation in seawater temperature may have some significance to corals growing at both sites although it can be anticipated that any effects would be minor because of the small annual range in temperature. It therefore seems unlikely that any differences in growth or physiology of P. porites at each site can be attributed to different temperature regimes per se.

2.5 Sediments

2.5.1 Methods

Sediments were collected between 18 November 1985 and 27 March 1986 using plastic centrifuge tubes 27 mm in diameter and 98 mm deep. Three traps were secured to cinder blocks with their tops approximately 15 cm above the substrate at each site and were left for 7 days. Placement and collection always took place between 08.30 and 11.30 hrs. Sediments from each trap were filtered onto individual pre-dried and pre-weighed 15 cm Whatman no. 1 filters. Macroscopic organisms including hermit crabs and the alga Dictyota spp. were removed before washing the sediments with distilled water. Washed sediments plus filter were dried to a constant weight at 60°C, cooled over SiO_2 and weighed to the nearest 10 µg on a Mettler H6 balance. The mean sediment load in the 3 traps from each location was extrapolated to g sediment.$m^{-2}.d^{-1}$.

2.5.2 Results

Mean sedimentation rates from the 3 traps for each period are shown in Table 2. Sedimentation rates were significantly higher at the CP site (Mann-Whitney U-test, U = 11, $n_1 = n_2 = 7$, P = 0.049), and the median rates were 24.59 $g.m^{-2}.d^{-1}$ (WFR site)and 33.94 $g.m^{-2}.d^{-1}$ (CP site). Sedimentation varied between sampling periods particularly at the WFR site where 122.93 $g.m^{-2}.d^{-1}$ was deposited between 23 and 30 of December 1985. This was a period of calm weather following a period of rough weather. A similar but reduced effect was shown over the same period at the CP site.

The sediment composition was not analysed but the sediments collected at the CP site were fine whilst those collected at the WFR site were coarser and contained sand from adjacent channels.

2.5.3. Discussion

The sedimentation rates in the present study were recorded between November and March and the absolute values cannot be extrapolated to the whole year. However the between-site differences are probably consistent throughout the year as waves are always proportionately reduced within the bay compared to the fore reef.

PAR transmission at the CP site was significantly lower than at the WFR site and the CP site was characterised by a high particulate load in the water column, a substrate with areas of unconsolidated sediments, and a significantly higher sedimentation rate. Ohlhorst (1980) looked at sedimentation rates at an 18 m depth Columbus Park site and also at a 15 m depth fore reef site at Discovery Bay and reported values of 303 $\pm$ 77 $g.m^{-2}.d^{-1}$ and 27 $\pm$ 15 $g.m^{-2}.d^{-1}$ respectively (mean $\pm$ s.d. of bi-weekly samples collected 1 m above the substrate over 1 year). These are consistent with the values at the WFR site but are much greater than the values at the CP site in the present study. Dodge *et al.* (1974) recorded sedimentation rates of

Trap placement		Sedimentation $g.m^{-2}.d^{-1}$	
Date down	Date up	WFR	CP
18-11-85	25-11-85	39.71*	62.38
2-12-85	9-12-85	24.59	33.94
16-12-85	23-12-85	25.52	29.86
23-12-85	30-12-85	122.93	50.37
6-01-86	13-01-86	15.14	29.90
6-03-86	13-03-86	14.09*	---
13-03-86	20-03-86	20.08*	30.86*
20-03-86	27-03-86	---	42.49
	Median	24.59	33.94

Table 2. Sedimentation rates at 10 m depth for the West Fore Reef (WFR) and Columbus Park (CP) study sites between 18 November 1985 and 27 March 1986. Each value is the mean for three traps unless marked with * when only two traps were analysed.

up to 11 $g.m^{-2}.d^{-1}$, 50 cm above the soft sediments near the rear zone of the Discovery Bay reef, whilst Rogers (1983) measured a sedimentation rate of 96 $g.m^{-2}.d^{-1}$., 10 cm above a reef in Puerto Rico. Ohlhorst's (1980) figure of 303 $g.m^{-2}.d^{-1}$ is exceptionally high and does not apply to the 10 m depth CP site. The particulate matter in the water column at the CP site does not settle out at 10 m depth and may either remain in suspension or may be exported towards the central bay depression and the 18 m depth where Ohlhorst recorded her sedimentation rates.

Sedimentation rates at the WFR site spanned almost an order of magnitude and were greater than expected in a location where the underwater visibility generally exceeded 20 m. The sediments collected at the WFR contained coarse sand with the same appearance as the sand in the channels between the buttresses. The WFR site was about 2m above the adjacent channels and it seems likely that sand becomes resuspended in the bottom 2 - 3 m of water during rough weather and then settles onto the buttresses. This would account for the clarity of the majority of the 10 m water column and the high sedimentation recorded between 23 and 30 December 1985.

As there were no continuous large scale inputs of sediments into the bay and the sediments collected in the CP traps were similar to those on the adjacent substrate, even the modest sedimentation rates reported in the present study are probably maintained by resuspension. The lower variation in sedimentation rates at the CP site, together with the likely source of sediments at the WFR site (the sand channels in rough weather) suggests that sedimentation was chronically high at the CP site but only sporadically high at the WFR site.

2.6 Nutrients

2.6.1 Methods

Water samples were collected between 18 November 1985 and 13 January 1986 with 50 ml plastic syringes whilst SCUBA diving. Samples were collected at 10 m depth from each study site and were returned to the laboratory for immediate analysis. Absorbances of distilled water and unfiltered seawater in 1 cm cuvettes in a Beckman DU2 spectrophotometer were not different at either 640 nm or 543 nm so that turbidity corrections or filtration of samples were unneccessary.

Ammonium nitrogen was assayed by the method of Strickland and Parsons (1972) scaled to a 5 ml sample size. Reagents were made up in single distilled water as environmental ammonium levels were low. Commercial bleach was used as a source of sodium hypochlorite and the absorption was measured at 640 nm on a Beckman DU2 in 1 cm cells.

A standard solution of $(NH_4)_2SO_4$ was diluted with 0.45 μm filtered seawater (FSW) to known concentrations which were assayed in duplicate to produce a calibration line. Absorbances were corrected for the background NH_4^+ concentration of sea water and for cell-cell absorbances.

Duplicate unknowns, blanks and standards (in FSW) were analysed together to ensure consistent accuracy. Unknowns were corrected for distilled water blanks, standards for FSW blanks and both unknowns and standards for cell-cell absorbances. NH_4^+ nitrogen concentrations were read from the calibration line.

Nitrate nitrogen was assayed by the method of Strickland and Parsons (1972) scaled to a 5 ml sample size and using copper-coated cadmium wire within a nylon tube for reduction (Stainton, 1974). Reagents were made up in single distilled water and absorbances were measured at 543 nm in 1 cm cells in a Beckman DU2. The flow rates

required (Stainton, 1974) for full reduction by the Cd-wire within the nylon tube were obtained by altering the height of a detachable 10 ml syringe above the outlet of the reduction tube. The reduction tube was prepared for use by using a syringe to flush through 10 ml each of 1N HCl, distilled water and 2% (w/v) $CuSO_4$ at approx. 20 $ml.min^{-1}$ followed by 40 ml of distilled water. This was repeated every 2 - 3 weeks. 10 ml of the sample was sucked into a clean 10 ml plastic syringe, the outlet port temporarily capped, and the plunger removed. 200 µl of 25% (w/v) NH_4Cl was added, the plunger replaced and the syringe shaken. The cap over the outlet port was removed and the syringe attached to the upstream side of the reduction tube at the predetermined height. When the plunger was removed the sample flowed throught the column by gravity feed at approximately 0.8 $ml.min^{-1}$. The first 3 ml of the reduced sample was discarded, and a 5 ml aliquot taken from the remainder for assay. In between samples the reduction column was flushed with 10 ml of distilled water at approx. 0.8 $ml.min^{-1}$. When not in use the tube was left filled with 0.7% (w/v) NH_4Cl.

A standard solution of KNO_3 in distilled water was diluted to known concentrations with FSW and each standard assayed in duplicate to produce a calibration line. Absorbances were measured at 543 nm in 1 cm cells in a Beckman DU2. All absorbances were corrected for cell-cell absorbances and NO_3^- levels in the FSW. Duplicate unknowns, blanks (distilled water) and standards (in FSW) were analysed together as a check on accuracy. Unknowns were corrected for distilled water blanks, standards for FSW blanks and both unknown and standards for cell-cell absorbances. Concentrations of NO_3^- nitrogen were read from the calibration line.

Nitrite nitrogen was assayed by the method of Strickland and Parsons (1972) scaled to a 5 ml sample size. This was the same as the nitrate assay above but without the reduction stage.

A standard KNO_2 solution in distilled water was diluted to known concentrations with distilled water, and each assayed in duplicate to produce a calibration line. Duplicate unknowns, distilled water blanks and standards were analysed together as a check on accuracy. All absorbances were corrected for distilled water blanks and cell-cell absorbances. Concentrations of NO_2^- nitrogen were read from the calibration line.

2.6.2 Results

The results are shown in Table 3. Nearly all the concentrations for NH_4^+-N, NO_2^--N and NO_3^--N at both sites were extremely low and below the limit of detection of the analyses in 1 cm cells, which are 1.0, 0.1 and 0.5 $\mu g.At\text{-}N.l^{-1}$ respectively (Strickland and Parsons, 1972). The mean for each nutrient concentration cannot be calculated because of the uncertainty over the figures. Six of the NO_3^--N concentrations at the CP site were above the limit of detection whereas only one NO_3^--N value was above the limit of detection at the WFR site

2.6.3 Discussion

The use of 1 cm cells with the methods of Strickland and Parsons (1972) is inadequate for the concentrations encountered in the present study. The high NO_3^--N concentration recorded on 13 January 1986 at the WFR site was unexpected and is greater than the values tabulated by Muscatine (1980b) from coral reefs throughout the world. The value in the present study is probably erroneous and NO_3^--N concentrations at the WFR site were probably < 0.5 $\mu gAt\text{-}N.l^{-1}$. Three of the nitrate concentrations at the CP site are below the limit of detection and lie between 0 - 0.5 $\mu gAt\text{-}N.l^{-1}$. The mean NO_3^--N concentration at the CP

Sampling date	WFR			CP		
	NH_4^+	NO_2^-	NO_3^-	NH_4^+	NO_2^-	NO_3^-
18-11-85	<1.0	<0.1	<0.5	<1.0	<0.1	1.8
25-11-85	<1.0	<0.1	<0.5	<1.0	<0.1	<0.5
2-12-85	<1.0	<0.1	<0.5	1.4	0.1	1.7
9-12-85	<1.0	<0.1	<0.5	<1.0	<0.1	1.9
16-12-85	<1.0	<0.1	<0.5	<1.0	0.1	1.3
23-12-85	<1.0	<0.1	<0.5	<1.0	<0.1	1.0
30-12-85	<1.0	<0.1	0.5	<1.0	<0.1	0.8
8-01-86	<1.0	0.2	<0.5	<1.0	<0.1	<0.5
13-01-86	<1.0	0.2	3.5	<1.0	<0.1	<0.5

Table 3. Concentrations of ammonium-, nitrite- and nitrate- nitrogen at 10 m depth at the West Fore Reef (WFR) and the Columbus Park (CP) sites. Each figure is the mean of two replicates and units are µg At-$N.l^{-1}$

site is therefore between 0.94 ± 0.26 µgAt-N.l^{-1}. and 1.11 ± 0.19 µgAt-N.l^{-1} (mean ± s.e.), taking the uncertain values as 0 or 0.5 µgAt-N.l^{-1} respectively.

On the Great Barrier Reef off the north Queensland coast, NH_4^+-N, NO_2^--N and NO_3^--N concentrations were < 0.2 µgAt-N.l^{-1}, < 0.9 µgAt-N.l^{-1} and < 0.5 µg At-N.l^{-1} respectively (Ryle et al., 1981). Thomas (1970) showed that concentrations of NO_3^--N, NO_2^--N and NH_4^+-N in tropical east Pacific waters along longitudes 105°W and 112°W ranged from 0.0, 0.00, and 0.52 µgAt-N.l^{-1} respectively to 5.6, 0.12, and 0.61 µgAt-N.l^{-1} respectively. He described the waters which gave the former 3 figures as nutrient depleted and the waters which gave the latter 3 figures as nutrient enriched. The concentration of NH_4^+-N, NO_2^--N and NO_3^--N in the present study agree with the dogma of nutrient depleted tropical reef waters, although NO_3^--N concentrations at the CP site are higher than at the WFR. D'Elia et al. (1981) reported significant enrichment of nitrate nitrogen to Discovery Bay from subterranean springs, whilst Muscatine et al. (1979) found NH_4^+-N concentrations up to 1.4 µgAt-N.l^{-1} in the same location. Spring water discharged into the bay less than 5 m from the CP site, and the Columbus Park tourist attraction had a septic tank drainage system that overflowed to the bay close to the study site. Nutrient levels at 10 m depth were not greatly increased suggesting that either the inputs to the bay were nutrient depleted or that the spring water was absent. Dilute sea water has a reduced density and it is possible that the fresh water inputs rises to the surface and is unavailable at 10 m depth.

2.7 Summary

Study sites at 10 m depth were established at Columbus Park and on the fore reef of Discovery Bay where energy budgets for the coral Porites porites could be calculated under different environmental conditions. Measurements of the light transmission, water temperature, sedimentation rates and nutrient concentrations were made at each site. Seasonal differences in light transmission at each site were not found, but the CP site received significantly less light than the WFR site. Seawater temperature showed similar trends at both sites. Sedimentation was chronic although lower than anticipated at the CP site but still significantly higher than at the WFR site which had sporadically high sedimentation rates. Sediments may remain suspended at the CP site and be exported from the area. Sedimentation at the WFR site probably results from the resuspension of sand from the channels which then settles onto the buttresses. Mineral nutrients were often below the level of detection at both sites but the CP site showed some evidence of NO_3^- enrichment. Unfortunately a refractometer was not available for frequent measurements of salinity. On the few occasions when it was possible to compare the sites the salinity at both was 35‰.

The CP and WFR sites differ significantly in their transmission of PAR to 10 m depth and perhaps NO_3^--N concentrations. These two factors may have a major effect on the energy budgets of P. porites. Quantification of isolated environmental characteristics does not, however, give a complete indication of their effect on organisms for any one factor may act synergistically with one or several others to enhance or reduce the effect.

CHAPTER 3: MATERIALS AND METHODS

3.1 Introduction

The energy budgets for Porites porites growing at the two sites were determined between April 1984 and March 1986 using identical methods. A number of experiments were only carried out on the WFR specimens and the results extrapolated to both sites. All these methods are described in this chapter.

3.2 The experimental animal

The symbiotic reef coral Porites porites (Pallas; Scleractinia) was chosen as the experimental animal because it is:

a. readily identifiable underwater,

b. abundant and occurs in a variety of habitats,

c. easily removed from the substrate,

d. comparatively free from boring organisms,

e. extremely hardy.

Goreau and Wells (1967) described 4 species of Porites commonly occurring below 2 m depth in Jamaica: P. astreoides, P. furcata, P. divaricata, and P. porites. Brakel (1976) carried out cluster analysis on 24 quantitative characteristics of these same 'species' in Jamaica, and distinguished three weakly defined phenons: P. astreoides, P. furcata and P. porites, with P. divaricata being a subset of P. furcata. Zlatarski and Estalella (1982) followed Brakel's approach and considered P. furcata, P. divaricata and P. porites to be different 'forma' of the single species P. porites. Much of this confusion has arisen from similarities in skeletal microarchitecture between the 4

'species', and the supposed species-specific colony morphologies for P. porites, P. divaricata and P. furcata which appear as points on a continuum with intermediate morphologies being common (pers. obs.).

To circumvent this 'species problem', specimens were only collected from colonies which were undoubtedly Porites porites, irrespective of whether this is a true species (sensu Goreau and Wells, 1967), phenon (sensu Brakel, 1976) or forma (sensu Zlatarski and Estalella, 1982) of the genus Porites. These colonies consisted of sturdy, finger-like branches ca. 2 - 2.5 cm in diameter and up to 15 cm long, with rounded or swollen tips (never laterally compressed or bifurcated). Many hundreds of upright branches formed colonies up to a metre in diameter. Live tissue covered only the top few cm of individual branches so that adjacent tips were often less than 5 mm apart, but were unconnected by living tissue. Some colonies had only a few short, widely spaced branches growing from a common attachment (never encrusting) and were interconnected with living tissue. Live P. porites was brown/green in colour with polyps invariably expanded 24 hours a day. Expanded polyps were 2 - 3 mm in diameter and up to 6 mm in length and carried a variable number (9 - 12) of short lobose tentacles surrounding the oral disc in a single ring. Tentacles were often paler than the rest of the colony.

Branch tips ("nubbins" after Birkeland, 1976; and Davies, 1984) of P. Porites were removed in situ at 10 m depth at each study site and used for all experiments. One specimen from each of 10 colonies at each site was used for determinations of photosynthesis vs irradiance (P/I) relationships. Single specimen collection from each colony was not possible for the remaining experiments (except where noted) because of the quantity of nubbins required. Specimens were transported in shaded buckets to the laboratory where their bases were filed smooth and perpendicular to the long axis of the branch, blotted

dry on paper towels, and glued onto pre-weighed and individually numbered 30 x 30 mm Perspex tiles using cyanoacrylate adhesive (superglue). Prepared nubbins were returned to their respective collection sites, usually within 24 hours, and no later than 48 hours after collection. Nubbins were slotted into Perspex racks secured onto cement blocks at 10 m depth and enclosed within wire cages (mesh size 10 x 10 mm) since nubbins were subject to grazing. Cages were cleaned every few days, but generally attracted few fouling organisms. These nubbins were left for at least a one-week recovery period on the reef and provided a reservoir of individuals which were used for all physiological experiments.

Experimental nubbins at each site are shown in Figures 7 and 8.

3.3 Specimen characteristics

The unit reference used throughout the study was dry skeletal weight obtained by buoyant weighing in sea water (Jokiel et al.,1978) to the nearest mg. The dry skeletal weight is given by:

$$W_{dry} = \frac{W_s}{1 - D_s.(D_a)^{-1}} \qquad 1.$$

where: W_{dry} = dry skeletal weight (g)

W_s = buoyant weight recorded in sea water (g)

D_s = density of sea water ($g.cm^{-3}$)

D_a = density of the skeleton ($g.cm^{-3}$)

Seawater density was calculated from the buoyant weight of a ground glass stopper (used as a reference weight) in sea water and in distilled water at a known temperature using the equation:

Figure 7. Porites porites nubbins at 10 m depth at the West Fore Reef site. The nubbins are glued onto tiles 30 x 30 mm. Note the clear water and the absence of sediment accumulation around the nubbins (photo: G. Bruno).

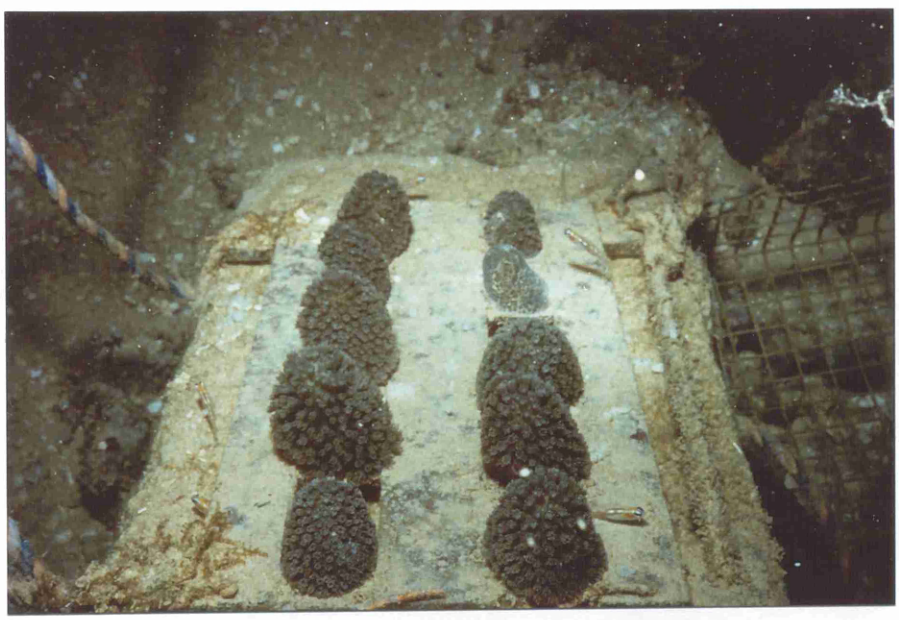


Figure 8. Porites porites nubbins at 10 m depth at the Columbus Park site. The nubbins are glued onto tiles 30 x 30 mm. Note the accumulation of sediments around the nubbins and the loose sediment on the substrate surrounding the cement blocks (photo: G. Bruno).

$$D_s = D_d \cdot \frac{(R_{dry} - W_s)}{(R_{dry} - W_d)} \qquad 2.$$

where D_d = tabulated density of distilled water at a known temperature ($g.cm^{-3}$)

W_d = buoyant weight in distilled water (g)

R_{dry} = dry weight of object (g)

At the start of this study, skeletal density of Porites porites from both sites was determined empirically by buoyant weighing tissue-free, freshly excised portions of skeleton in sea water and then steeping and weighing in distilled water of known densities. Skeletal density is given by:

$$D_a = \frac{W_s \cdot D_d - W_d \cdot D_s}{W_s - W_d} \qquad 3.$$

The density of each Perspex tile was obtained by the same process and the resultant value substituted in equation 1 in place of D_a together with the tile dry weight (in place of W_{dry}) and the density of sea water (from equation 2) to give the predicted buoyant weight of the tile by rearrangement of the equation. This was subtracted from the measured buoyant weight of the nubbin (coral + tile) to give the buoyant weight of the coral alone. Groups of nubbins were sacrificed to provide data on surface area, dry tissue, ash, tissue energy and protein content, together with numbers of polyps and zooxanthellae.

In order to produce a calibration line relating surface area to skeletal dry weight, aluminium foil of a known $weight.cm^{-2}$ was cut and fitted to the surface of nubbins which had been dried after buoyant weighing. Surface area was determined from the weight of aluminium foil, and was related to the skeletal dry weight by a linear regression line fitted by the method of least squares. The calices were also counted to determine the number of polyps per cm^2.

In order to produce a calibration line relating dry tissue content to skeletal dry weight, buoyant-weighed nubbins were fixed in 5% formalin in sea water for 24 hours prior to decalcification in a solution of 10% HNO_3 in distilled water. The resulting tissue tunics were filtered onto pre-dried and pre-weighed Whatman 1 qualitative filters and dried to a constant weight at 60°C. Dry tissue weights were measured to the nearest mg after cooling over SiO_2, and were related to the dry skeletal weight by a linear regression line fitted by the method of least squares. Tunics were also collected onto pre-dried and pre-weighed Whatman GF/C filters, dried to a constant weight and then ignited at 450°C for 5 hours to give the ash-free weight.

Tissue energy was determined by wet oxidation with $K_2Cr_2O_7$ (after Golterman and Clymo, 1970; Tytler, 1982), and a spectrophotometric determination of the quantitative reduction of Cr^{6+} to Cr^{3+}. A 4 ml aliquot of standard 0.1 N $K_2Cr_2O_7$ in concentrated H_2SO_4 was added to each 4 ml aliquot of several standard sucrose solutions and blanks of distilled water, heated in a boiling water bath for 3 hours, removed, cooled to room temperature and made to 25 ml with distilled water. The absorption was measured at 440 nm in 1 cm cells against distilled water in a Beckman DU2 spectrophotometer. A calibration line was plotted from the decrease in absorption of the standards relative to the unreduced 0.1 N $K_2Cr_2O_7$ in conc. H_2SO_4 (reacted with distilled water) against the energy equivalent of the $Cr_2O_7^{2-}$ reduced by the sucrose:

where: $8Cr_2O_7^{2-} = 12O_2 = C_{12}H_{22}O_{11}$

and 1 Mol O_2 = 452.48 KJ from the general oxy-calorific coefficent of Elliott and Davison (1975) assuming that the unknown biological samples contained a heterogeneous mixture of carbohydrates, proteins and lipids.

Unpreserved nubbins were decalcified over 36 hours in 10% HNO_3 in distilled water after buoyant weighing. The resulting tissue-acid mixtures were homogenised, made to 250 ml with distilled water and 4 ml aliqouts (2 replicates) oxidised with 4 ml of 0.1 N $K_2Cr_2O_7$ in H_2SO_4 as described for the standards. Halide ions also reduce $Cr_2O_7^{2-}$, but were precipated with an empirically determined quantity of $HgSO_4$ solution (approx. 2% w/v in distilled water acidified with H_2SO_4; Mackereth et al., 1978). The decrease in absorbance of $Cr_2O_7^{2-}$ was converted to an energy equivalent using the calibration line and extrapolated to the tissue energy content of the whole nubbin. In order to test whether decalcification in HNO_3 had any effect on the energy content of the tissues, fresh unpreserved tissue was removed from P. porites by water piking (Johannes and Wiebe, 1970) and homogenised. Seven 1 ml aliquots of the homogenate were each treated with 1 ml of 20% HNO_3 in distilled water. Another seven 1 ml aliquots each had 1 ml distilled water added and were frozen. After 36 hours both groups were wet oxidised as above, and their energy content was not found to be significantly different (t-test; t = 0.6411, d.f. = 12, P = 0.05).

Typically 40% of the protein remains unoxidised by wet oxidation (Forster and Gabbott, 1971). Therefore, a correction for unoxidised protein was applied to the energy content of the tissue using the equation:

$$(T \times P \times 23.6 \times 0.4)/100 = 0.0944.T.P$$

where T = dry tissue biomass (mg), P = % protein content of dry tissue, 23.6 is the energy content of a typical protein ($J.mg^{-1}$) (Brafield and Llewellyn, 1982), and 0.4 is the proportion of protein

unoxidised. The dry tissue content and surface area of the nubbins were determined from the regression of dry tissue and surface area on dry skeletal weight. Energy content was expressed as $J.mg^{-1}$ dry tissue and $J.cm^{-2}$.

Homogenised "blastate" obtained by water piking was used for tissue protein determination using the procedure of Lowry et al. (1951) scaled to 1 ml sample size and using bovine serum albumen as a standard. Samples were centrifuged before measuring their absorbances in 1 cm cells at 750 nm against distilled water in a Beckman DU2. Duplicate 5 ml aliquots of each homogenate were dried to a constant weight at 60°C to give the dry tissue content of the homogenate, and protein content was expressed as a percentage of the dry tissue.

The total zooxanthellae content was determined in buoyant weighed nubbins fixed in 5% formalin in sea water and decalcified in 10% HNO_3 in sea water. Tissue tunics were homogenised and the mixture centrifuged until the supernatant was clear. The pellet was resuspended, made to a known volume, and 10 replicate counts of zooxanthellae were made using a haemocytometer. Dry tissue content and surface area of the nubbins were determined from the regression of dry tissue and surface area on dry skeletal weight, and these data used to express zooxanthellae content as zooxanthellae.g^{-1}dry tissue and zooxanthellae.cm^{-2}.

3.4 Isolation of zooxanthellae

3.4.1 For chlorophyll analysis

Specimens of P. porites from each site were water piked with 0.45 µm filtered sea water (FSW) and the blastate homogenised. The homogenate was filtered through cheese cloth and the debris pelleted by centrifugation. The pellet was washed 4 times by resuspending it in

40 ml of fresh FSW, repelleting by centrifugation at approximately 1000 x g and discarding the supernatant. The final pellet was resuspended in 5 ml of FSW and 10 replicate counts of zooxanthellae were made using a haemocytometer. Two 1 ml aliquots were each filtered onto Whatman GF/C filters under suction to give a spot of zooxanthellae which was washed with 1 ml of distilled water (McCloskey and Muscatine, 1984). Individual spots were cut out and placed in foil-covered screw-capped test-tubes, and extracted overnight at 5°C in 100% acetone containing a small amount of $MgCO_3$ to prevent acidic decomposition of the chlorophyll. After centrifugation, absorbances of the chlorophyll extracts were measured against 100% acetone using 1 cm cells at 663 nm and 630 nm on a Beckman DU2. Mass of chlorophyll a and c_2 was calculated according to the formulae of Jeffrey and Humphrey (1975) for dinoflagellates and results expressed as $(\mu g \text{ pigment}).x10^6 zoox^{-1}$.

3.4.2 For energy, protein and respiration determinations

Zooxanthellae were isolated using a modification of the procedure of Tytler and Davies (1984). Equimolar equivalents of sucrose were substituted for sorbitol in their salines and separation of zooxanthellae was carried out on a step gradient of 90%, 75% and 50% Tris-buffered sucrose-Percoll saline (TBSuPS) (5 ml of each) using a MSE Minor centrifuge. Each preparation of zooxanthellae was obtained from a single colony of P. porites by water piking with FSW, homogenising the blastate and filtering it through cheese cloth. Zooxanthellae were pelleted by centrifugation of the filtrate and were resuspended in 2 ml of Tris-buffered sucrose artificial saline (TBSuAS) by forcing through a 19G needle with a 10 ml syringe. The suspension was layered onto the top of the 90% TBSuPS and spun at approximately 1200 x g for 20 minutes. Zooxanthellae were collected

from the 50%/75% density interface with a Pasteur pipette, and were washed twice by pelleting from 10 ml of FSW by centrifugation. Washed cells were made to a known volume in FSW and 10 replicate counts of zooxanthellae were made using a haemocytometer.

The energy content of zooxanthellae was determined on two 1 ml aliquots of each suspension filtered onto Whatman GF/C filters under suction. Control filters had 1 ml of FSW sucked through. After washing with 5 ml of a 4.5% w/v solution of Na_2SO_4 (Strickland and Parsons, 1972), filters were dried at 60°C until wet oxidised. Filters were put into individual test tubes and an empirically determined quantity of $HgSO_4$ solution was added (Mackereth et al., 1978), before being wet oxidised by the procedure described previously for whole tissue with 4 ml of 0.1 N $K_2Cr_2O_7$. Oxidised filters were centrifuged until the supernatant was clear. The absorbances of the supernatants were measured and corrected for control filter absorbance. Energy content was expressed as $J.x10^6 zoox^{-1}$. and was corrected for incomplete protein oxidation as for the whole tissues. Zooxanthellae protein was assayed by the procedure of Lowry et al. (1951), scaled to 1 ml samples of the cell suspension and carried out as described for the whole tissues. Protein content was expresed as μg protein.$x10^6$ $zoox^{-1}$.

Zooxanthellae prepared by this method were used for the respiration measurements detailed in section 3.5.

3.5. Oxygen flux measurements

Colony respiration and photosynthesis were measured as oxygen flux in a temperature-regulated, 120 ml confined Perspex respirometer containing a rotating (130 rpm) magnetic stirrer. The partial pressure of oxygen (PO_2) was measured using a Stathkelvin 781 oxygen meter with a Radiometer E5046 oxygen electrode inserted into the side of the

respirometer and the PO_2 plotted on a 20 cm chart recorder. The oxygen electrode was calibrated using a mixture of 0.01 M disodium tetraborate and Na_2SO_3 as a chemical zero and then in air saturated 0.45 µm FSW at 28°C. All measurements were made in 0.45 µm FSW at 28°C. Salinity was measured with a refractometer and values for oxygen solubility in seawater taken from Weiss (1970). Background oxygen consumption of FSW alone was measured in the same chamber and experimental oxygen fluxes adjusted accordingly.

The lighting during the photosynthesis measurements was provided by an overhead bank of 6 x 15W Westinghouse Daylight fluorescent tubes located in an aluminium foil-lined enclosure surrounding the respirometer. An ascending series of irradiances were obtained by raising the respirometry chamber from approximately 26 cm to 5 cm beneath the lights which were also switched on independently. The experimental nubbins received a maximum of up to 430 $\mu E.m^{-2}.s^{-1}$ as measured with a LiCor LI 185A meter and LI 192S sensor. The directional distribution of light was measured with a silicon photocell connected to a voltmeter. The photocell was inserted through the electrode port of the clean and dry respirometer. The relative irradiance was recorded horizontally and at $\pm$ 45° and $\pm$ 90° to normal for the front to rear, and left to right of the incubation enclosure.

Between 74% and 90% of the light passing vertically down into the chamber was received at the 4 points (left-right, front-rear of the incubation enclosure) at 45° to the vertical axis, and between 29% and 41% at the 4 points at 90° to the vertical axis. Brakel (1979) recorded the irradiance at $\pm$ 45° and $\pm$ 90° to the vertical axis for north-south and east-west at 9 m depth on the fore reef of Discovery Bay at 09.45 hrs. His figures range from about 14% to 78% at the 4

points 45° to the vertical and 5% to 38% at the 4 points 90° to the vertical with the lowest values recorded in the shaded direction from the morning sun. The directional distribution of the light in the incubation enclosure was similar to that at 9 m depth on the fore reef, but may have exagerated the irradiance received by the vertical surfaces.

3.6 Respiration and photosynthesis/ irradiance relationships

Upon removal from the reef and return to the laboratory, the Perspex tiles bearing the nubbins were scraped clean of encrusting organisms. The nubbins were then placed into darkened, running sea water until use at various times of the following day. This ensured that individuals had similar light histories. A single nubbin was transferred in darkness to the respirometry chamber and left to settle for 5 - 10 minutes. The respiration rate, measured in darkness, was constant with decreasing PO_2 down to at least 75% saturation. All experiments were completed between 100 and 75% saturation by adding temperature equilibrated FSW, bubbled with either N_2 or O_2. After determining dark respiration, the net photosynthesis/irradiance (P/I) relationship was measured as the oxygen evolution over 5 to 10 minute periods at different irradiances.

The use of net rather than gross productivity was preferred in the present study as the former does not require the assumption that the colony respiration rate is the same in the light and in the dark (see Chapter 6.2 for evidence for an elevated daytime respiration rate). When the use of gross photosynthesis was unavoidable as in the calculations of the energy budget, it was taken as the sum of the net photosynthesis and the respiration rate measured after overnight darkness. After each experiment, nubbins were buoyant weighed and

their displacement volume measured and used to determine the volume of sea water in the chamber. Oxygen flux data were expessed as μlO_2 at S.T.P and normalised to dry tissue content and surface area of the nubbins.

As oxygen-flux experiments were not carried out at a fixed time, respiration and photosynthesis of nubbins were compared at various times of the day to determine whether daily variation occurred.

Five nubbins, collected from the 10 m depth WFR site, were cleaned and retained in darkened running seawater until their dark respiration was measured the following day at each of 07.00, 09.00. 12.00, 15.00 and 18.00 hrs ($\pm$ 30 minutes), after 5 minutes settling in the chamber. Nubbins were retained in darkness between measurements, and their buoyant weight and displacement volume determined after the 18.00 hrs experiment.

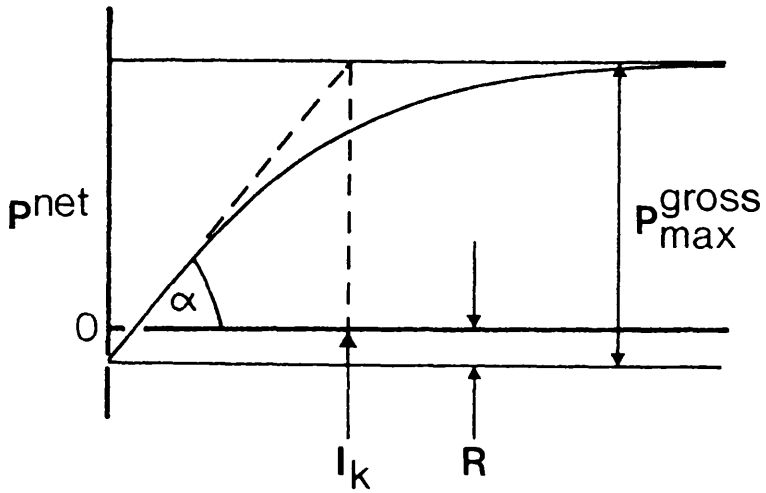
Groups of 5 nubbins were also collected from the 10 m depth WFR site and their net photosynthesis at 285 $\mu E.m^{-2}.s^{-1}$ immediately determined at 12.00, 15.00, 18.00 or 09.00 hrs. ($\pm$ 90 minutes; total of 20 nubbins) after cleaning their tiles and allowing them to acclimate for 15 minutes in the chamber. Buoyant weight and displacement volume were determined after removal from the chamber.

Respiration measurements were made on zooxanthellae isolated on a Percoll gradient by the method already described and then maintained in darkness with periodic aeration to keep the water saturated with O_2 and the cells in suspension. Three ml of each preparation (2 replicates, approximately 10^6 zoox.ml^{-1}) were placed in a water-jacketted chamber at 28°C, containing a magnetic spin bar rotating at 130 rpm. The zooxanthellae were allowed to equilibrate for 5 - 10 minutes before measuring their dark respiration using the same meter and oxygen electrode.

In order to obtain aposymbiotic nubbins for respiration determinations, symbiotic nubbins from the WFR site were maintained at a high irradiance until they became white and transluscent (up to 10 weeks). These were kept in a glass bowl surrounded externally by aluminium foil and continually supplied with a high flow of unfiltered sea water. Nubbins were exposed to direct sunlight during the day and to a 500W quartz-halogen lamp filtered through an infra-red filter (Edmund Scientific; stock 4009: 350 $\mu E.m^{-2}.s^{-1}$, 20 cm above the nubbins) at night and on heavily overcast days. The initial attempts at obtaining aposymbionts in the present study by exposing nubbins to high and low temperatures, aerial exposure, abrasion, darkness or 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) were unsuccessful. The respiration rate of aposymbionts was measured as described above and specimens were then buoyant weighed. As the dry tissue content of aposymbionts was not measured, oxygen uptake was normalised to surface area. Values for surface area obtained from the regression of surface area on skeletal weight for symbiotic individuals from the WFR site. At the end of the experiment after fixing, decalcifying and homogenising, nubbins were inspected for the presence of zooxanthellae.

3.7 Analysis of photosynthetic data

Net photosynthesis ($\mu lO_2.g^{-1}$ dry tissue.min^{-1}) vs irradiance data were fitted to Chalker's (1981) model based upon the hyperbolic tangent function (Figure 9):



$$P^{net} = P^{gross}_{max}.Tanh(I/I_k) + R$$

Figure 9. Generalised hyperbolic tangent function. P^{net} = net oxygen evolution (measured as $\mu lO_2.g^{-1}$dry tissue.min^{-1}) at an irradiance I ($\mu E.m^{-2}.s^{-1}$), P^{gross}_{max} = maximum gross photosynthesis = maximum net photosynthesis minus dark respiration (R, where R is expressed in the same units but with a negative sign) and I_k = the irradiance ($\mu E.m^{-2}.s^{-1}$) at which the initial slope (defined as alpha) of the curve intercepts the horizontal asymptote. $I_{0.95}$ is the irradiance at which photosynthesis is 95% of the maximum, and is used as an estimate of the saturating irradiance, where $I_{0.95}$ = 1.632 x I_k.

A computer programme was used to determine the best-fit curve for the unweighted data points by a least-squares regression analysis on the linear transformation of the hyperbolic tangent function. In order to produce a 'representative' P/I curve for P. porites at each site, a

best fit curve was fitted to the mean productivities at each irradiance for a group of nubbins from both of the WFR and the CP sites. Individual curves were also fitted to the P/I data for each nubbin.

3.8 Daily productivity

The percentage transmission of surface PAR to 10 m depth was used together with continuous recordings of surface PAR to predict the *in situ* PAR curve at 10 m depth. This curve was divided into 15 minute increments and the PAR was interpolated from the curve at the median time for each increment. Net photosynthetic rates at these irradiances were calculated for each nubbin from its best-fit hyperbolic tangent function and converted to absolute net production over each 15 minute increment. Net photosynthesis over each 15 minute period were summed over the whole day to give the integrated net photosynthetic oxygen production. The mean of these values for each group of nubbins was added to the daytime oxygen consumption (calculated from the mean measured dark respiration rate for the same group). This gave the mean integrated gross daily photosynthetic oxygen production. This method was used to calculate the productivities incorporated into the energy budgets in Chapter 4.

Assuming that lipid is the main respiratory substrate (Patton *et al.*, 1977), respiratory oxygen consumption was converted to energy using the oxy-joule equivalent of 19.63 J.mlO_2 (from Elliott and Davison, 1975) Photosynthetic oxygen production in the present study was converted to energy by assuming that 1 mol of O_2 resulted in the formation of 0.167 mol of glucose with an energy content of 469.5 KJ (Lehninger, 1973). However, the Calvin cycle reactions in photosynthesis fix CO_2 into glyceraldehyde-3 phosphate and then into

various products including glucose and lipids, although the proportional significance of each route is unknown (Bassham and Buchanan, 1982). In the photosynthetic pathway leading to glyceraldehyde-3 phosphate 1 mol O_2 = 488.7 KJ (Bassham and Buchanan, 1982), which is less than 5% higher than the value for the formation of glucose used in the present study. Until information on the proportion of carbon channeled into glucose, lipid or other compounds becomes available, the assumption that all the carbon is converted into glucose is valid and the estimate of photosynthetically fixed energy cannot be more than 5% in error.

3.9 Growth

In situ growth was measured for nubbins maintained at each study site but returned to the laboratory for buoyant weighing approximately every 3 weeks. Nubbins were away from the reef for less than 24 hours, and received no aerial exposure during the process. The skeletal increment, obtained from the buoyant weight using the empirically determined skeletal density, was used to determine the dry tissue increment from the regression of dry tissue on skeletal weight. Zooxanthellae growth was estimated by assuming a constant proportion of zooxanthellae to coral tissue biomass (Patton and Burris, 1983) so that a coral tissue growth increment would contain the same proportion of zooxanthellae. Skeletal and tissue growth increments were divided by the number of days between successive measurements to give the daily growth rates. These growth rates were then divided by the mean of the tissue biomass present at the start and end of the relevent observation period to give the daily tissue-specific growth rates. All regression equations involving growth rates were calculated by least squares linear regression.

3.10 Reproduction

Reproductive expenditure of Porites porites was predicted from measurements of the number of mature planulae produced. Two different pairs of colonies were sampled at various times of day each week from each site between November 1984 and March 1985. One branch from each colony was broken off underwater and put into a plastic bag which was sealed and immediately injected with concentrated formalin to approximately 5% v/v. Fixed specimens were returned to the laboratory, decalcified and dissected and 20 polyps from each colony examined under a binocular microscope at 20x magnification. The number of fecund polyps (those containing mature and/or immature planulae and/or gonads) and the number of mature planulae per polyp were recorded. The length of mature planulae was recorded using an eyepiece graticule at 20x magnification.

On two occasions live planulae were released overnight from nubbins collected from the WFR site and retained in the aquarium. These planulae were sucked onto Whatman GF/C filters and their energy content determined by the wet oxidation procedure already described for zooxanthellae. No correction for incomplete protein oxidation was applied since planulae protein content was not determined.

3.11 Heterotrophy

Heterotrophic input, as zooplankton capture, was assessed by microscopic inspection at 20x magnification of decalcified and dissected polyps, which were fixed in situ at various times of the day and night at the WFR site. On one night zooplankters were attracted to colonies of P. porites at the WFR site with a white lamp prior to fixation. These polyps were also decalcified, dissected and inspected. In addition, all polyps dissected for reproductive assessment at both sites were examined for the presence of zooplankters.

3.12 Mucus release

In order to investigate the loss of energy as mucus, mucus release was measured under 'unstressed' conditions *in situ* and also during 'unstressed' and 'stressed' conditions in the laboratory using nubbins from the WFR site only.

Three Perspex incubation boxes were used for *in situ* mucus collection. Each had a volume of 300 ml, an integral battery operated stirrer and a removable lid containing a 50 x 100 mm teflon FEP membrane (pore-size 10 nm; thickness 0.025 mm (Dupont)), which allowed flux of oxygen and carbon-dioxide, but retained large molecules. One nubbin was place in each of two boxes *in situ* at 10 m depth at the WFR site, and the third box contained only sea-water as a control. After up to 72 hours the boxes were recovered and drained into separate screw-capped jars with minimal disturbance to the nubbins.

In the laboratory 'unstressed' mucus release was measured in beakers containing 150 ml of aerated 0.45 μm FSW, 5 each containing 1 nubbin and 5 as controls with no nubbin. These were incubated over 1 day with exposure to natural sunlight shaded with plastic mosquito netting to a quantitative equivalent of the PAR received at 10 m depth. 'Stressed' mucus release was stimulated in the laboratory by chilling nubbins in 150 ml of FSW to 21^{o}C for up to 60 minutes. Control jars contained no nubbin and were also chilled.

All incubation water samples were filtered through precombusted Whatman GF/C filters which were rinsed with 4.5% w/v solution of Na_2SO_4 (Strickland and Parsons, 1972) and wet oxidised as previously described for zooxanthellae. Filtrates were dialysed (dialysis tubing with 2000 M.W. cut off; preboiled in 5% w/v $NaHCO_3$ to remove residual

organics) for 48 hours against running tap water to remove halides, either before or after concentration by pervaporation and 4ml aliquots (2 replicates) were then removed for energy determination by wet oxidation by the procedure described for whole coral tissues.

CHAPTER 4: RESULTS AND THE ENERGY BUDGETS

4.1 Introduction

Measurements of specimen characteristics, respiration, photosynthesis, growth, heterotrophy, reproduction and mucus release were made for Porites porites growing at two sites and used to construct energy budgets. These data are presented, compared and discussed in this chapter and energy budgets calculated on an 'ideal' sunny day using the summer mean transmission of surface PAR to 10 m depth for each site. Energy budgets on 'non-ideal', days with reduced PAR and more turbid water will be constructed in Chapter 5.

Porites porites collected at both sites conformed to P. porites as described in Chapter 3, although specimens at the CP site were a darker brown than those at the WFR site and grew with more spindly, widely spaced branches in smaller colonies. The large colonies such as occur at the WFR site containing hundreds of branches, were not found at the CP site.

The living tissue in Porites porites extends into the skeleton to about 5 mm depth and appears as a brown zooxanthellae-containing ring in cleaved branches. A number of branches of P. porites at each site contained the siphonaceous green alga Ostreobium spp. within the skeleton. Only Ostreobium-free nubbins were used.

Porites porites nubbins at both sites had approximately 300 mg of dry tissue and survived well in the field. Both skeleton and tissue grew out over the tiles after several months.

4.2 Specimen characteristics

In order to construct energy budgets and to allow normalisation of all data, the characteristics of Porites porites from both sites were measured (Table 4). These data were compared between sites by the t-test.

The skeletal densities were not significantly different between sites. Dry tissue and skeletal dry weight were significantly correlated at both sites and the highest correlation coefficient obtained with a power relationship of $\log_{10}$ dry tissue versus $\log_{10}$ skeletal weight data (WFR site: r = 0.8471, d.f. = 20, P < 0.001, size range 2.451 g - 11.085 g skeleton, cf. untransformed data, r = 0.7848, P < 0.001 ; CP site: r = 0.9246, d.f. = 15, P < 0.001, size range 3.213 g - 10.509 g skeleton, cf. untransformed data, r = 0.9203, P < 0.001). These regression lines are shown in Figure 10. The slope of the regression line for nubbins from the CP site was significantly different from that for the nubbins from the WFR site (ANCOVA, $F_{(Slopes)1,33} = 4.1761$, P < 0.05).

Surface area (SA) and skeletal dry weight were significantly correlated with a linear regression at both sites (Table 4: WFR site, P < 0.001, size range 3.285 g - 11.734 g skeleton; CP site, P < 0.001, size range 2.679 g - 7.494 g skeleton). These regression lines are shown in Figure 10. Neither the slopes nor the elevations were significantly different between sites (ANCOVA, $F_{(slopes)1,34} = 0.4932$, $F_{(elevations)1,35} = 2.6973$, P = 0.05 for both cases). The regressions of dry tissue on skeletal weight were used to predict the dry tissue content of nubbins with a known surface area, and the dry tissue content was then expressed on a unit area basis. Nubbins from the WFR site had significantly more dry tissue per cm^2 than nubbins from the CP site.

Table 4. Porites porites, at the West Fore Reef (WFR) and Columbus Park (CP) sites: specimen characteristics. All values are mean ± 95% confidence limits or means with the 95% ranges in the case of percentage data (calculated as arcsine transformed data; Sokal and Rohlf, 1969). The regressions of dry tissue content and surface area on skeletal weight were compared between sites by ANCOVA analysis and the results presented in the text. The remaining data were compared between sites by the t-test and the t values are shown together with the probability (P) for a significant difference. In the case of percentage data, t-tests were carried out on arcsine transformed data. N.S. = not significantly different at P = 0.05.

CHARACTERISTIC	WFR SITE	CP SITE	t	SIGNIFICANCE
Skeletal density $g.cm^{-3}$	2.822 ± 0.190 (21)	2.683 ± 0.317 (20)	0.7853	N.S.
Dry tissue content $mg\ dry\ tissue.cm^{-2}$	18.59 ± 0.99 (22)	15.51 ± 1.14 (16)	4.2502	P < 0.001
regression of dry tissue on skeletal weight. $y = \log_{10}(mg\ dry\ tissue)$ $x = \log_{10}(g\ skeleton)$	y = 0.7437x + 1.9034 r = 0.8471 (21)	y = 1.1145x + 1.5547 r = 0.9246 (16)		
Surface area				
regression of surface area on skeletal weight. $y = cm^2$ surface area $x = g$ skeleton	y = 5.9917 + 1.7179x r = 0.9272 (22)	y = 3.9458 + 1.9364x r = 0.9604 (16)		
Ash content of tissue % of dry tissue	22.0% (12) (17.2% to 27.2%)	12.1% (15) (9.6% to 14.8%)	4.0226	P < 0.001
Tissue energy content $J.mg^{-1}$ dry tissue	16.18 ± 1.05 (21)	14.40 ± 1.43 (18)	2.1085	P < 0.05
Tissue protein content % of dry tissue	23.30% (10) (20.64% to 26.07%)	24.40% (7) (21.28% to 27.66%)	0.6207	N.S.
Number of polyps $polyps.cm^{-2}$	25.0 ± 2.4 (8)	22.6 ± 1.7 (0)	1.9427	N.S.
Zooxanthellae content $x10^7 zoox.g^{-1}$ dry tissue	15.52 ± 1.78 (18)	18.97 ± 4.54 (11)	1.5656	N.S.
$x10^6 zoox.cm^{-2}$	3.13 ± 0.53 (18)	3.16 ± 0.77 (11)	0.0656	N.S.
Zooxanthellae characteristics				
Chlorophyll a $\mu g\ pigment.x10^6 zoox^{-1}$.	6.81 ± 1.31 (18)	6.89 ± 1.87 (8)	0.1151	N.S.
Chlorophyll c2 $\mu g\ pigment.x10^6 zoox^{-1}$.	2.13 ± 0.50 (18)	2.33 ± 0.69 (8)	0.5017	N.S.
energy content $J.x10^6 zoox^{-1}$.	11.69 ± 2.41 (10)	7.76 ± 0.73 (8)	3.2017	P < 0.01
protein content $\mu g\ protein.x10^6 zoox^{-1}$.	85.30 ± 13.77 (10)	74.67 ± 17.27 (8)	1.1290	N.S.

Table 4

Figure 10. Porites porites from both the West Fore Reef (WFR) and the Columbus Park (CP) sites: relationships between skeletal weight and dry tissue content (a,b) and skeletal weight and surface area (c,d). The best-fit linear regression lines are drawn, togetner with the 95% prediction limits (Sokal and Rohlf, 1969). The equations of the lines are given in Table 4.

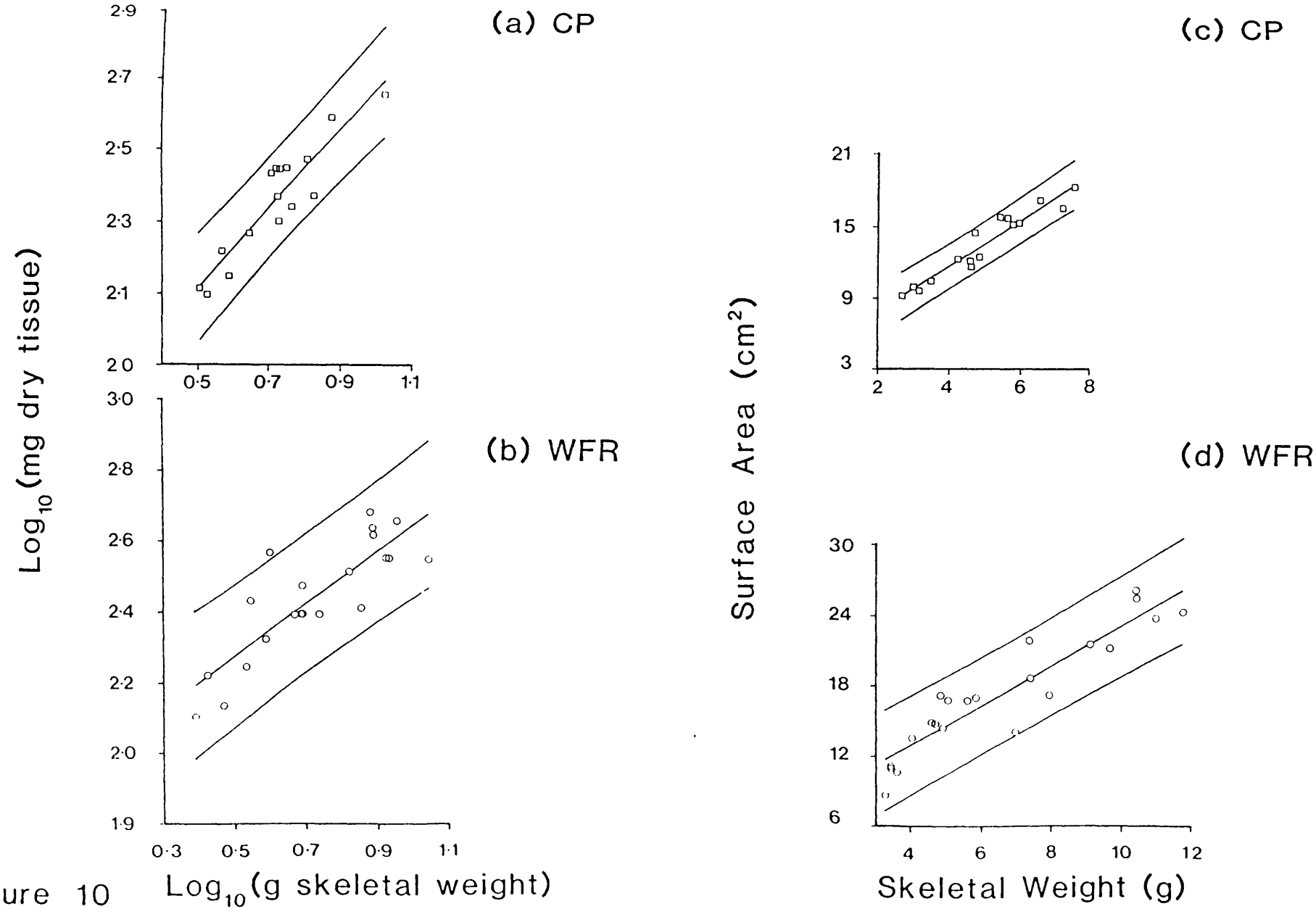

(a) CP
(b) WFR
(c) CP
(d) WFR
Log10 (mg dry tissue)
Log10 (g skeletal weight)
Surface Area (cm2)
Skeletal Weight (g)
2·9
2·7
2·5
2·3
2·1
2·0
0·5
0·7
0·9
1·1
3·0
2·8
2·6
2·4
2·2
2·0
1·9
0·3
0·5
0·7
0·9
1·1
21
15
9
3
2
4
6
8
30
24
18
12
6
4
6
8
10
12

Figure 10

The power regression between the dry tissue content and skeletal weight suggests that the unit area tissue content increased with skeletal weight and this effect was greater at the CP site where the gradient of the regression line was steeper. Small nubbins at the CP site had less tissue.cm^{-2} than equivalent nubbins at the WFR site, but this disparity was reduced as the skeletal weight increased. However, as the same data also gave a good fit for a linear regression the unit area increase in tissue with increasing skeletal weight was minimal within the size range studied. The dry tissue contents for normalising growth, oxygen flux and zooxanthellae content were obtained from the more accurate power regression.

The ash content of dry tissue and the tissue energy content at the WFR site were significantly higher than at the CP site. There was no significant difference in zooxanthellae content, protein and polyp content between the two sites.

Zooxanthellae isolated by repetitive washing from Porites porites were contaminated with animal debris and were only used for chlorophyll determinations. Chlorophyll a and c_2 contents are shown in Table 4 and were not significantly different between sites.

Zooxanthellae isolated on a step gradient of Percoll from Porites porites were free of animal debris when inspected at 400x magnification. Their energy and ana protein content are shown in Table 4. Zooxanthellae from P. porites at the WFR site had a significantly higher energy content than those from the CP site, but their protein content was not significantly different.

4.3 Respiration and photosynthesis

4.3.1. Daily variation in respiration and photosynthetic ability

To determine whether Porites porites had an endogenous respiratory rhythm which would affect the results obtained depending on the time of measurement, the respiration rate of nubbins from the WFR site was measured under constant darkness at 07.00, 09.00, 12.00, 15.00 or 18.00 hrs. (Table 5) and was found to be the same (the same 5 nubbins at each time, variance between times not significantly greater than residual, two-way ANOVA, $F_{(times)4,16} = 1.8707$, $P = 0.05$). Similarly to determine whether photosynthetic ability varied throughout the day, net photosynthesis at 285 $\mu E.m^{-2}.s^{-1}$ was measured for nubbins freshly collected from the WFR site at 09.00, 12.00, 15.00 or 18.00 hrs. (Table 6) and was found to be the same (5 different individuals at each time, one-way ANOVA, $F_{3,16} = 2.13$, $P = 0.05$).

4.3.2 Photosynthesis/irradiance relationships

In order to obtain a mathematical relationship between the irradiance and photosynthetic productivity, best-fit hyperbolic tangent functions were fitted to net photosynthesis vs irradiance data for 10 nubbins from each site (Appendix I, Table 1 and 2). Five nubbins from the WFR site and 4 nubbins from the CP site reproduced only the initial portion of the curve without reaching a P_{max} at the experimental irradiances available. This accounted for the high variance in the I_k and P_{max} values.

Mean photosynthetic characteristics derived from each individual curve for the 10 nubbins at each site are shown in Table 7 together with the results of t-test comparisons between sites. The

	TIME OF DAY (HOURS)				
REPLICATE	07.00	09.00	12.00	15.00	18.00
1	8.58	11.29	7.40	6.88	10.52
2	4.87	7.09	8.29	8.76	7.79
3	8.74	11.95	12.27	11.20	13.16
4	7.61	8.54	5.13	4.65	7.22
5	6.94	7.52	6.28	6.89	6.65
MEAN	7.35	9.28	7.87	7.68	9.07
S.D.	1.57	2.22	2.73	2.45	2.73

Table 5. Porites porites, from the West Fore Reef site: dark respiration recorded at different times of day. All units $\mu l O_2 . g^{-1}$ dry tissue.min^{-1}. The same 5 individuals were recorded at each time and were kept in darkness in between measurements.

	TIME OF DAY (HOURS)			
REPLICATE	09.00	12.00	15.00	18.00
1	36.87	14.67	24.67	15.79
2	24.87	24.09	25.92	8.23
3	22.58	19.35	16.68	10.67
4	18.69	19.84	13.62	10.34
5	15.07	14.78	11.89	22.64
MEAN	23.62	18.55	18.56	13.53
S.D.	8.30	3.95	6.40	5.80

Table 6. Porites porites, from the West Fore Reef site: net photosynthesis at 285 $\mu E.m^{-2}.s^{-1}$ recorded at different times of the day. All units $\mu lO_2.g^{-1}$ dry tissue.min^{-1}. 5 different nubbins were measured for each time.

Table 7. Porites porites at both the West Fore Reef (WFR) and Columbus Park (CP) sites: mean photosynthetic characteristics taken from individual curves for each of 10 nubbins at each site. All units as shown, values given as mean ± 95% confidence limits, sample size in parenthesis, d.t. = dry tissue. Statistical comparisons were carried out by the t-test and the t values and the probability (P) for a significant difference are shown. N.S = not significantly different at P = 0.05

[A] Calculated using dry tissue content of 18.59 $mg.cm^{-2}$ (WFR site) and 15.51 $mg.cm^{-2}$ (CP site).

[B] Calculated using the protein content of the dry tissue (Table 4).

[C] Calculated using zooxanthellae content of dry tissue and the chlorophyll a content of zooxanthellae (Table 4).

CHARACTERISTIC	WFR SITE	CP SITE	t	SIGNIFICANCE
Colony Respiration				
$\mu lO_2.mg^{-1}(d.t.).h^{-1}$	0.64 ± 0.21 (10)	0.45 ± 0.11 (10)	1.7914	N.S.
$^{A}\mu lO_2.cm^{-2}.h^{-1}$	11.91 ± 4.00 (10)	7.01 ± 1.70 (10)	2.5482	$P < 0.05$
Maximum Gross Photosynthesis				
$\mu lO_2.mg^{-1}(d.t.).h^{-1}$	4.43 ± 1.87 (10)	4.13 ± 1.25 (0)	0.3011	N.S.
$\mu lO_2.x10^6zoox^{-1}.h^{-1}$	28.53 ± 12.07 (10)	21.78 ± 6.60 (10)	1.1118	N.S.
$^{A}\mu lO_2.cm^{-2}.h^{-1}$	82.34 ± 34.82 (10)	64.08 ± 19.40 (10)	1.0365	N.S.
$^{A}\mu gO_2.cm^{-2}.h^{-1}$	117.58 ± 49.63 (10)	91.45 ± 27.68 (10)	1.0377	N.S.
$^{B}\mu molO_2.mg^{-1}$ protein.h^{-1}	0.85 ± 0.36 (10)	0.76 ± 0.23 (10)	0.4759	N.S.
I_k $\mu E.m^{-2}.s^{-1}$	456 ± 250 (10)	215 ± 39 (10)	2.1510	$P < 0.05$
95% Irradiance ($I_{0.95}$)				
$\mu E.m^{-2}.s^{-1}$	835 ± 459 (10)	393 ± 71 (10)	2.1197	$P < 0.05$
Alpha (α)				
$\mu lO_2.mg^{-1}(d.t.).h^{-1}.uE^{-1}.m^2.s.$	0.011 ± 0.003 (10)	0.019 ± 0.004 (10)	3.852	$P < 0.01$
$^{A}\mu gO_2.cm^{-2}.h^{-1}.uE^{-1}.m^2.s$	0.292 ± 0.080 (10)	0.421 ± 0.089 (10)	2.4414	$P < 0.05$
$^{C}\mu molO_2.h^{-1}.(mgChla)^{-1}.uE^{-1}.m^2.s$	0.463 ± 0.126 (10)	0.648 ± 0.137 (10)	2.2461	$P < 0.05$
Zooxanthellae Respiration				
$\mu lO_2.x10^6zoox^{-1}.h^{-1}.$	1.84 ± 0.34 (19)	1.82 ± 0.33 (16)	0.0630	N.S.

Table 7

'representative' P/I curve for each site is shown in Figure 11 (the 'representative' P/I curves are used in Chapter 5). P_{max}^{gross} was not significantly different between sites irrespective of method of normalising, whilst I_k and $I_{0.95}$ were significantly lower at the CP site and alpha was significantly higher at the CP site. Colony respiration was significantly lower at the CP site on a unit area basis but not on a unit dry tissue basis.

Zooxanthellae freshly isolated on a Percoll gradient showed no signs of lysis and remained photosynthetically active for at least 9 hours after isolation, as measured by oxygen evolution in the light. The dark respiration of isolated zooxanthellae was not significantly different between sites.

4.3.3. Respiration rate of aposymbionts

Aposymbiotic Porites porites were obtained for respiration measurements by exposing symbiotic nubbins from the WFR site to a high irradiance for 8 - 10 weeks. Zooxanthellae were expelled in large numbers over the first 2 weeks and were seen as a brown ring around the base of the nubbin. The residual zooxanthellae population then decreased slowly over the following 3 - 8 weeks. The mean respiration rate of the aposymbionts at the end of the 10 week period was 7.2 $\pm$ 1.5 $\mu l O_2.cm^{-2}.h^{-1}$ (n = 5) which was significantly lower than the respiration rate of symbiotic nubbins from the WFR site (from Table 7; t-test, t = 2.5454, d.f. = 13, $P < 0.05$). Aposymbiotic nubbins were white and opaque when fully expanded and did not have a measurable net photosynthetic oxygen production at 240 $\mu E.m^{-2}.s^{-1}$. When fixed, decalcified, homogenised and inspected, zooxanthellae were found at a mean of 7.4% (n = 4) of the zooxanthellae population size of symbiotic nubbins of equivalent size and from the same location.

Figure 11. 'Representative' net photosynthesis/irradiance curves for Porites porites at the West Fore Reef (WFR) and the Columbus Park (CP) study sites. Mean ± S.E. are plotted and the best-fit hyperbolic tangent functions fitted to the mean net photosynthesis at each irradiance are drawn in. n = 10 for all points at the WFR site except for ★ where n = 8; n = 10 for all points at the CP site except for ☆ and ✪ where n = 5 and 9 respectively.

The equations for the "representative" P/I curves are:

$$\text{WFR:} \quad P^{net} = 56 \times \text{Tanh}(I/334) - 8.09$$

$$\text{CP:} \quad P^{net} = 61 \times \text{Tanh}(I/174) - 9.06$$

where I = irradiance ($\mu E.m^{-2}.s^{-1}$)

P^{net} = net productivity ($\mu l O_2.g^{-1}$ dry tissue.min^{-1})

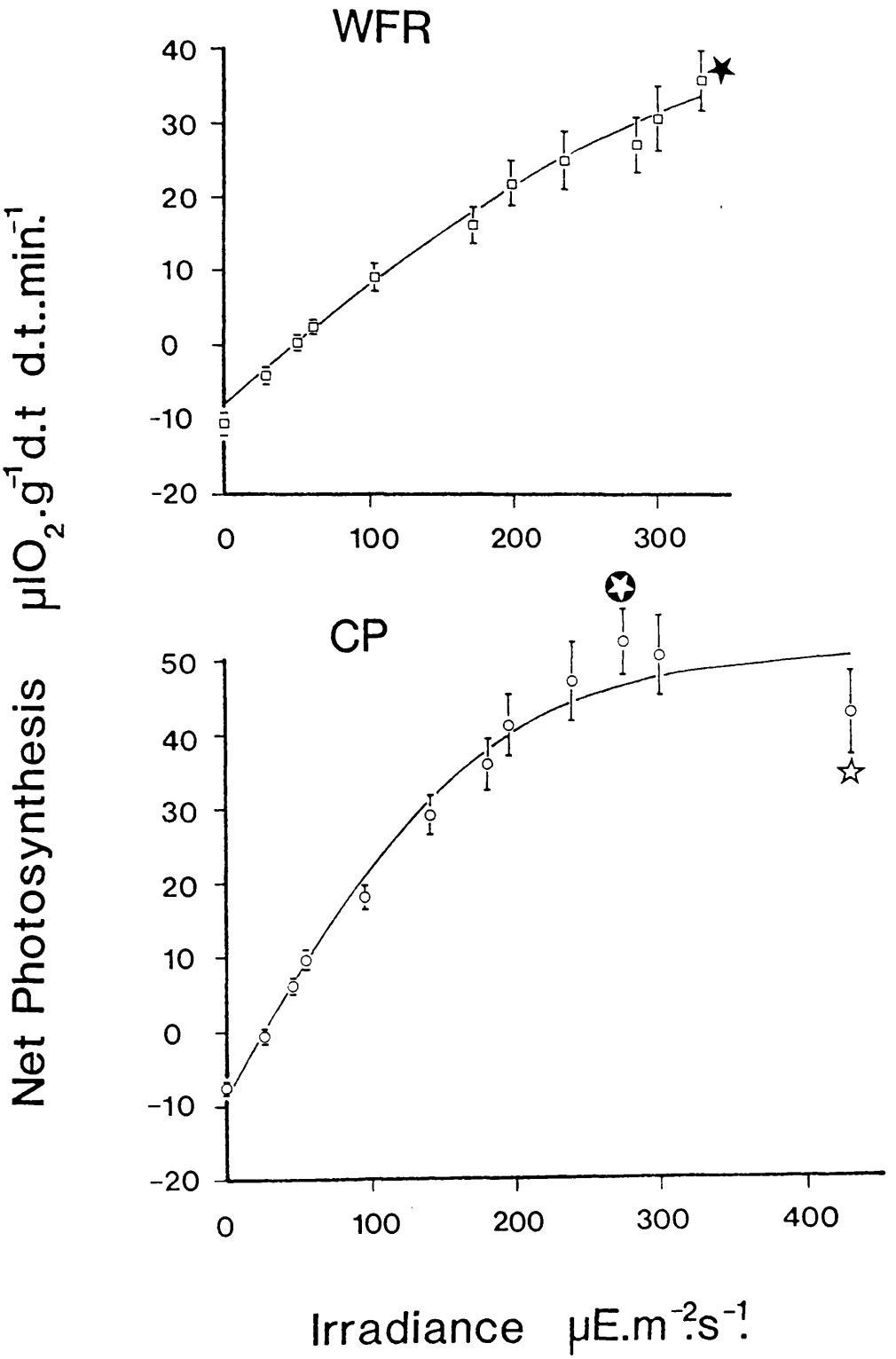

WFR
CP
Net Photosynthesis μlO2.g-1d.t d.t..min-1
Irradiance μE.m-2.s-1
40
30
20
10
0
-10
-20
0
100
200
300
50
40
30
20
10
0
-10
-20
0
100
200
300
400

Figure 11

4.4 Growth

4.4.1. Mean growth rates

Porites porites grew almost linearly over a 9 week observation period at the WFR site and a 14 week observation period at the CP site (Figure 12; Appendix I, Table 3, 4). These data were normalised to unit biomass of dry tissue (Table 8; Appendix I, Table 5, 6) to allow incorporation into the energy budgets and between site comparisons. Mean tissue-specific skeletal growth (TSSG) was 81.7 $mg.g^{-1}$dry $tissue.d^{-1}$ (WFR site) and 47.1 $mg.g^{-1}$ dry $tissue.d^{-1}$ (CP site), and mean tissue-specific tissue growth (TSTG) was 2.8 $mg.g^{-1}$dry $tissue.d^{-1}$ (WFR site) and 2.3 $mg.g^{-1}$ dry $tissue.d^{-1}$ (CP site) for bulked data for all measurement periods. Tissue-specific skeletogenesis and tissue-specific growth rates were significantly higher at the WFR site than at the CP site (Table 8), and similary for the unit area growth rates calculated from the same data (Table 8).

With a constant zooxanthellae to coral-tissue biomass ratio and using the tissue specific growth rates over the whole growth period at each site 4.35×10^5 zooxanthellae and 4.36×10^5 zooxanthellae were added each day to a nubbin with 1 g dry tissue at the WFR and CP site respectively. These are equivalent to algal-specific growth rates (μ) of 0.0028 (WFR site) and 0.0023 (CP site) $zooxanthella.zooxanthella^{-1}.d^{-1}$. Although Porites porites at both sites was not observed extruding zooxanthellae-containing pellets similar to those described by Steele (1977) the expulsion of individual zooxanthellae other than in pellets was not investigated.

Figure 12. Porites porites at both the Columbus Park (CP) and the West Fore Reef (WFR) sites: absolute tissue and skeletal growth increments over the observation period. The mean growth increment for each group of nubbins at each site are shown at each measurement period ± 95% confidence limits. 14 replicates at each point for the WFR site (★ n = 13, for tissue and skeleton) and 12 replicates at each point for the CP site.

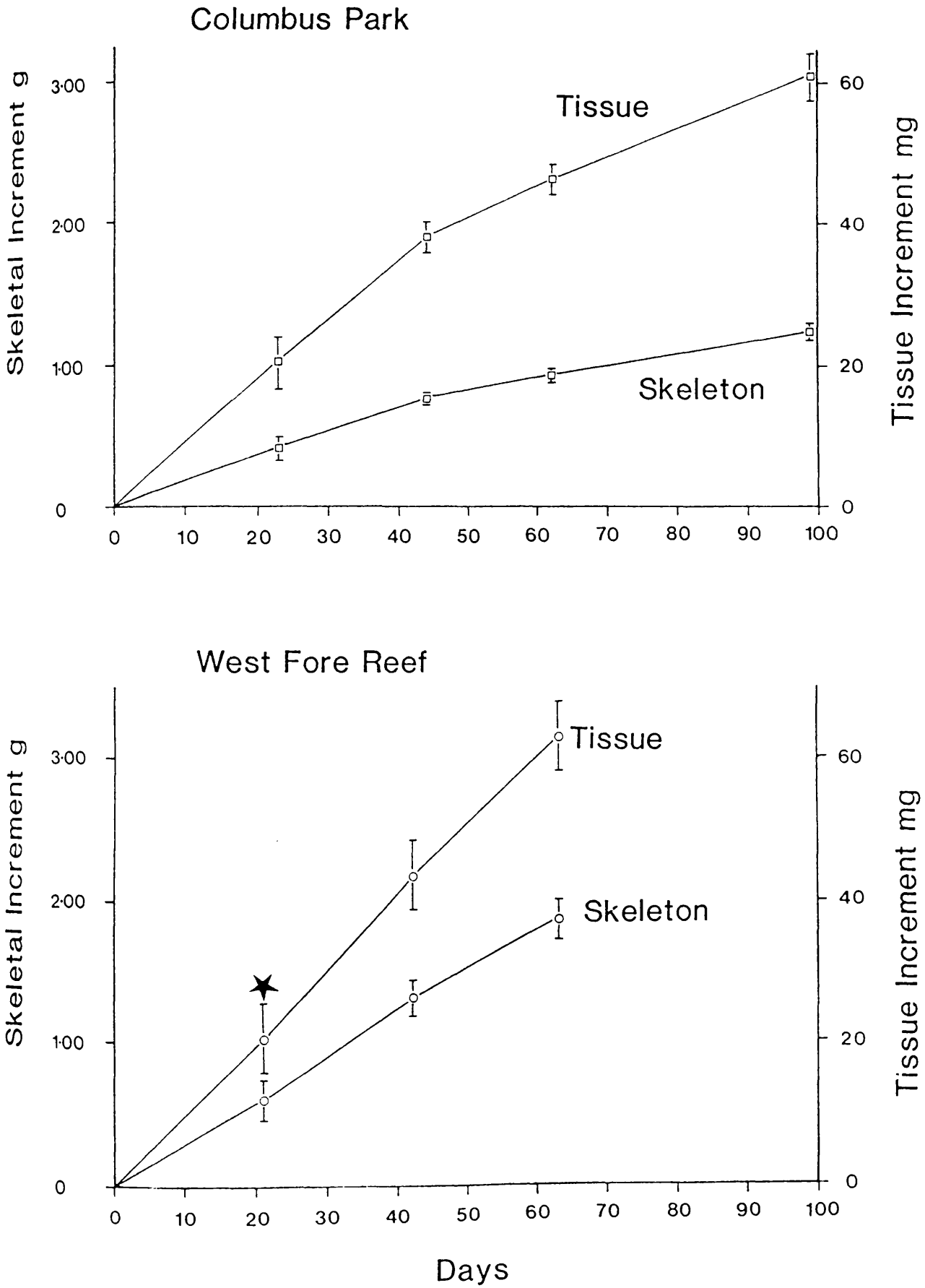

Columbus Park
Skeletal Increment g
Tissue Increment mg
Tissue
Skeleton
3·00
2·00
1·00
0
60
40
20
0
0 10 20 30 40 50 60 70 80 90 100
West Fore Reef
Skeletal Increment g
Tissue Increment mg
Tissue
Skeleton
3·00
2·00
1·00
0
60
40
20
0
0 10 20 30 40 50 60 70 80 90 100
Days

Figure 12

	WFR	CP	t	SIGNIFICANCE
SKELETON				
$mg.g^{-1}$dry tissue.day^{-1}	81.7 ± 7.3 (41)	47.1 ± 7.3 (48)	6.7231	$P < 0.001$
$A_{mg.cm^{-2}.day^{-1}}$	1.52 ± 0.14 (41)	0.73 ± 0.11 (48)	7.8326	$P < 0.001$
TISSUE				
$mg.g^{-1}$dry tissue.day^{-1}	2.8 ± 0.2 (41)	2.3 ± 0.4 (48)	2.3917	$P < 0.02$
$A_{mg.cm^{-2}.day^{-1}}$	0.052 ± 0.004 (41)	0.036 ± 0.006 (48)	4.5619	$P < 0.001$

Table 8. Pooled growth rates of Porites porites taken from the West Fore Reef (WFR) and the Columbus Park (CP) sites. Mean ± 95% confidence limits are shown with the number of measurements in parenthesis. 41 measurements were made on 14 individuals at the WFR site, and 48 measurements were made on 12 individuals at the CP site. Growth rates were compared between sites by the t-test: t values and probability (P) for a significant difference are shown.

A: calculated using the unit area dry tissue content of 18.59 $mg.cm^{-2}$ (WFR site) and 15.51 $mg.cm^{-2}$ (CP site).

4.4.2. Size specific and time specific effects

To determine the effect of time and nubbin size on the observed growth rates, correlation and ANOVA analyses were used to investigate the relationships between tissue-specific growth rates and dry tissue content and between tissue-specific growth rates and time of measurement.

At the WFR site the tissue-specific growth rates over each of the three measurement periods were similar irrespective of the size of the nubbins (Appendix I, Table 5) and were not significantly correlated with the corresponding dry tissue content ($0.450 > r > 0.063$, not significant at $P = 0.05$). However, both TSTG and TSSG were significantly different between each measurement period and between replicates (two-way ANOVA: TSTG, $F_{(times)2,24} = 19.6984$, $P < 0.001$; TSSG, $F_{(times)2,24} = 15.8436$, $P < 0.001$). The mean TSTG and the mean TSSG for the third measurement period were significantly lower than the TSTG or TSSG over the first or second periods (Table 9, Student-Newman-Keuls test (SNK; Sokal and Rohlf, 1969) using the error mean square from the two-way ANOVA, $P < 0.05$).

At the CP site the tissue-specific growth rates over each measurement period (Appendix I, Table 6) showed a significant negative correlation with the corresponding predicted dry tissue content over the first three measurement periods ($-0.678 > r > -0.760$, significant at $P < 0.02$), but not the final period ($-0.290 > r > -0.360$, not significant at $P = 0.05$). Both TSTG and TSSG were significantly different between each measurement period and between replicates (two-way ANOVA; TSTG: $F_{(times)3,33} = 28.9650$, $P < 0.001$; TSSG, $F_{(times)3,33} = 30.6685$, $P < 0.001$). The mean TSTG and the mean

WEST FORE REEF

	OBSERVATION PERIOD (DAYS)		
	FIRST	SECOND	THIRD
n	13	13	13
TSTG	2.9	3.2	2.3
TSSG	85.7	93.1	64.6

COLUMBUS PARK

	OBSERVATION PERIOD (DAYS)			
	FIRST	SECOND	THIRD	FOURTH
n	12	12	12	12
TSTG	3.4	3.0	1.5	1.4
TSSG	70.7	60.2	29.3	28.0

Table 9. Porites porites, at the West Fore Reef (WFR) and the Columbus Park (CP) sites: mean tissue specific growth rates over each of the approximately 3 week observation periods. Tissue specific tissue growth (TSTG) in $mg.g^{-1}$ dry $tissue.day^{-1}$, tissue specific skeletal growth (TSSG) in mg skeleton. g^{-1} dry $tissue.day^{-1}$. n = sample size in ANOVA analysis (the data from one specimen was omitted from the WFR analysis, see Appendix I, Table 3). The means which are not significantly different are underlined (P = 0.05; Student-Newman-Keuls test).

TSSG for the first two periods were not significantly different (SNK test, P = 0.05) but were significantly higher than the mean TSTG and the mean TSSG respectively for the final two periods (Table 9; SNK test, P < 0.05).

4.5 Heterotrophy

To determine the heterotrophic input as zooplankton capture, specimens of Porites porites were collected at 07.55 hrs (2 colonies, 25 polyps), 19.55 hrs (1 colony, 32 polyps) and 12.00 hrs (1 colony, 25 polyps) and individual polyps inspected for the presence of zooplankters. No zooplankters were found in these polyps, although two calanoid copepods (1mm long) were found on the oral discs of separate polyps on the colony collected at night after attracting zooplankters with a white light . After examining more than 650 polyps at each site, 2 polyps were each found to contain one cyclopoid copepod at the WFR site.

4.6 Reproduction

To determine the energy expenditure on reproduction, the frequency of planulation and the number of planulae were estimated by weekly inspections of dissected polyps.

At each site reproductive state often differed between two colonies with only one of each pair being fecund in some of the weeks sampled. In fecund colonies only a proportion of the polyps were fecund. These contained combinations of mature planulae, immature planulae and gonads. Mature planulae were free in the coelenteron and contained zooxanthellae, mesenteries and sometimes an oral aperture.

Immature planulae often contained zooxanthellae but no mesenteries or oral apertures were observed. These planulae appeared attached to and were surrounded by the mesenteries, as were the gonads.

Mature planulae (preserved) had a mean maximum diameter of 0.455 $\pm$ 0.014 mm (n = 205, WFR site) and 0.463 $\pm$ 0.013 mm (n = 190, CP site) which were not significantly different (t-test, P = 0.05). Mean data for all colonies and polyps at the WFR site showed that each week 46.1% (95% range: 28.8% to 69.8%, n = 18) of the polyps were fecund and that 10.7% (95% range: 3.2% to 21.9%, n = 18) of the polyps each contained 2.0 $\pm$ 0.3 mature planulae (n = 124). Mean data for all colonies and polyps at the CP site showed that each week 40.1% (95% range: 23.9% to 57.4%, n = 18) of the polyps were fecund and that 13.1% (95% range: 3.4% to 27.7%, n = 18) of the polyps each contained 1.7 $\pm$ 0.2 mature planulae (n = 105). The percentage of the polyps which were fecund or which contained mature planulae were not significantly different between sites (t-test; t = 0.4276, d.f. = 34; t = 0.3975, d.f. = 34 respectively, P = 0.05 for each; percentage data arcsine transformed), nor were the number of mature planulae per polyp (t-test; t = 1.7241, d.f. = 227, P = 0.05). Neither the number of polyps containing planulae nor the number of planulae per polyp (for mature or immature planulae alone, or mature plus immature planulae together) displayed a significant cyclical behaviour at either site (one-sample runs test, n = 18, P = 0.025). However the highest proportion of fecund polyps containing mature planulae showed evidence of a monthly cycle at both sites (Figure 13, Appendix I, Table 7), but this was not significantly related to time at each site (one-sample runs test, P = 0.025). These data were used to give a first approximation to the time between initiation and release of planulae.

Figure 13. Porites porites at both the Columbus Park (CP) and West Fore Reef (WFR) sites: proportion of fecund polyps containing mature planulae from approximately weekly samples between November 1984 and March 1985.

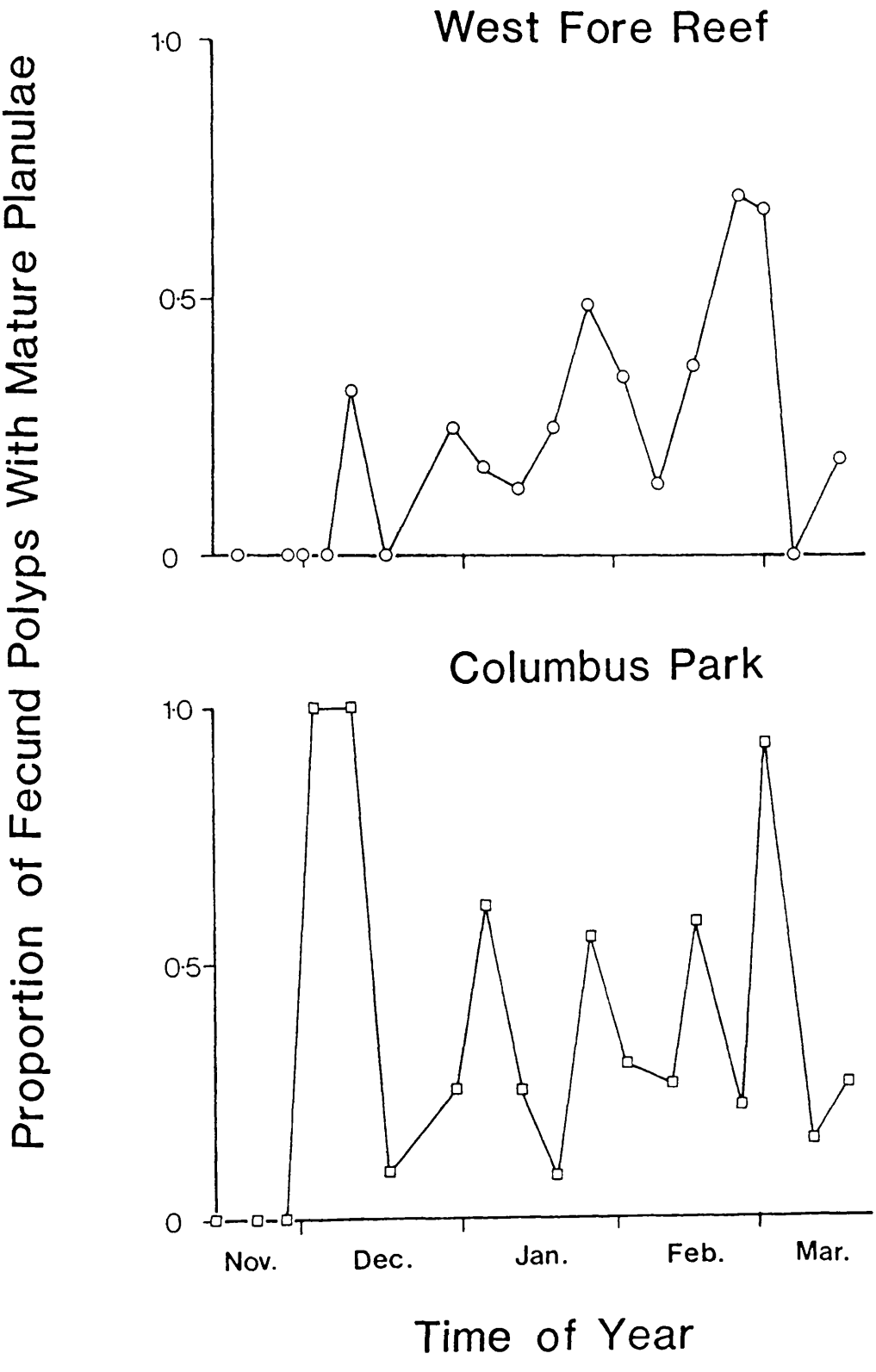

West Fore Reef
1·0
0·5
0
Columbus Park
1·0
0·5
0
Nov.
Dec.
Jan.
Feb.
Mar.
Proportion of Fecund Polyps With Mature Planulae
Time of Year

Figure 13

Two specimens of Porites porites collected from the WFR site released mature, free swimming planulae when retained in an aquarium over night. These had a mean energy content of 0.27 J.planula^{-1} (2 determinations of 70 and 27 planulae).

4.7 Mucus release

The energy loss as mucus from Porites porites was assessed by wet oxidation of both the soluble and particulate fractions released during incubation in situ and also in the laboratory. The wet oxidation method used could detect approximately 2.5 J.sample^{-1} (approx. 6% of a 4 ml aliquot of $K_2Cr_2O_7$ being reduced) for either solid or fluid (4 ml) samples.

In the first experiments designed to measure in situ mucus release from Porites porites, the seawater used had an energy content at or below the limit of detection of the method used for both particulate and soluble materials. In order to reduce the error caused by particulate materials normally present in seawater, mucus release was also measured in controlled laboratory conditions using 0.45 um FSW. The seawater from 'unstressed' laboratory incubations of P. porites did not contain measurable amounts of dissolved materials, but the energy content of particulate materials was not significantly different from the controls (t-test, t = 1.0418, d.f. = 18, P = 0.05) although the energy contents were only just detectable (9% of the $K_2Cr_2O_7$ reduced by experimental filters). In the laboratory, nubbins chilled to 21°C for 25 or 60 minutes released mucus containing cellular debris including nematocysts and zooxanthellae. The particulates represented a mean loss rate of 39 ± 14 J.g^{-1} dry tissue (25 minutes) and 128 ± 53 J.g^{-1} dry tissue (60 minutes) (n = 10 for each), but the filtrate energy content was below the limit of detection.

4.8 The 24 hour energy budget

The energy budgets for Porites porites growing at both study sites is calculated using the data presented above. All values are calculated for a specimen with 300 mg dry tissue, which is near the mean size used at both sites.

4.8.1 Dark respiration

The colony dark respiration represents the combined algal and animal respiration and was 0.64 $\mu lO_2.mg^{-1}$ dry tissue.h^{-1} at the WFR site and 0.45 $\mu lO_2.mg^{-1}$ dry tissue.h^{-1} at the CP site (Table 7). Assuming that the night-time respiration rate is the same as the daylight respiration rate, the 24 hour colony respiratory demand for a nubbin with 300 mg of dry tissue is therefore 0.64 x 24 x 0.3 = 4.61 ml oxygen (WFR site) and 0.45 x 24 x 0.3 = 3.25 ml oxygen (CP site), equivalent to 90.50 J and 63.86 J respectively (at 1 mlO_2 = 19.63 J). The dark respiration of isolated zooxanthellae was 1.84 $\mu lO_2.x10^6$zoox.$^{-1}.h^{-1}$ (WFR site) and 1.82 $\mu lO_2.x10^6$zoox.h^{-1} (CP site) (Table 7), equivalent to a zooxanthellae respiratory energy demand of 40.36 J.$24n^{-1}$ and 48.80 J.$24h^{-1}$ respectively in colonies with 300 mg of dry tissue and the predetermined zooxanthellae population at each site (from Table 4). By subtraction, the respiratory energy consumption due to animal tissue alone is 50.14 J (WFR site) and 15.06 J (CP site).

4.8.2 Photosynthesis

The energy budget is initially calculated on an 'ideal' clear sunny day, such as 16 June 1985 which had an integrated daily PAR of 56.3 $E.m^{-2}.d^{-1}$ over a 14 hour daylight period (Figure 5). The mean

surface PAR transmissions to 10 m depth at each site recorded between May/July 1985 (Table 1; WFR site, 26.2%; CP site, 20.4%) are used to predict the *in situ* light intensities. The daily integrated net photosynthetic oxygen productions were 6.41 mlO_2 (WFR site) and 9.00 mlO_2 (CP site) (calculated as described in Chapter 3.8 for a nubbin with 300 mg of dry tissue). The integrated gross photosynthetic oxygen production (= integrated net photosynthesis + integrated dark respiration over 14 hours) are therefore 6.41 + 2.69 = 9.10 $mlO_2.d^{-1}$ = 190.62 J (WFR site) and 9.00 + 1.90 = 10.90 $mlO_2.d^{-1}$ = 228.32 J (CP site).

4.8.3 Growth

Using the mean growth rates observed over the whole of the observation periods at both sites (2.8 mg dry tissue.g^{-1} dry tissue.d^{-1} (WFR site) and 2.3 mg dry tissue.g^{-1} dry tissue.d^{-1} (CP site); Table 8), a nubbin with 300 mg of dry tissue would add 0.84 mg (WFR site) and 0.69 mg (CP site) of coral dry tissue each day. Using the values in Table 4 the growth rates have a predicted energy equivalent of 0.84 x 16.18 = 13.59 $J.d^{-1}$ and 0.69 x 14.40 =9.94 $J.d^{-1}$ respectively. With a constant zooxanthellae number to coral-tissue biomass ratio, tissue growth adds 1.30 x 10^5 zoox.d^{-1} at both sites (Table 4; WFR site, 15.52 x10^7 zoox.g^{-1}dry tissue; CP site; 18.97 x 10^7 zoox.g^{-1} dry tissue) which are equivalent to 1.52 $J.d^{-1}$ (at the WFR site; 11.69 J.x10^6zoox.$^{-1}$; Table 4) and 1.01 $J.d^{-1}$ (at the CP site, 7.76Jx10^6 zoox^{-1}; Table 4). The energy costs of animal tissue growth alone are therefore 13.59 - 1.52 = 12.07 $J.d^{-1}$ (WFR site) and 9.94 - 1.01 = 8.93 $J.d^{-1}$ (CP site).

4.8.4 Heterotrophy

Zooplankters were found on or in a few polyps from a large sample size at the WFR site. Porites porites therefore has the ability to capture zooplankton, but no evidence was found for habitual zooplankton ingestion. Until further data are available this input will be taken as zero.

4.8.5 'Losses' from zooxanthellae, including translocation

No data are available on in situ zooxanthellae culling which is therefore ignored in the present study. Photosynthetically fixed energy in excess of that required for zooxanthellae growth or respiration will be assumed to be translocated to the animal tissue. This amounts to 148.74 J (WFR site) and 178.51 J (CP site).

4.8.6 Reproductive expenditure

A 300 mg (dry tissue) nubbin has 403 polyps at the WFR site (18.59 mg dry tissue = 1 cm^2 = 25 polyps) and 437 polyps at the CP site (15.51 mg dry tissue = $1cm^2$ = 22.6 polyps) (both from Table 4). In any one week 10.7% of the polyps on a nubbin at the WFR site will each contain 2 mature planulae (total of 86 planulae) equivalent to 86 x 0.27 = 23.22 J (planula energy content = 0.27 $J.planula^{-1}$ from Chapter 4.6), whilst at the CP site 13.1% of the polyps on a nubbin will each contain 1.7 mature planulae (total 97 planulae) equivalent to 97 x 0.27 = 26.19 J.

Planula development time and periodicity of planula release were not accurately measured. Data on the proportion of fecund polyps containing mature planulae suggest that initiation to release of

planulae may take one month (Figure 13). If the mature planulae present in a nubbin each week represent one months (30 days) reproductive effort, the daily reproductive expenditure is 0.77 J (WFR site) and 0.87 J (CP site).

4.8.7 Losses from the whole colony: DOM, enzymes, nematocysts, cell debris etc.

Continual losses of energy as mucus were not detected under 'unstressed' conditions either *in situ* or in the laboratory for nubbins from the WFR site, even though losses of 85.75 J (WFR site) and 153.65 J (CP site) are predicted by subtraction. These surpluses of energy remain unaccounted for with the present assumptions.

The complete energy budgets are shown in Figure 14.

WEST FORE REEF SITE

ZOOXANTHELLAE

PHOTOSYNTHESIS	= RESPIRATION +	GROWTH +	LOSSES
190.62J	40.36J	1.52J	148.74J
100%	21.2%	0.8%	78.0%

ANIMAL TISSUE

PHOTOSYNTHETICALLY FIXED EXCESS ENERGY	= RESPIRATION +	GROWTH +	REPRODUCTION +	LOSSES
148.74J	50.14J	12.07J	0.77J	85.75J
	26.3%	6.3%	0.4%	45.0%

COLUMBUS PARK SITE

ZOOXANTHELLAE

PHOTOSYNTHESIS	= RESPIRATION +	GROWTH +	LOSSES
228.32J	48.80J	1.01J	178.51J
100%	21.4%	0.4%	78.2%

ANIMAL TISSUE

PHOTOSYNTHETICALLY FIXED EXCESS ENERGY	= RESPIRATION +	GROWTH +	REPRODUCTION +	LOSSES
178.51J	15.06J	8.93J	0.87J	153.65
	6.6%	3.9%	0.4%	67.3%

Figure 14. Porites porites from 10 m depth at the West Fore Reef and the Columbus Park site: partitioning of the 24 hour energy budget into zooxanthellae and animal components. The budgets are calculated for specimens with 300 mg of dry tissue for an 'ideal' sunny day with the mean summer light transmission at each site. Absolute joule values and percentage of the gross photosynthetic input are shown.

4.9 DISCUSSION

4.9.1 Specimen characteristics

The empirical skeletal densities for Porites porites in the present study represent the combined density of $CaCO_3$ and the skeletal organic matrix, and were therefore lower than 2.93 $g.cm^{-3}$ which is the density of pure aragonite. The organic matrix was not measured in the present study, but accounts for up to 0.1% of the skeletal weight in Pocillopora damicornis (Wainwright, 1963). The lower skeletal density of P. porites at the CP compared to the WFR site site may reflect a higher percentage of organic matrix present in the skeleton.

The fixation and acid treatment of coral tissue can result in about 10% loss in the dry tissue (Davies, 1980) so that tissue specific rates in the present study may be over estimated by about 10%. Nevertheless the unit area dry tissue contents are higher than for Pocillopora eydouxi (5m depth, 2.15 $mg.cm^{-2}$; Davies, 1984), Montastrea annularis and Acropora cervicornis (10 m depth, 9.65 $mg.cm^{-2}$ and 15 m depth, 2.00 $mg.cm^{-2}$ respectively; from Davies, 1980) and Porites porites (2 - 5 m depth, 10.3 $mg.cm^{-2}$; Lewis, 1982) all recorded using the same technique as in the present study.

The higher unit area dry tissue content of Porites porites at the WFR site may reflect the greater number of $polyps.cm^{-2}$ or an increased thickness of the tissue layer compared to specimens at the CP site. A decrease in number of $polyps.cm^{-2}$ was found in shade vs light adapted Stylophora pistillata (Porter et al.,1984) and deep (50 m) vs shallow (1 m) Montastrea annularis (Porter et al., in press). The decrease in polyp content with depth for M. annularis was implied to occur

together with a decrease in unit area tissue content, although the reverse trend is suggested by the data of Davies (1980). A reduction in the number of polyps.cm^{-2} with reduced irradiance may be a common process involved in photoadaptation.

The percentage protein compositions of dry tissues of Porites porites measured in this study are lower than the 33% recorded by Patton et al. (1977) for Pocillopora capitata, but per unit area (WFR site, 4.33 mg protein.cm^{-2}; CP site, 3.78 mg protein.cm^{-2}; from Table 4) the protein contents are within the range reported for a variety of corals including Fungia scutaria, 1.0 mg protein.cm^{-2} (Johannes, 1974) and Stylophora pistillata, 12.17 mg protein.cm^{-2} (McCloskey and Muscatine, 1984). The protein content of P. porites is also lower than the mean protein content of 44.9% (of the dry tissue weight) from 37 species of marine invertebrate (from Conover, 1978). However the same group of invertebrates had a mean lipid content of 11.6% which compares to lipid contents of approximately 20% in P. porites (Chapter 6.4.4) and 35% in Pocillopora capitata (Patton et al., 1977). The high lipid content of P. porites may account for the comparatively low percentage protein content.

The percentage ash content of dry tissue from Porites porites at the CP site is similar to 13.5% reported for fed Anthopleura elegantissima (Fitt and Pardy, 1981). The significantly higher ash content of dry tissue from P. porites at the WFR site may be an artifact of a higher proportion of volatile components as there is little reason for a larger proportion of non-combustable material.

The tissue energy content of Porites porites in the present study compares favourably with 18.05 J.mg^{-1} for tissue from the coral Heliofungia sp. (Davies, 1984), and 27.20 J.mg^{-1} ash-free dry weight for 5 tropical gorgonians (Lewis and Post, 1982). The significantly higher tissue energy content of P. porites at the WFR site compared

to the CP site may represent a higher lipid content which would be consistent with a higher ash content caused by lipid volatilisation. The zooxanthellae in P. porites at the WFR site had a significantly higher energy content than those in P. porites at the CP site and both are higher than 6.43 Jx10^6zoox. recorded by Tytler (1982; in Davies, 1984) for the temperate anemone Anemonia sulcata. The high zooxanthellae energy content in P. porites at the WFR site partly accounts for the high coral tissue energy content at this site.

Corals usually photoadapt to a reduced irradiance by increasing the chlorophyll content of their zooxanthellae (Chang et al., 1983; Porter et al., 1984; Titlyanov et al., 1980) while the numbers of zooxanthellae.cm^{-2} may decrease with depth (Dustan, 1979; Porter et al., in press) or remain almost constant (Drew, 1972; Porter et al., 1984). P. porites at the CP site receives significantly less light than at the WFR site, but the zooxanthellae chlorophyll content and the zooxanthellae.cm^{-2} were not significantly different. The chlorophyll contents at both sites are more similar to values for "shade" adapted corals (Stylophora pistillata, 12.13 µg Chla.x10^6zoox^{-1}., Porter et al., 1984; Porites nigrescens, 6.7 ± 0.6 µg Chla.x10^6zoox^{-1}. Titlyanov et al., 1980) than for "light" adapted corals (S. pistillata, 2.98 µg Chla.x10^6zoox.$^{-1}$, Porter et al., 1984; P. nigrescens, 5.4 ± 0.3 µg Chla.x10^6zoox.$^{-1}$, Titlyanov et al., 1980). The zooxanthellae contents in the present study (Table 4) are similar to the ranges reported by Drew (1972), 0.90 - 2.48 x10^6zoox.cm^{-2} (11 genera of hard corals, 2 genera of soft corals) and Dustan (1979), 3.65 x 10^6 - 8.76 x 10^6zoox.cm^{-2}, (Montastrea annularis, 42 - 1 m depth respectively). However, on a per unit biomass basis (Table 4) the zooxanthellae contents are approximately 40% lower than the

equivalent figure of 28.2 x 10^7 zoox.g^{-1} dry tissue for the imperforate coral Pocillopora eydouxi (Davies, 1984). This is a direct result of the greater thickness of tissue in the porous skeleton of P. porites.

4.9.2 Components of the Energy Budgets

4.9.2.1. Respiration and photosynthesis

Free living marine phytoplankton show diel periodicity in photosynthetic characteristics (Harding et al., 1982; Sournia, 1974). Photosynthesis/irradiance responses also vary throughout the day in the anemone Aiptasia pulchella (Muller-Parker, 1984), the coral Acropora acuminata (Barnes and Crossland, 1978) and freshly isolated zooxanthellae from Acropora cervicornis (Chalker, 1977). Since these effects alter the calculated productivity depending on the time of the experiment, experiments were carried out to see whether they were significant in Porites porites.

In the present study there was no evidence of an endogenous daily variation in colony respiration rate for P. porites maintained in total darkness, and photosynthesis at a single irradiance was constant throughout the day (Chapter 4.3.1). The P/I relationships in the present study were therefore not affected by the time of measurement and accurately represent the photosynthetic ability of nubbins. However, there was some evidence that the colony respiration rate of P. porites increased after exposure to light, but this was minimised by keeping corals in darkness overnight before experimentation. The concept of an elevated daytime respiration rate will be expanded in Chapter 6.2.

Dark respiration of Porites porites at 10 m depth at both sites (0.64 $\mu lO_2.mg^{-1}$ dry tissue.h^{-1} = 11.91 $\mu lO_2.cm^{-2}.h^{-1}$, WFR site; 0.45 $\mu lO_2.mg^{-1}$ dry tissue.h^{-1} = 7.01 $\mu lO_2.cm^{-2}.h^{-1}$, CP site) are comparable to 11.38 $\mu lO_2.cm^{-2}.h^{-1}$ recorded for expanded polyps of P. lobata (7 m depth) by Johannes and Tepley (1974) and 8.76 $\mu lO_2.cm^{-2}.h^{-1}$ (0.85 $\mu lO_2.g^{-1}$ dry tissue.h^{-1}) for P. porites in Barbados (2 - 5 m depth; Lewis, 1982). They are lower than equivalent unit tissue biomass rates and somewhat higher than equivalent surface unit area rates obtained for other whole scleractinians: Pocillopora eydouxi (5 m depth) 3.8 $\mu lO_2.mg^{-1}$ dry tissue.h^{-1} = 8.1 $\mu lO_2.cm^{-2}.h^{-1}$ (Davies, 1984) and Stylophora pistillata (2 m depth) 9.74 $\mu lO_2.cm^{-2}.h^{-1}$ (Porter et al. 1984). On the basis of surface area, the respiration rates are comparable to those of other corals. On a unit tissue-biomass basis, however, they are lower than found for other corals. This could be a result of Porites spp. having a mass of deep tissue which may be metabolically rather inactive. Similar observations have been reported for Acropora species (Davies, 1980).

The respiration of isolated zooxanthellae from P. porites at 10 m depth at both sites (Table 7) are similar to 2.61 $\mu lO_2.x10^6 zoox.^{-1}h^{-1}$ for zooxanthellae from Montastrea cavernosa (Davies, 1984) and ca. 3.0 $\mu lO_2.x10^6 zoox.^{-1}h^{-1}$ for zooxanthellae from M. annularis (10 m depth, Dustan, 1982). Zooxanthellae respiration in P. porites accounts for 45% (WFR site) and 76% (CP site) of the colony respiration rate which are considerably higher than the value of 19% in Pocillopora eydouxi (Davies, 1984), or 3% in light adapted Stylophora pistillata at 2 m depth (Muscatine et al., 1984). Muscatine and co-researchers have assumed that zooxanthellae respiration is proportional to the zooxanthellae protein: whole colony protein ratio ($1 - \beta$; where β is the ratio of animal protein:colony protein) (Muscatine and Porter, 1977) and have found support for their assumption in the 7 to 8 fold

discrepancy between direct measurements of zooxanthellae respiration and the prediction using $1 - \beta$ for Stylophora pistillata (McCloskey and Muscatine, 1984). The ratio $1 - \beta$ in the present study is 0.06 at both sites which compares with 0.09 for Pocillopora damicornis (Muscatine et al., 1981). The prediction of zooxanthellae respiration rates in P. porites using $1 - \beta$ are 0.25 $\mu lO_2.x10^6 zoox.^{-1}h^{-1}$ (WFR site) and 0.14 $\mu lO_2.x10^6 zoox.^{-1}h^{-1}$ (CP site), which are less than 14% of the measured values.

The reported values for respiration rates of isolated zooxanthellae have been criticised because of contamination with animal debris and the effects of mechanical disturbance (Downton et al., 1976; McCloskey and Muscatine, 1984), but the assumptions in the B ratio method have not been verified. However, zooxanthellae isolated on a Percoll gradient in the present study were very clean and it seems beyond coincidence that the respiration rate of aposymbiotic P. porites plus the respiration rate of the zooxanthellae in an equivalent sized symbiotic colony closely approximates the respiration of symbiotic colonies (7.2 $\mu lO_2.cm^{-2}.h^{-1}$ (aposymbiont) + 5.8 $\mu lO_2.cm^{-2}.h^{-1}$ (using the respiration rate of zooxanthellae from the WFR site; Table 7) = 13.0 $\mu lO_2.cm^{-2}.h^{-1}$ cf. 11.91 $\mu lO_2.cm^{-2}.h^{-1}$ for symbiotic colonies at the WFR site; Table 7). Although aposymbionts do not have translocates from the zooxanthellae, which are normally used as respiratory substrates, it seems likely that the measured respiration rates of zooxanthellae in the present study are a closer approximation to the in situ respiration rates than values predicted by the protein biomass ratio method.

A depth-dependent reduction in coral respiration rate was shown by Davies (1977, 1980) and McCloskey and Muscatine (1984), and similar changes occurred with shading at a constant depth

(Porter et al., 1984). A lower respiration rate can counteract a reduced gross photosynthetic input at a lower irradiance to maintain the proportional contribution of autotrophy to the nutritional requirements of a coral colony. A lower unit biomass respiration of P. porites at the CP site compared to the WFR site becomes significantly lower on a unit area basis (Table 7) and may represent a similar light dependent response. Whilst unit area respiration rates differ by 41% between sites, unit biomass respiration rates differ by only 30%. This suggests that a higher unit area tissue content may combine with a greater proportion of deeper, metabolically inactive tissue in P. porites at the WFR site to reduce the unit biomass respiration rate to a greater extent than at the CP site.

As the zooxanthellae content of Porites porites and zooxanthellae respiration rate were not significantly different between sites (Table 4, 7), the reduction in colony respiration rate at the CP site must therefore be a function of the animal tissue alone. A similar effect was suggested for Montastrea annularis which displayed a depth specific reduction in colony respiration rate (Davies, 1980) whilst the zooxanthellae respiration rate remained almost constant between 0 and 50 m depth (Dustan, 1982). The zooxanthellae from Stylophora pistillata, however, showed some evidence of a reduction in respiration rate between 3 and 35 m depth (McCloskey and Muscatine, 1984).

The unit biomass zooxanthellae content is higher (not significantly higher, Table 4) in P. porites at the CP site whilst unit area zooxanthellae contents are almost identical (Table 4). The reduction in host respiration may therefore be the result of a decrease in the amount of host tissue present. A reduction in unit area polyp content could then be construed as a photoadaptive process to reduce the amount of respiring animal tissue.

The hyperbolic tangent function was a good fit for the photosynthesis/irradiance data obtained in the present study as shown by the high correlation coefficients (Appendix I, Table 1 & 2). The main advantage of using this function is that it allows standardisation and comparison between studies and provides a mathematical relationship for predicting photosynthesis from a known irradiance. However, when the rate of photosynthesis does not reach a plateau at the highest irradiances available in the experimental conditions, the best-fit hyperbolic tangent for these data should be interpreted with care. Although the hyperbolic tangent models the actual data it can also be used to extrapolate beyond the data to predict P_{max} values which can be misleading. If the in situ irradiance throughout each day is similar to the irradiance range reproduced in the laboratory as in the present study (see Chapter 2.3 and 3.5), photosynthetic rates for the full in situ irradiance range can be estimated from the hyperbolic tangent functions without extrapolation beyond the range of the data. Under these conditions the absence of a measured P_{max} in the laboratory has little effect on the calculated in situ productivity.

The photosynthesis/irradiance responses of 5 nubbins at the WFR site and 4 at the CP site failed to show a measured plateau in photosynthesis, and their P_{max} and I_k values were extrapolated using the best-fit curve beyond the range of the data. These were higher than the equivalent values for nubbins which reached a measured P_{max}, and increased the mean and variance in P_{max}, I_k and alpha for nubbins at each site. At the WFR site the mean P_{max} would not be attainable on an 'ideal' sunny day at 10 m depth. The mean P_{max} for all the nubbins at the CP site was attained on an 'ideal' sunny day at 10 m depth.

Porter (1980) also failed to find a maximum productivity for any of the coral species he studied *in situ* including *Acropora cervicornis* from 10 m depth. He suggested that the horizontal and undersurfaces prevented the whole colony from reaching saturation. Crossland and Barnes (1977) suggested that zooxanthellae are mutually shaded in the tissues of *A. acuminata*, whilst Dustan (1982) found that zooxanthellae of *Montastrea annularis* to be light-limited in their natural habitat and implicated self shading of the zooxanthellae as the cause.

Sufficient zooxanthellae are present in *Porites porites* to form more than 3 layers of closely packed zooxanthellae (at 11 µm diameter), but instead they are dispersed through a ca. 5 mm thick tissue layer within a porous skeleton. Algal cells are shaded by each other, skeletal elements and animal tissue. Shading of deep zooxanthellae may have prevented some nubbins from reaching a P_{max} and the effect might be enhanced at the WFR site by a greater unit area tissue biomass. Vertical surfaces receive only about 5% to 38% of the irradiance falling on a horizontal surface at 9 m depth on the fore reef at Discovery Bay (Brakel, 1979) and this reduction in light was approximated in the experimental incubation enclosure (Chapter 3.5). With an increasing irradiance from a light source vertically above a nubbin, zooxanthellae on the horizontal surface would reach their P_{max} before zooxanthellae on the vertical surfaces, and a similar effect would occur with shaded zooxanthellae within the coral tissue, unless within-colony photoadaptation occurs. The observed P/I response for each nubbin was therefore the sum of a family of P/I responses for zooxanthellae at different locations on the nubbin.

The values of P_{max}^{gross}, I_k and alpha for *Porites porites* at both sites (Table 7) compare with a P_{max}^{gross} of 17.2 $\mu l O_2 . mg^{-1}$ dry tissue.h^{-1} = 36.1 $\mu l O_2 . cm^{-2} . h^{-1}$ for *Pocillopora eydouxi* at 5 m

depth (Davies, 1984) and a P^{gross}_{max} of 32.7 $\mu gO_2.cm^{-2}.h^{-1}$ an I_k of 273 $\mu E.m^{-2}.s^{-1}$ and an alpha of 0.12 $\mu gO_2.cm^{-2}.h^{-1}.uE^{-1}.m^2.s$ for "light adapted" Stylophora pistillata at 2 m depth (Porter et al., 1984). P^{gross}_{max} in P. porites at both sites were lower on a unit dry tissue basis but higher on a surface area basis than equivalent values for other coral species, which may be caused by a mass of deep metabolically inactive tissue as previously suggested to explain the low tissue specific respiration rates.

Photoadaptation of corals in response to reduced irradiance usually results in reduction in both P^{gross}_{max} and I_k and an increase in alpha (Chalker et al., 1983; Porter et al., 1984; Wethey and Porter, 1976). Porites porites at the CP site shows similar adaptations, although photoadaptation is not due to changes in zooxanthellae pigment content or zooxanthellae numbers. Changes in pigment distribution within algal cells and the light absorbing qualities of chlorophyll, or differences in the quantum efficiency can also be important in photoadaptation (Dubinsky et al., 1984) and may be important in P. porites at the CP site. As zooxanthellae pigment content was determined on a mixture of cells from various depths within the tissue layer, and different locations on the same nubbin in the present study, within-colony photoadaptation cannot be ruled out. The similarity in pigment content of zooxanthellae from P. porites with other shade-adapted corals suggests that the mean colony pigment content may be biased by a high pigment content of shade adapted zooxanthellae located on the vertical surfaces or deep within the tissue.

Any reduction in zooxanthellae shading by the redistribution of the algae to superficial tissues and polyps could effectively increase the colony alpha and decrease I_k without having to alter the

photosynthetic characteristics of the zooxanthellae. This may be achieved in P. porites at the CP site by decreasing the unit biomass and thickness of the tissue layer.

4.9.2.2 Growth

In the present study, growth was measured as a skeletal increment and used to predict the tissue growth. Emphasis was placed on the tissue growth as the organic energy content of the skeleton is likely to be small. The mean colony growth rates (Table 8) suggest that nubbins with 300 mg of dry tissue would double their tissue biomass in approximately 8 months at the WFR site and 10 months at the CP site. There are few comparable data in the literature, but Pocillopora eydouxi at 5 m depth had a tissue-specific tissue growth rate of 1.90 $mg.g^{-1}$ dry $tissue.day^{-1}$ and a tissue-specific skeletogenesis of 404 $mg.g^{-1}.day^{-1}$ (from Davies, 1984). These suggest that Porites porites at both sites in the present study has a high tissue growth rate supported by a low rate of skeletogenesis. The mean growth rates can be converted to 36.6 $\mu gCa.mg^{-1}\text{-}N.h^{-1}$ (WFR site) and 20.2 $\mu gCa.mg^{-1}\text{-}N.h^{-1}$ (CP site) using the specimen characteristics in Table 4 and the nitrogen content from (mg protein)/6.25. These values compare favourably with those reported by Goreau and Goreau (1959) for P. porites (18.6 to 29.3 $\mu gCa.mg^{-1}\text{-}N.h^{-1}$) and a variety of other corals (5.2 to 73.7 $\mu gCa.mg^{-1}\text{-}N.h^{-1}$), all measured as ^{45}Ca uptake at approximately 1.5 m depth in the sunshine.

The mean growth rates for Porites porites in the present study apply to nubbins within the size range studied for the duration of the observations. At the WFR site tissue-specific growth rates were similar irrespective of nubbin size but at the CP site tissue-specific growth rates decreased with increasing tissue biomass (Chapter 4.4.2).

These results are interpreted as suggesting that growth is slower on the sides of nubbins at the CP site than at the tip, so that large nubbins contain proportionately more slow-growing lateral tissue which decreases the overall tissue-specific growth rates. This favours linear extension over radial increase which could keep branch tips above the sediments and would cause the more spindly growth morphology of P. porites at the CP site. Branch extension and radial increase probably proceeded at similar rates in P. porites at the WFR site where there was less need for rapid linear extension above the substrate. Similar within-branch growth gradients have been found in Acropora cervicornis and Porites furcata (Goreau and Goreau, 1959) and Stylophora pistillata (Rinkevich and Loya, 1984), although between environment comparisons have not been made.

Although mass accretion of $CaCO_3$ by Porites porites is lower at the CP site than at the WFR site, specimens at both sites could increase in physical size at similar rates if the skeletal porosity was lower at the CP site. Schneider and Smith (1982) showed that the bulk density of Porites spp. varied between 1.2 $g.cm^{-3}$ and 1.6 $g.cm^{-3}$ in the Pacific, whilst Brown et al. (1985) recorded a porosity of between 0.8% and 84.0% for Acropora aspera growing in exposed or sheltered conditions (respectively) in Indonesia. Unit area dry tissue growth rates of P. porites were reduced by 31% at the CP site compared to the WFR site whilst unit area skeletogenesis was reduced by 52% (Table 8). As tissue growth and skeletal growth must occur together, it is possible that the bulk skeletal density was lower at the CP site so that the increase in skeletal volume and therefore tissue biomass, were not decreased by the same proportion as the mass accretion of $CaCO_3$.

Small corals increase their height, diameter or area proportionately faster than big corals of the same species (Connell, 1973; Stephenson and Stephenson, 1933). Similar data suggest that coral growth rates are not determinate but proceed at a reduced rate after an initial rapid growth in young colonies (Connell, 1973). However, only Goreau and Goreau (1960) have shown that unit area calcification can be higher in small vs large colonies. Kinzie and Sarmiento (1986) recently showed that the linear growth rate of Pocillopora damicornis was independent of colony size. They corroborated their results with a re-analysis of the data of Stephenson and Stephenson (1933) for the same species which showed that the increment in colony diameter was independent of the initial diameter.

The growth of Porites porites in the present study, however, cannot be entirely explained in terms of determinate or indeterminate effects. Although tissue-specific growth rates were not size dependent at the WFR site they decreased with size at the CP site. This can be explained by a preferential linear as opposed to a radial growth of branches at this site. Tissue-specific growth rates decreased during the study period at both sites which suggests that nubbins may behave as fast growing "young" colonies which grow more slowly as they get older as suggested by Connell (1973). This is not necessarily contrary to the findings of Kinzie and Sarmiento (1986) if they studied "old" colonies of Pocillopora damicornis, where growth had slowed to a constant rate independent of colony size. However, the possibility that the higher initial growth rates for P. porites in the present study were an artifact of the 'nubbins methodology' cannot be ruled out. The current information on coral growth rates remains equivocal, but the significance and interrelationship of size- and time-dependent effects clearly requires further investigation.

Algal specific growth rates (μ) in Porites porites of 0.0028 (WFR site) and 0.0023 (CP site) were required to keep the zooxanthellae number: coral tissue biomass constant (Chapter 4.4.1). Although Steele (1977) described zooxanthellae-containing pellets being extruded from some tropical anemones and also Porites spp., such pellets were not observed during the present study for P. porites. As the algal-specific growth rates in the present study are lower than those estimated using the in situ algal mitotic index for light adapted Stylophora pistillata (μ = 0.013; Muscatine et al., 1984) and the anemone Aptasia pulchella (μ = 0.007; Muller-Parker, 1985), it is possible that the zooxanthellae growth was underestimated and that the excess were being lost from the colony.

4.9.2.3 Reproduction

Reproduction in Porites porites was almost identical at both sites. Mature planulae were found every week during the 5 month observation period and free swimming planulae were seen on several different occasions in the aquarium. The possibility that P. porites has dioecious colonies, like P. murrayensis (Kojis and Quinn, 1982), would account for the absence of planulae in some colonies sampled each week, but should not affect the data obtained as colonies were sampled at random. Continuous planulation over 5 or more months has been recorded for P. lutea (Marshall and Stephenson, 1933) and P. murrayensis (Kojis and Quinn, 1982), whilst Goreau et al. (1981) documented a November planulation in a single colony of P. porites in Jamaican waters. The mature planulae found in the polyps of P. porites in the present study were probably released on a monthly cycle (Figure 13).

Embryos develop encompassed by mesenterial tissue in Acropora cuneata and some of the eggs may be reabsorbed (Kojis, 1986). Immature planulae were enclosed in mesenterial tissue in Porites porites and it is possible that not all of the immature planulae developed to a mature stage. The reproductive expenditure was therefore measured as the number of mature planulae found within polyps and assumed to be released. The energy content of planulae from P. porites at the WFR site is lower than the range 1.5 to 4.1 J.planula^{-1} reported from Pocillopora damicornis by Richmond (1982). He suggested that the threefold range in planula energy content was important in determining how long the larvae can remain planktonic. The low energy content of planulae from P. porites suggests that these larvae only have a brief planktonic phase.

The best approximation for the time from initiation to release of planulae from P. porites is 1 month taken from the peaks of the proportion of fecund polyps containing mature planulae (Figure 13). This is similar to approximately 1.5 months suggested as the minimal time for planula development in P. murrayensis (Kojis and Quinn, 1982) but less than the 4.5 months in Acropora cuneata (Kojis, 1986).

4.9.2.4 Heterotrophy

Porites porites at both sites obtains insignificant heterotrophic nutrition from the capture of zooplankton as revealed by the almost total absence of zooplankton in the coelenteron. Specimens collected at 19.55 hrs did not contain zooplankters even though reef zooplankton are most abundant at this time (Ohlhorst, 1982; Porter, 1974) and evidence of zooplankton capture would remain within the polyps for at least 3 hours (Yonge and Nicholls, 1930). The present observations agree with the "capturing ineffectiveness" of P. lobata observed in situ by Johannes and Tepley (1974), although Lewis and Price (1975)

and Hubbard (1973) had described a typical feeding response by P. porites in the laboratory. The ability to capture zooplankton in the laboratory clearly does not indicate the realised in situ zooplankton capturing ability.

4.9.2.5 Mucus release

The absence of a continuous energy loss as mucus from P. porites at the WFR site was surprising as Lewis and Price (1975, 1976) had described P. porites using mucus in feeding and sediment shedding. Coles and Strathmann (1973) also observed mucus "streaming" from the surface of some Pacific Poritids. It was also contrary to the 40% loss of photosynthetically fixed carbon as mucus from Acropora acuminata (Crossland et al., 1980) and the 50% loss of net carbon fixed in shade adapted Stylophora pistillata (Muscatine et al., 1984). Mucus release from Porites porites at the CP site was not measured but may be higher than at the WFR site since the former site has a higher sedimentation rate (Chapter 2.5) and mucus is required in the sediment rejection mechanism (Hubbard and Pocock, 1972). Stressed corals release mucus containing macromolecular mucus-polysaccharides, glycoproteins, muco-lipids and lipoproteins (Crossland et al., 1980; Daumas and Thomassin, 1977; Ducklow and Mitchell, 1979b; Krupp, 1982) which may further polymerise in seawater (Ducklow and Mitchell, 1979b).

All macromolecular mucus components and cell debris were retained by the Teflon membrane in the in situ incubation experiments in the present study, but no significant losses of energy from P. porites were found. This may reflect a methodological difference to many of the previous studies in which corals were stressed to enhance mucus

release. This also results in quantitative and qualitative differences in the mucus (Benson and Muscatine, 1974), including contamination with cellular debris (Krupp, 1982). In the present study, Porites porites stressed in the laboratory released significant amounts of energy as a mixture of 'mucus', zooxanthellae and cell debris. Similar losses may be incurred under severe stress in situ. Although unstressed P. porites at the WFR site did not release significant amounts of soluble or particulate macromolecular mucus, taut mucus coats were periodically formed over the whole colony surface at both sites and represented an alternative route for the loss of mucus energy. Mucus tunics are fully investigated in Chapter 6.3.

Muscatine et al. (1984) measured a 50% loss of net carbon fixed by shade adapted Stylophora pistillata in whole subsamples (no dialysis, filtration or concentration) of the incubation water. Since S. pistillata did "not secrete copious amounts of mucus" they concluded that the material released was "largely dissolved organic carbon". Similar losses were observed for Montastrea annularis and Siderastrea siderea by Cooksey and Cooksey (1972) who concluded that the carbon was lost from a metabolic pool close to the respiratory pathway.

At least 21 species of marine invertebrates from 7 phyla release free amino acids (Ferguson, 1982) including the coral Pocillopora elegans (D'Elia and Webb, 1977), and a variety of cnidarians have also been shown to absorb dissolved organic material (DOM) (Schlichter, 1982; Stephens, 1962). Schlichter (1980) has interpreted the presence of numerous epidermal microvilli together with an active uptake of DOM in cnidarians to suggest that they are well adapted cytologically and physiologically for the influx of DOM. Since these adaptations can probably also be used for the efflux of DOM it is possible that corals can lose carbon and energy as DOM (including low molecular weight

compounds such as free amino acids) instead of as mucus. However, most analyses of coral mucus have included procedures to remove or exclude low molecular weight compounds and these data do not therefore indicate the total or perhaps the major loss of organic compounds from corals. Low molecular weight compounds could also explain the losses of photosynthetically fixed carbon measured by Muscatine et al. (1984) and Cooksey and Cooksey (1972). However, the flux of low molecular weight compounds which pass through the Teflon membrane (10 nm pore size) or the dialysis tube (2000 M.W. cut off) used in the present study remains unquantified.

4.9.3 The energy budget

The energy budgets presented in this chapter are those which would be expected for Porites porites on an 'ideal' day with the mean summer transmission of surface PAR to 10 m depth at each site. The objectives were similar to those of Davies (1984), Falkowski et al. (1984) and Muscatine et al. (1984), but in the present study a greater number of measurements over a longer time scale were made.

The two sites had an identical temperature regime but the CP site received significantly less light, had a significantly higher sedimentation rate with large amounts of unconsolidated sediments on the substrate, a high particulate load in the water column and perhaps a higher nitrate concentration (Chapter 2). Although the WFR site received more light and had a mainly solid substrate, high sedimentation occurred after rough weather (Table 2). Temperature, light, sedimentation and mineral nutrients have been shown to influence coral growth and physiology (references in Chapter 2), and yet the energy budgets at the two sites are broadly similar (Figure 14), suggesting that considerable adaptation has occurred.

As the energy input to Porites porites at both sites as zooplankton capture was found to be insignificant it will be assumed that the energy content of the photosynthetically fixed carbon is the major source of the energy input into the colonies, and this will be available for the processes which form the right-hand side of the equations over a 24 hour period (Figure 14). No data were collected on the availability or use of DOM, detritus or bacteria and these potential sources will be ignored.

Although Porites porites at the CP site has the same number of zooxanthellae.cm^{-2} with the same chlorophyll a and c_2 content as P. porites at the WFR site, the specimens at the CP site have a higher gross productivity under a significantly lower PAR regime. Photadaptation has significantly increased alpha so that P_{max} is reached at a lower irradiance than at the WFR site (see Figure 11).

The major use of the energy input (to Porites porites) is for the colony respiration which accounted for 47.5% (WFR site) and 28.0% (CP site). These compare with values of 51.1% for Pocillopora eydouxi from 5 m depth (Davies, 1984) and 77.9% for light adapted Stylophora pistillata from 2 m depth (Muscatine et al., 1984). Zooxanthellae respiration accounts for 21.2% (WFR site) and 21.4% (CP site) of the gross photosynthetic input for P. porites in the present study, which are considerably higher than the value of 9.8% in Pocillopora eydouxi (Davies, 1984) or 2.5% in light adapted Stylophora pistillata (Muscatine et al., 1984). Although respiration measurements on isolated zooxanthellae have been criticised, the present values for P. porites are likely to be closer to the in situ respiration rates as they are consistent with the value derived by subtracting the respiration rate of aposymbiotic colonies from that of symbionts. As zooxanthellae respiration rate and zooxanthellae content are the same

in P. porites at both sites whilst specimens have significantly less tissue.cm^{-2} at the CP site, the respiration rate of the animal tissue alone is reduced from 26.3% of the gross photosynthetic input at the WFR site to 6.6% at the CP site. A reduction in the host tissue-specific respiration rate may also enhance the reduction in respiratory energy consumption by the host tissue at the CP site.

The energy diverted into tissue growth of Porites porites accounted for only 7.1% (WFR site) and 4.3% (CP site) of the gross photosynthetic input, representing an absolute reduction in energy expenditure on growth at the CP site. This may be analogous to the unverified depth dependent reduction in energy required for tissue growth in Caribbean corals suggested by Davies (1980), and further supported by the reduced host respiration at the CP site.

As sediment shedding is an energy-requiring process (Dallmeyer et al., 1982; Hubbard and Pocock, 1972), the respiration rates measured in the present study do not necessarily represent the in situ respiration rates under the chronic sedimentation regime at the CP site. It is possible that more energy is expended in situ than is suggested by the respiratory energy consumption in the energy budgets in Figure 14.

The algal specific growth rates (μ) for P. porites in the present study suggest that the energy diverted to zooxanthellae growth is almost negligible. If μ at each site is taken as 0.013 as in light adapted Stylophora pistillata (Muscatine et al., 1984), zooxanthellae would be produced in excess of the numbers required to maintain a constant zooxanthellae: coral biomass ratio. If surplus zooxanthellae were culled and expelled from the colony this would represent a loss of only 5.56 J (WFR site) and 4.73 J (CP site) (calculated from figures in Tables 4, 7, and 8).

An important effect of the high zooxanthellae respiration rate calculated for Porites porites in the present study is the reduction in the gross photosynthetically fixed energy available for translocation to 78% at both sites. This compares to 90% in Pocillopora eydouxi (Davies, 1984) and 97% in light adapted Stylophora pistillata (Muscatine et al., 1984). The high translocation predicted for S. pistillata is a result of a low zooxanthellae respiration rate determined by the protein biomass ratio (B) method.

The production of planulae by Porites porites, which has not been measured in previous work, utilised only 0.4% of the gross photosynthetically fixed energy at each site. Although planulae were found throughout the 5 months of observations, it is possible that this period represented the breeding season. Although some corals reproduce all year (Agaricia agaricites f. purpurea, van Moorsel, 1982; Pocillopora damicornis, Stimson, 1978) most reproduce seasonally (see Fadlallah, 1983 for a review). The energy allocated to planula production in the present study has been calculated assuming that the reproductive activity measured between November 1984 and March 1985 is representative of the whole year, and may potentially overestimate the reproductive expenditure.

Of the total gross photosynthetically fixed energy going into Porites porites colonies on an 'ideal' sunny day at both the WFR and CP sites, 45.0% and 67.3% respectively remains unaccounted for with the present assumptions, and P. porites has the potential for total autotrophy in terms of its energy demands under these conditions. Davies (1984) found an energy surplus of 48% in Pocillopora eydouxi at 5 m depth which lead him to suggest that corals are nutritionally analogous to aphids and may have to produce and lose excess carbon in order to obtain limiting mineral nutrients. A similar strategy was described for the herbivorous sea urchin Strongylocentrotus

droebachiensis by Miller and Mann (1973) and may be a common solution to the problem of obtaining protein and mineral nutrients from a diet high in carbon content. Shade adapted Stylophora pistillata lost 54.4% of its gross photosynthetically fixed carbon but only 6.5% in the light adapted individuals (Muscatine et al., 1984). The shade vs light differences may be analogous to the WFR site vs CP site differences in surplus energy from P. porites in the present study, but Muscatine et al. were unable to explain why the shade adapted corals should lose more carbon. The energy surplus was not lost from P. porites as soluble macromolecular mucus in the present study, which contradicts the pathway for surplus energy suggested by Davies (1984) and Edmunds and Davies (1986). However the excess carbon may be lost as low molecular weight compounds. This argument will be developed further in Chapter 7 after the annual energy budgets have been calculated (Chapter 5) and the role of lipid storage, mucus tunics and daytime respiration considered (Chapter 6).

CHAPTER 5: ANNUAL ENERGY BUDGETS

5.1 Introduction

The energy budgets constructed in Chapter 4 show that Porites porites growing at two different sites can be fully autotrophic on an 'ideal' sunny day with the mean transmission of surface PAR to 10 m depth. However daily integrated suface PAR ranges from 4 $E.m^{-2}.d^{-1}$ (Porter, 1985) to 56.3 $E.m^{-2}.d^{-1}$ (Figure 5) and transmission of surface PAR to 10 m depth ranges from 18.3% to 39.2% at the WFR site and from 10.3% to 41.3% at the CP site (Table 1). Both 'ideal' and unfavourable environmental conditions must be endured by sedentary corals which have no choice in their environments after the initial settlement of the planula larva. Annual energy budgets are therefore of greater interest to coral reef biologists studying the nutritional strategies of corals and attempting to explain their success in the tropical marine environment.

Although numerous researchers have estimated annual reef productivities (reviewed by Lewis, 1977) none have been supported by long term measurements of either environmental variables or the energy demands of the corals themselves. Surface PAR and attenuation through the water column have the greatest direct affect on productivity, but annual recordings of daily PAR for a tropical reef location have only just become available (Porter, 1985), and the recordings of percentage transmission of surface PAR to 10 m depth in the present study are the first of their kind. These data will now be used to extend the daily energy budgets for Porites porites over a whole year.

5.2 Methods

In order to make a prediction of the daily *in situ* productivity of *Porites porites*, the annual record of daily surface light regimes at Discovery Bay for 1983-84 (Porter, 1985) was combined with data on the transmission of photosynthetically active radiation (PAR) to 10 m depth at both sites (Chapter 2, Table 1) to predict the *in situ* daily PAR regimes. These were then used together with the 'representative' photosynthesis/ irradiance response of *P. porites* at both sites (Chapter 4, Figure 11) to calculate daily productivities.

The rate of photosynthesis is determined by the instantaneous PAR, and the maximum rate (P_{max}) is often achieved below the maximum ambient PAR. Although PAR greater than the value required to attain P_{max} contributes to the daily integrated PAR (IntPAR), photosynthesis does not increase beyond P_{max}. Daily integrated photosynthesis can therefore only be accurately calculated from a continuous recording of PAR throughout the day.

Unfortunately, the only annual record of daily surface PAR at Discovery Bay is in the form of daily IntPAR values (Porter, 1985). Before the *in situ* productivity of *P. porites* could be calculated, it was therefore necessary to predict the daily PAR curve corresponding to each surface daily IntPAR value.

The daily surface IntPAR values from Porter (1985) were assumed to have occurred on 12 hour days with a sine wave distribution of the daily PAR, so that the area beneath the sine curve was equivalent to the IntPAR. The equation of this curve was taken as:

$$I = I_{max} \times \mathrm{Sin}[(3.142xT)/D] \qquad 1.$$

where I = irradiance ($E.m^{-2}.h^{-1}$) at time T (hours after sunrise), D = daylength (taken as 12 hours), I_{max} = the maximum irradiance ($E.m^{-2}.h^{-1}$) and (3.142xT)/D changes the time of day into radians (see Appendix II).

The integral of equation 1 gives the area beneath the sine curve and by substituting IntPAR for the area it is possible to obtain a value for the unknown I_{max} as described in Appendix II. A sine curve of surface PAR against time of day can then be predicted for any given daily surface IntPAR.

In order to reduce the computation involved, sine curves of daily surface PAR were only used to model twelve daily surface IntPAR values arbitrarily chosen to cover the full annual range of surface IntPARs reported by Porter (1985) (2.8 $E.m^{-2}.d^{-1}$ to 63.3 $E.m^{-2}.d^{-1}$ in steps of 5.5 $E.m^{-2}.d^{-1}$).

The next stage was to calculate the daily PAR regimes at 10 m depth at each site from the sine curves of surface PAR. During the present study the transmission of surface PAR to 10 m depth at each site was measured between May and July and also between December and January (Chapter 2.3). The mean and the two extremes of all these values at each site (Table 1; WFR site, 26.9% and 18.3% to 39.2%; CP site, 19.4% and 10.3% to 41.3%) were representative of the range of water clarities expected over a whole year. These were used to calculate the *in situ* PAR regimes at each site using the 12 sine curves of surface PAR described above. This gave 36 sine curves at each site each modelling daily PAR at 10 m depth. These curves covered the full annual range of daily surface IntPAR and the annual range of water clarities at each site. Each curve was in the form of equation 1 from which the *in situ* PAR could be calculated at any time of the day.

Finally, the integrated gross daily productivities of Porites porites were calculated for each of the 36 sine curves of in situ 10 m depth PAR at both sites. The net photosynthetic rates were calculated using the 'representative' P/I curves for each site (Figure 11). Each sine curve was divided into 0.25 hour increments and the PAR at the median time of each increment was calculated. The net photosynthetic rate was calculated for each PAR value, converted to absolute oxygen production over each 0.25 hour increment and summed over the whole day (as modelled by the sine curve) to give the integrated net photosynthetic oxygen production. The net photosynthetic oxygen production was then added to the daytime respiratory oxygen consumption calculated from the mean, measured dark respiration rate at each site (Table 7), to give the integrated gross daily photosynthetic oxygen production. These were converted to Joules as in Chapter 3.8.

The end result was 36 gross daily productivities for Porites porites at each site, corresponding to 12 daily surface IntPARs and 3 transmissions of surface PAR to 10 m depth. Gross daily productivity was plotted against daily surface IntPAR to give a single curve for each of the 3 transmissions at each site.

In addition to calculating the daily gross productivities of Porites porites at both sites for the range of daily surface IntPARs expected over a year, the integrated gross productivities at each site were also calculated for an actual year. 366 daily surface IntPAR values for the year 1983-84 were taken from Porter (1985) (including previous day extrapolated values for 3 missing October dates) and were modelled with sine curves as described above. Since the percentage transmissions of surface PAR to 10 m depth was not measured on every day of the year, the mean value recorded at each site (Table 1; WFR site, 26.9%; CP site, 19.4%) was used to predict the in situ 10 m

depth daily PAR for each of the 366 sine curves of daily surface PAR. Daily integrated gross productivities were then calculated as above for each of the 366 in situ daily light curves at each site, and were summed to give the integrated annual productivities.

5.3 Results

A sine curve accurately models the daily PAR of an 'ideal' day, but heavily overcast days show departures from the curve (Chapter 2, Figure 5). However, gross daily productivities of Porites porites calculated using the 'representative' P/I curves (Figure 11) for the actual PAR recordings for 16 June 1985 and 13 January 1986 (Figure 5) as described in Chapter 3.8 and also for the sine curve models for the same two days (as described in this chapter), differed by less than 7% at both sites (Table 10). The daily IntPAR for 16 June and 13 January were 56.3 $E.m^{-2}.d^{-1}$ and 13.4 $E.m^{-2}.d^{-1}$ respectively, and the PAR vs time curves were very different (Figure 5). The prediction of daily PAR from daily IntPAR values using sine curves therefore provides a good approximation to the actual PAR irrespective of the magnitude of the daily IntPAR or the shape of the actual PAR curve.

Gross productivities vs daily surface IntPAR are shown as curves for each transmission of surface PAR to 10 m depth at each site in Figure 15. The daily energy requirements for Porites porites at both sites (from Figure 14) are drawn in as a horizontal line. On the days with less surface IntPAR than the value indicated by the intercept of the curves and the horizontal lines (showing the daily energy expenditure), P. porites no longer has the potential for complete autotrophy in terms of energy. The 363 recordings of daily surface IntPAR values for 1983-84 (Porter, 1985) had a mean of 37.4 $E.m^{-2}.d^{-1}$

SITE	DATE	GROSS PRODUCTIVITY FROM SINE CURVE	GROSS PRODUCTIVITY FROM LIGHT TRACE	% ERROR
WFR	16 June 1985	30.19	31.00	-2.6
	13 January 1986	11.61	11.28	+2.9
CP	16 June 1985	33.66	34.31	-1.9
	13 January 1986	13.17	12.32	+7.0

Table 10. Porites porites at the West Fore Reef (WFR) and the Columbus Park (CP) sites: integrated gross daily productivity (mlO_2.g^{-1} dry tissue) calculated from actual light traces and from the sine curve model of the same integrated daily surface PAR with transmission of surface PAR to 10 m depth of 26.9% (WFR site) and 19.4% (CP site). 16 June was an 'ideal' day and 13 January was heavily overcast (Figure 5). The percentage error is the difference between the two estimates of gross productivity: a negative indicates that the sine curve prediction is lower than the estimate from the actual recording.

Figure 15a and b. Porites porites at 10 m depth at the West Fore Reef (a; WFR) and the Columbus Park (b; CP) sites: daily gross productivity (Joules) as a function of daily surface integrated photosynthetically active radiation (IntPAR) and water clarity. The percentage frequency distribution of the integrated daily light levels throughout 1983-84 (Porter, 1985) is shown by the histogram with a class interval of 4.9 $E.m^{-2}.d^{-1}$., and the curves represent the productivity at the mean (WFR, 26.9%: CP; 19.4%) and the two extremes of all the recorded PAR transmissions to 10 m depth at each site (for the bulked May/July and the December/January data, Table 1). The horizontal lines at 350 J (WFR site) and 250 J (CP site) represents the daily energy expenditure. All energy values are calculated for a specimen with 1 g dry tissue.

When the curves pass below the daily energy expenditure the corals can no longer be totally autotrophic. Even with the most turbid water at each site (18.3% transmission at the WFR site: 10.3% transmission at the CP site) P. porites can remain autotrophic until the daily light values fall below 31.5 $E.m^{-2}.d^{-1}$ (WFR site) or 22.7 $E.m^{-2}.d^{-1}$ (CP site), which accounted for less than 24% (WFR site) or 4% (CP site) of the days in 1983-84.

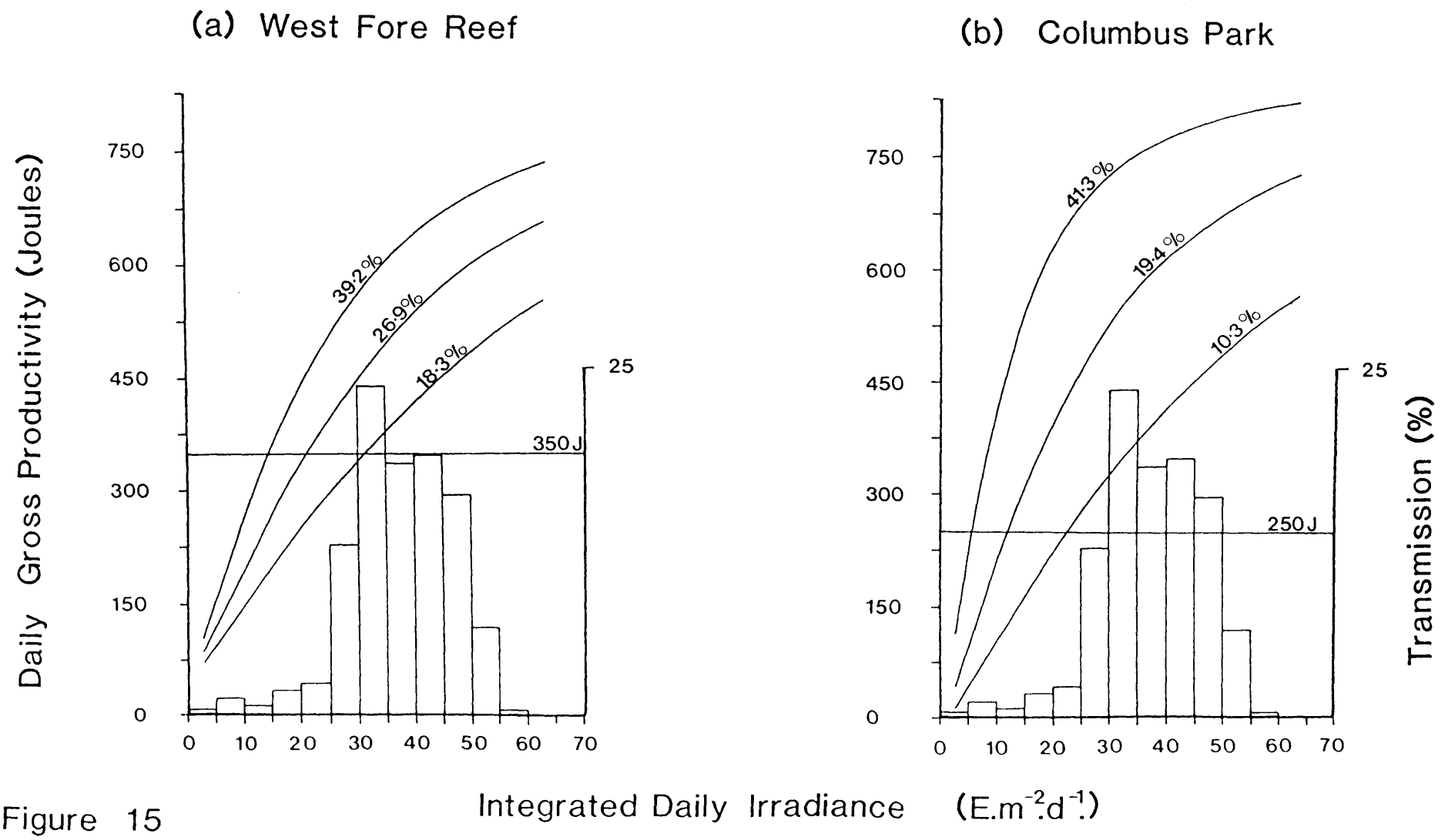

(a) West Fore Reef
(b) Columbus Park
Daily Gross Productivity (Joules)
Transmission (%)
Integrated Daily Irradiance (E.m⁻².d⁻¹)
39.2%
26.9%
18.3%
41.3%
19.4%
10.3%
350J
250J
25
0
150
300
450
600
750
0
10
20
30
40
50
60
70

Figure 15

and were normally distributed for a class interval of 4.9 $E.m^{-2}.d^{-1}$ (Kolmogorov-Smirnov Test, D = 0.262, n = 12, not significantly different from a normal distribution at P = 0.05). These data are plotted as a histogram in Figure 15.

The percentage transmission of surface PAR to 10 m depth varies continuously throughout a year (see Table 1) and this has a direct effect on coral productivity independent of surface PAR. However, by fixing the value of the percentage transmission of surface PAR to 10 m depth at the upper extreme, mean or lower extreme of the transmission data recorded at each site, the least, average and the highest possible number of days in a year that Porites porites can be autotrophic can be estimated from Figure 15. During 1983-84 P. porites received insufficient daily PAR to be fully autotrophic on 6, 14 or 86 days corresponding to 39.2%, 26.9% or 18.3% transmission of surface PAR to 10 m depth at the WFR site, and similarly on 2, 5 or 14 days corresponding to 41.3%, 19.4% or 10.3% transmission at the CP site.

The gross annual productivity of Porites porites over 1983-84 was 8803 $mlO_2.g^{-1}$dry tissue = 163.7 $mlO_2.cm^{-2}$ (at 18.59 mg dry tissue.cm^{-2}) at the WFR site and 10203 $mlO_2.g^{-1}$ dry tissue = 158.3 $mlO_2.cm^{-2}$ (at 15.51 mg dry tissue.cm^{-2}) at the CP site. These gross productivities are equivalent to 184.39 $KJ.g^{-1}$dry tissue (WFR site) and 213.72 $KJ.g^{-1}$dry tissue (CP site) (1 mlO_2 = 20.9467 J; from Chapter 3.8). If the annual energy expenditure is 366x the daily energy expenditures (Figure 14), during 1983-84 there was a net surplus of 56.29 $KJ.g^{-1}$dry tissue at the WFR site (31% of the gross annual productivity) and 122.22 $KJ.g^{-1}$dry tissue at the CP site (57% of the gross annual productivity).

5.4 Discussion

As the rate of photosynthesis in corals is asymptotic to irradiance, the *in situ* daily IntPAR is not directly proportional to productivity. A sine curve was used to predict a 12 hour irradiance distribution for each daily surface IntPAR value, which was used to calculate the *in situ* PAR at any time of the day and hence the integrated daily photosynthesis of *P. porites* at 10 m depth at both sites using the predetermined photosynthesis/irradiance response. Although actual days can differ from the sine wave model in both daylength (16 June = 14 hours, 13 January = 11 hours) and irradiance distribution (cf. Figure 5), the errors in the estimated productivities from the sine curve are small (Table 10) and tend to counteract each other over a whole year (for daylength).

Integrated daily gross productivities vs surface daily IntPar curves were only plotted for the mean and the two extremes of the percentage transmission of surface PAR to 10 m depth, even though a range of percentage transmissions occur in any one year. However the bulked data for the percentage transmission to 10 m depth were normally distributed at each site (Chapter 2.3.2). Therefore the gross daily productivities corresponding to any combination of surface daily IntPAR and percentage transmission to 10 m depth at each site should lie between the integrated gross daily productivity vs surface daily IntPAR curves for the two extreme percentage transmissions at each site (Figure 15). The different shapes of the curves indicate photoadaptation of *P. porites* at the CP site compared to the WFR site, and the non-zero intercepts are a result of the differences between the mean measured respiration rate (Table 7) and the respiration rate predicted from the best-fit hyperbolic tangent curve for the net

productivity/irradiance data. The best-fit hyperbolic tangents usually did not pass through the measured respiration point since data points were unweighted (Chapter 3.7).

The worst possible annual light conditions experienced by Porites porites would be approached by a year with similar daily surface IntPAR values to those recorded in 1983-84 (Porter, 1985) and the highest recorded turbidity occurring every day of the year at each site (WFR site; transmission of surface PAR to 10 m depth = 18.3%: CP site; transmission = 10.3%). Even under these conditions P. porites at 10 m depth could remain fully autotrophic for more than 76% (WFR site) or 96% (CP site) of the year (from Figure 15).

The gross annual productivities for Porites porites in 1983-84 (calculated using the mean percentage transmission of surface PAR to 10 m depth) exceed the annual energy requirements at the respective sites (from Figure 14). The annual energy budgets are therefore similar to the energy budgets on an 'ideal' day. Porites porites can be autotrophic over a whole year at both sites, although the annual surpluses of photosynthetically fixed energy (PFE) are reduced to 31% of the gross PFE at the WFR site (cf. 45% surplus on an 'ideal' day) and 57% of the gross PFE at the CP site (cf. 67.3% surplus on an 'ideal' day).

Porter (1985) used the same surface daily IntPAR values for 1983-84 to show that Montastrea annularis was autotrophic in terms of respiratory carbon at 1 m depth, but that exogenous sources of carbon were required to meet respiratory demands over the remainder of its depth range to 50 m. Similar results were predicted by Davies (1977) based on short term laboratory experiments. Porter (1985) calculated gross productivities for M. annularis of 1025 $gC.m^{-2}.y^{-1}$ (1 m depth), 510 $gC.m^{-2}.y^{-1}$ (10 m depth) and 293 $gC.m^{-2}.y^{-1}$ (50 m depth) which are very similar to those predicted by Davies (1977) and which compare to

797 $gC.m^{-2}.y^{-1}$ (WFR site) and 771 $gC.m^{-2}.y^{-1}$ (CP site) for P. porites at 10 m depth in the present study (calculated with a photosynthetic quotient of 1.1; after Muscatine et al., 1981). Although these productivities are all in the same order of magnitude, it is clear that not all Caribbean corals are as autotrophic as Porites porites.

Porites porites can be autotrophic on an 'ideal' day in two different environments and this nutritional status can be maintained for most of the year. As 95% of the figures for the percentage transmissions of PAR to 10 m depth are between 25.9% and 27.9% (WFR site) or 18.2% and 20.6% (CP site) (from the 95% ranges in Table 1) the high annual gross productivities can probably be maintained irrespective of most water clarities experienced. However, an important factor in determining the survival of P. porites in the two locations may be the ability to survive a run of 'bad' days with low daily surface IntPAR and low transmissions of PAR to 10 m depth. This hypothesis will be expanded in Chapter 7 after the roles of lipid reserves have been considered.

CHAPTER 6: ACCOUNTING FOR THE SURPLUS ENERGY

6.1 Introduction

The zooxanthellae in Porites porites at 10 m depth at both the WFR and CP sites can fix sufficient carbon to meet and surpass the energy demands of the colony, and the current methodology suggests that the surplus energy is 'lost' from the colony. Similarly, previous short term studies have shown that photosynthesis can meet all the respiratory oxygen requirements in a variety of corals (Yonge et al., 1932; Kawaguti, 1937; Roffman, 1968; Drew, 1973; Wethey and Porter, 1976), that photosynthetically fixed carbon or energy can meet the energy or carbon demands of the colony (Davies, 1984; Muscatine et al., 1984) and that significant amounts of photosynthetically fixed carbon can be lost from the colony (Cooksey and Cooksey, 1972; Crossland et al., 1980).

The present study represents the most comprehensive energy budget for any coral to date but a significant proportion of the photosynthetically fixed energy is still accounted for by subtraction. However, since the initial hypothesis that the surplus energy was lost from the colony as soluble or particulate mucus was not substantiated by the measured losses (Chapter 4.7), alternative routes for the apparent surplus of energy need to be explored. In Chapter 7 a good argument will be developed to suggest that surplus energy can be lost from the colony as low molecular weight compounds rather than as macromolecular mucus, but in this chapter the assumption that the daytime and the night-time colony respiration

rates are the same will be challenged and the effect of an elevated daytime respiration rate on energy requirements will be considered. The roles of lipid storage and mucus tunics in utilising photosynthetically fixed energy will also be considered.

6.2 Elevated daytime respiration

6.2.1. Introduction

There was no evidence that the respiration rate of Porites porites varied throughout the day under continuous dark conditions (Chapter 4.3.1) but during the early experiments it was noted that the respiration rate was higher in the dark period following the irradiance sequence used to construct the P/I curves (Chapter 4.9.2.1). Similar observations have been made for a variety of corals (Yonge et al., 1932; Porter et al., 1984) and symbiotic anemones (Muller-Parker, 1984; Svoboda and Porrmann, 1980). However, the significance and magnitude of the effect have been consistently ignored. A series of experiments was therefore carried out to determine the magnitude of the daytime respiration rate in P. porites and its significance to the daily energy budgets.

The respiration rate of corals in the light cannot be directly measured by oxygen flux techniques because of the simultaneous production of oxygen by photosynthesis. The daytime respiration rate was therefore taken as the respiration rate measured in a dark period immediately following a light period. The proportional increase in the respiration rate during the day was taken as the difference in the respiration rate measured from overnight darkness and also after a light period in the laboratory.

6.2.2 Methods

In the initial experiments, the effect of 3 hours of sunlight on the respiration of Porites porites was measured. Six nubbins recovered from the WFR site were placed in an outdoor blacked out aquarium receiving running seawater. Their respiration rates were measured the following day between 10.00 and 12.00 hrs as described in Chapter 3 and they were then returned to the blacked out aquarium. When the measurements were completed the lid of the aquarium was replaced with mosquito netting which exposed nubbins to a quantitative equivalent of the PAR at 10 m depth at the WFR site. After 3 hours the lid was replaced and the dark respiration of each nubbin was again measured within 1 hour. Ten control nubbins were treated identically but received 3 hours of darkness between respiration measurements.

In order to determine the speed of onset and the magnitude of the elevated daytime respiration rate, nubbins were also collected from both sites and their respiration rates measured the following day before and after exposure to a known irradiance in the laboratory. Respiration measurements were carried out as described in Chapter 3. After measuring the dark respiration rate of nubbins maintained in darkness overnight, the overhead lights were switched on to expose the nubbins to 140 $\mu E.m^{-2}.s^{-1}$ as measured with a Li Cor LI 192SB sensor. An infra-red filter (Edmund Scientific, stock 4009) was placed between the chamber and the lights to prevent heating within the chamber as the water jacket and fan were found to be inadequate for this purpose during lengthy exposures to light. After 10 minutes the lights were switched off and the respiration rate measured in darkness. The sequence of a light period followed by a measurement of dark respiration was repeated for the same nubbin retained in the chamber for an additional 10, 20 and then 40 minutes exposure to the same

irradiance. A dark respiration rate was therefore obtained for each nubbin after an accumulative exposure to light of 10, 20, 40 and 80 minutes. After the final respiration measurement the nubbin was buoyant weighed. To control for the effect of approximately 120 minutes in the respirometry chamber (if each respiration measurement took 10 minutes), a nubbin (11 replicates) was retained in the chamber during 3 hours in darkness and the respiration rate measured before and after the treatment.

In order to determine whether the elevated daytime respiration was caused by the algal or animal component of the symbiosis, the dark respiration rate of zooxanthellae was measured before and after a light period. Zooxanthellae were isolated from Porites porites at both sites as described in Chapter 3.4.2, and their dark respiration measured with the apparatus described in Chapter 3.6, before and after a 15 minute light period at approximately 60 $\mu E.m^{-2}.s^{-1}$ (recorded beneath the cell preparation with a Li Cor LI 192S sensor). Control preparations received a 15 minute dark period. PO_2 was maintained between 100% and 75% saturation by bubbling the suspension with N_2 or O_2. Zooxanthellae respiration was adjusted for background O_2 uptake and expressed as $\mu lO_2.x10^6 zoox^{-1}.min^{-1}$.

6.2.3. Results

The mean respiration rates before and after exposure to 3 hours of sunshine were significantly different (Table 11; Appendix I, Table 8) and showed a mean elevation of 39.3% after exposure to light (95% range 8.2% to 76.4%; arcsine transformed data). The control respiration rates were not significantly different before or after the 3 hours in darkness (Table 11).

TREATMENT	MEAN	S.D.	N	t	d.f.	SIGNIFICANCE.
Before light period	8.18	2.11	6			
				3.190	5	$P < 0.05$
After light period	11.16	2.46	6			
Before dark period	7.92	1.40	10			
				0.011	9	N.S.
After dark period	7.91	0.67	10			

Table 11. Porites porites from the West Fore Reef site: respiration rates ($\mu lO_2.mg^{-1}$ dry tissue.min^{-1}) before and after a light period and also before and after a control dark period. The respiration rates before and after each treatment were compared by the paired sample t-test; t values, degrees of freedom (d.f.) and the probability (P) for a significant difference are shown. N.S. = not significantly different at P = 0.05.

In the second experiment with exposure to a known irradiance in the laboratory, the dark respiration rates increased after exposure to light and were significantly different between replicates and between light treatments at both sites (Figure 16; Appendix I, Table 9, 10). With Porites porites from the WFR site the mean respiration rate was not significantly higher than the respiration rate from overnight darkness until after 20 minutes exposure to light (Student-Newman-Keuls test (SNK), $P < 0.05$; Appendix I, Table 9). However, at the CP site the mean respiration rate was significantly higher than the mean respiration rate from darkness after 10 minutes of exposure to light (SNK test, $P < 0.05$; Appendix I, Table 10). The dark respiration rate of P. porites increased faster upon exposure to light at the CP site compared to the WFR site. In the control experiment, the respiration rates of nubbins retained in the respirometry chamber for 3 hours in darkness did not significantly change (paired sample t-test, $t = 0.0215$, d.f. = 10, $P = 0.05$).

An elevated colony respiration rate could be caused by either an animal or algal effect or both. In order to determine whether zooxanthellae show a light-enhanced respiration rate, the respiration rates of zooxanthellae from Porites porites at both sites were measured before and after a 15 minute experimental light period or a 15 minute control dark period. Respiration rates were not significantly different before or after experimental or control treatments (Table 12).

6.2.4. Discussion

The dark respiration rate of Porites porites increased after exposure to light. The respiration rate of the WFR specimens increased by 39% after exposure to sunlight whilst the respiration

Figure 16. Porites porites from the West Fore Reef (WFR) and the Columbus Park (CP) sites: the respiration rate ($\mu l O_2 . g^{-1}$ dry tissue.min^{-1}) measured in a dark period after an accumulative exposure to 0, 10, 20, 40 and 80 minutes of PAR at 140 $\mu E . m^{-2} . s^{-1}$. The mean $\pm$ standard errors are shown for 5 replicates at each point (★ = 4 replicates).

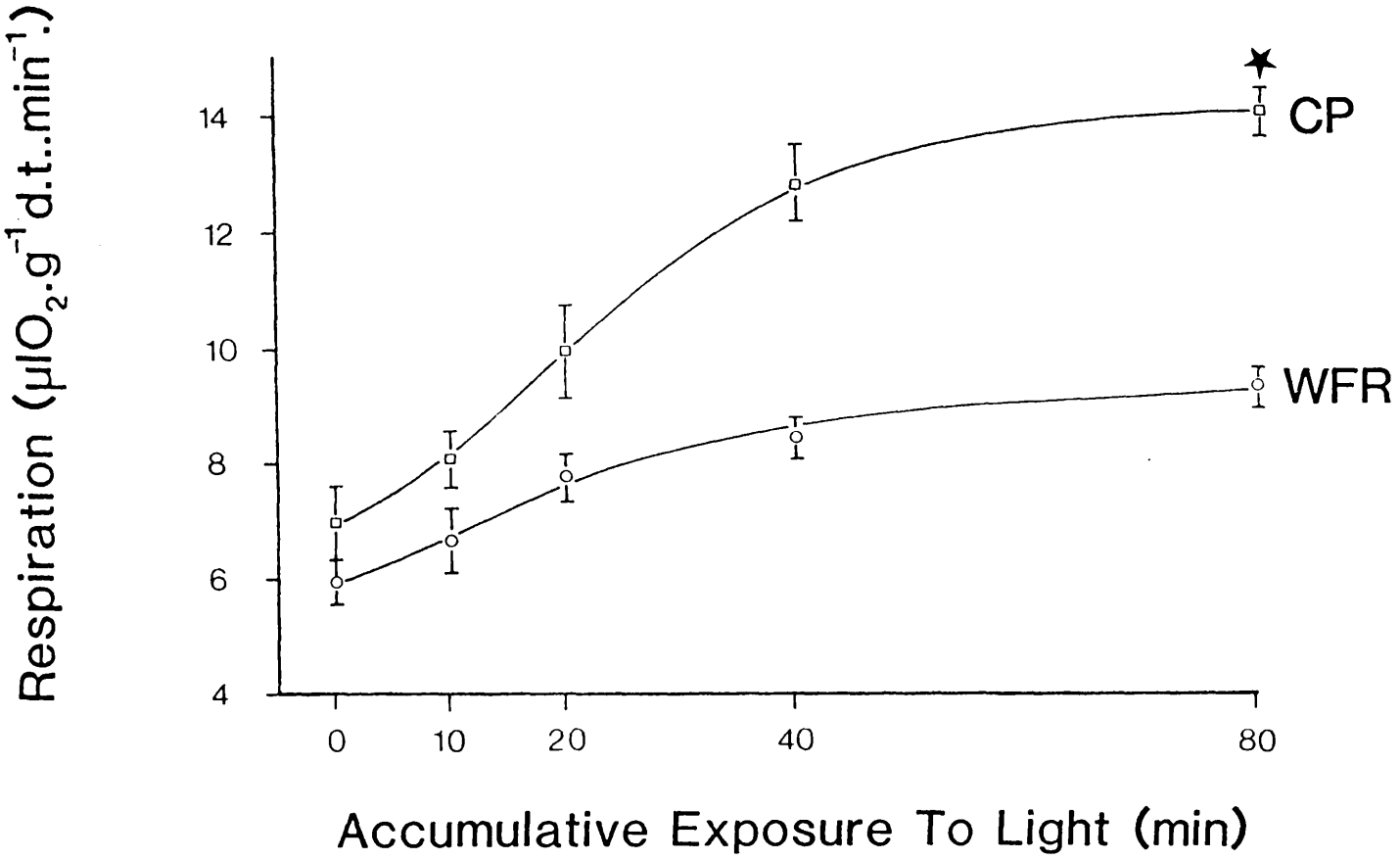

Respiration (μlO2.g-1d.t..min-1.)
14
12
10
8
6
4
0
10
20
40
80
CP
WFR
Accumulative Exposure To Light (min)

Figure 16

	CONDITION	BEFORE	AFTER	t	
WFR	EXPERIMENTAL	0.030 ± 0.005 (9)	0.034 ± 0.007 (9)	1.4306	N.S.
	CONTROL	0.031 ± 0.011 (10)	0.025 ± 0.004 (10)	1.9043	N.S.
CP	EXPERIMENTAL	0.037 ± 0.018 (8)	0.027 ± 0.008 (8)	0.9027	N.S.
	CONTROL	0.032 ± 0.008 (8)	0.028 ± 0.005 (8)	1.3599	N.S.

Table 12. Respiration rate of zooxanthellae ($\mu l O_2 . 10^6 zoox^{-1} . min^{-1}$) from P. porites at the West Fore Reef (WFR) and Columbus Park (CP) sites, before and after exposure to 15 minutes of light (experimental) or 15 minutes of darkness (control). Means ± 95% confidence limits shown, sample size in parenthesis. Before and after treatments compared by paired sample t-test, not significantly different (N.S.) at P = 0.05.

rate of specimens in the laboratory increased by approximately 56% (WFR site) and 103% (CP site) (from Figure 16) after 80 minutes illumination. The length of time the corals spent in the chamber did not affect the respiration rate.

An elevated dark respiration rate after a light period has been noted in a variety of symbiotic cnidarians (Muller-Parker, 1984; Porter et al., 1984). Some symbiotic cnidarians have a higher dark respiration when maintained in the laboratory under a high, as opposed to a low light regime (Kevin and Hudson, 1979; Svoboda and Porrmann, 1980; Tytler and Davies, 1984). This may be analogous to the reduction in coral respiration rate with depth (Davies, 1980; McCloskey and Muscatine, 1984) and shading (Muscatine et al., 1984).

An elevated respiration rate after a light period has been described in both plants and phytoplankton (Falkowski et al., in press; Jackson and Volk, 1970). It is often attributed to photorespiration (Jackson and Volk, 1970), a process whereby photosynthetically produced glycolate is metabolised to carbohydrate with the production of CO_2 and consumption of O_2, but with no net production of ATP (Goldsworthy, 1976). Photorespiration is usually diagnosed by the inhibition of photosynthesis by high concentrations of O_2 (the Warburg effect), by a post illumination burst in CO_2 production and O_2 consumption, or by a decreasing photosynthetic quotient with increasing concentrations of O_2 (Burris, 1980)

Crossland and Barnes (1977) found evidence for photorespiration in zooxanthellae from Acropora acuminata by using carbon-14 techniques to demonstrate the presence of the Warburg effect, as did Burris (1977) for zooxanthellae from Pocillopora capitata. Burris (1977) further showed that there was a post-illumination burst of CO_2 production and O_2 consumption in the isolated zooxanthellae. However, Burris (1977) and Crossland and Barnes (1977) noted that zooxanthellae

photorespiration was somewhat different to the equivalent effect in phytoplankton, and Burris (1977) suggested that zooxanthellae may have a different biochemical pathway for photorespiration. Photorespiration may not be the only mechanism for light enhancement of respiration in phytoplankton (Falkowski et al., in press), and the whole question of photorespiration in zooxanthellae remains equivocal (Muscatine, 1980a). Zooxanthellae from Porites porites in the present study showed no signs of an enhanced respiration rate after exposure to light (this chapter). Any change in the post-illumination respiration rate of symbiotic colonies of P. porites is therefore probably a function of the animal tissue alone.

Symbiotic cnidarians also show an increased respiration rate after feeding on particulate food (Svoboda and Porrmann, 1980; Szmant-Froelich and Pilson, 1984), and the post-prandial respiration rate can be 96% higher than the pre-prandial rate (Tytler and Davies, 1984). This has been described as specific dynamic action (SDA) and is generally considered to represent the metabolic expenditures resulting from the processing of nutrients (Jobling, 1981). The exact cause of SDA remains unclear, but it can probably be explained in terms of the energy required for protein synthesis and growth (Jobling, 1983).

Svoboda and Porrmann (1980) suggested that the increased respiration rate in light adapted Aiptasia diaphana was due to metabolism of photosynthetic products, and a similar effect was implied for Stylophora pistillata (McCloskey and Muscatine, 1984). Battey and Patton (1984) suggested that zooxanthellae translocated both glycerol as an immediate respiratory substrate and lipid as a long term energy reserve. Most recently they (Battey and Patton, in press) used cyanide to inhibit respiration in the symbiotic anemone

Condylactis gigantea and found that the intracellular glycerol concentrations in the host increased. They concluded that under normal conditions glycerol was rapidly catabolised by the host.

There is therefore good evidence in the literature to suggest that zooxanthellae photosynthetically fix carbon into both lipid and glycerol which are then translocated to the host (see also references in Chapter 1.2) where they have separate and distinct fates. Lipid is stored as a long term energy store whilst glycerol is immediately respired during the day to supply an increased energy expenditure. The catabolism of glycerol is manifest as a higher daytime colony respiration rate. Although photosynthesis ceases in darkness, zooxanthellae probably continue to translocate organic compounds (Lewis and Smith, 1971; Trench, 1971b) and it is likely that the translocation of glycerol from the zooxanthellae continues in darkness for at least several hours until the photosynthetically produced precursors are used up. This would account for the observed elevated respiration rate in a period of darkness following exposure to light.

An elevated daytime respiration in symbiotic cnidarians clearly represents a general light enhancement of metabolism in its broadest sense, and more specifically may be analogous to SDA (sensu Jobling, 1981) involving metabolism of glycerol. For Porites porites in the present study it is impossible to determine whether the increased daytime respiration represents substrate limitation in the dark, or whether the increased energy yield is an essential requirement for processes enhanced in the day, possibly by light itself. The former hypothesis would seem unlikely since P. porites has a surplus of energy on nearly every day of the year (Chapter 5), whilst both calcification and mineral nutrient uptake in corals are enhanced by

light (Goreau and Goreau, 1959; Muscatine, 1980b) and could require additional energy as suggested in the second hypothesis. These intriguing possibilities require further investigation.

The information on the daytime respiration rate is inadequate to make a valid modification of the energy budgets. The P/I responses would need to be recalculated, incorporating measurements of the respiration rate at each irradiance in order to give a true estimate of gross photosynthesis. In addition, a 103% increase in colony respiration at the CP site would require a 537% increase in host respiration alone, as zooxanthellae respiration does not increase in the light (this chapter). Such a large increase in animal respiration would seem unlikely and therefore some of these experiments need repeating. However, the present data together with similar observations in the literature become overwhelming in their rejection of the dogma of an identical respiration rate in the light and dark for symbiotic cnidarians.

6.3 Mucus tunics

6.3.1. Introduction

Although mucus release from corals has been observed *in situ* (Coles and Strathmann, 1973) and measured both *in situ* (Richman *et al.*, 1975) and in the laboratory (Krupp, 1982), release of soluble or particulate macromolecular mucus does not account for a significant proportion of the daily photosynthetically fixed energy in *P. porites* (Chapter 4.7). However, *Porites porites* also produces mucus coats ("tunics") over their entire surface when in the field and in the laboratory. The frequency, duration and energy content of mucus tunics were measured in order to quantify this potential route for the loss of photosynthetically fixed energy.

6.3.2. Methods

The frequency of occurrence and duration of mucus tunics on Porites porites was determined on 18 nubbins collected from the WFR site and maintained in an outdoor aquarium. The aquarium was shaded with mosquito netting to a quantitative equivalent of the PAR at 10 m depth and supplied with unfiltered seawater. Nubbins were scored daily over 26 days for the presence of complete (over their entire surface) or incomplete (only part of their surface covered) mucus tunics.

The energy content of mucus tunics was determined by wet oxidation. Nubbins which had formed complete mucus tunics in situ, were collected from the WFR site and were placed into individual beakers containing 50 ml of 0.45 µm FSW. The tunic was removed with jets of FSW from a Pasteur pipette and the nubbin was then buoyant weighed and its surface area determined from the regression of surface area on dry skeletal weight previously determined for specimens from the WFR site (Table 4). Individual mucus tunics were collected onto Whatman GF/C filters, washed with 5 ml of 4.5% w/v solution of Na_2SO_4 to remove halide ions (Strickland and Parsons, 1972) and wet oxidised as previously described for zooxanthellae (Chapter 3.4.2) but without correction for incomplete protein oxidation. Control filters had 50 ml of FSW sucked through and were wet oxidised by the same procedure. The energy content of each mucus tunic was expressed as Joules per cm^2 of coral surface.

6.3.3 Results

Individual branches of Porites porites observed on the reef at both sites were periodically covered with thin, taut sheets of mucus (mucus "tunics"), although not all the branches in any one colony had

mucus tunics at the same time. All the polyps and tissues were fully contracted beneath the tunics, but tunics split apart as if under tension when cut with a sharp object and healthy polyps then expanded from the exposed coral surface.

Nubbins of Porites porites spent a mean total of 6.3 ± 1.95 days (± 95% confidence limits) out of 26 days covered with complete or partial tunics. This included specimens which had tunics present at the start of the observation period and also those which had tunics present when the observation period ended. In order to get an estimate of the time from the start of the formation of a tunic to its total loss from the colony, only tunics which were formed and fully lost from the colony within the observation period were considered. Tunics or tunic-free periods which both commenced and terminated during the observation period, lasted a mean of 5.2 days (mode = 6, 6 observations) and 6.2 days (mode = 1, 23 observations), respectively.

Microscopic inspection of mucus tunics showed that they contained pores (ca. 0.5 mm dia.) above some of the underlying polyps and a wide variety of particulate material including zooxanthellae, nematocysts and protozoa. The mean energy content of tunics was 6.88 ± 2.86 $J.10cm^{-2}$ (± 95% confidence limits, n = 6).

6.3.4 Discussion

Mucus tunics on Caribbean Poritids have been previously described in situ and in the laboratory by both Lewis (1973) and Coffroth (1984). During the present laboratory observations P. porites was covered by partial or complete mucus tunics for 24% of the time it was retained in a flowing seawater tank. The small number of tunics which

both formed and were lost from nubbins during the course of the experiment suggest that 2 to 3 complete tunics (each lasting approximately 5.2 days with 6.2 days in between) occur each month (30 days). For a nubbin with 300 mg dry tissue = 16.1 cm^2 a single tunic contains 11.1 J equivalent to 1.1 $J.day^{-1}$ if three are formed each month. This represents an insignificant energy loss to the colony, (cf. Figure 14) particularly since embedded protozoa, bacteria etc. were included in the tunic energy determinations.

The functional significance of mucus tunics remains obscure. Polyps contracted into the skeleton and covered by a mucus tunic cannot capture zooplankton and have a reduced photosynthetic rate (pers. obs.). The contracted polyps may also be oxygen depleted and contain high concentrations of metabolic wastes. It would seem likely that tunics act as a physical barrier for particulate material, whilst dissolved materials can probably pass through the pores without difficulty. Even if Porites porites has dioecious colonies, fertilisation of the mesenterial-bound ova is internal, and it is possible that the tunics retain gametes during the fertilisation periods.

6.4 Lipid Content

6.4.1 Introduction

Since Bergmann et al. (1956) showed that the dry tissues of tropical anemones contained more than 33% lipid it has become clear that lipids play an important role in the metabolism of corals and probably form the basis of their energy economy (Patton et al., 1977). Gross photosynthesis in Porites porites provides more energy than the

colony can use on nearly every day of the year and this surplus is presumed to be lost from the colony in the energy budgets presented in Chapter 4. Lipid reserves provide an alternative route for surplus energy, and the lipid content of P. porites was therefore measured to see whether lipid energy reserves could account for the predicted net energy fluxes under different lighting regimes.

6.4.2. Methods

Lipid content was determined by a modification of the method of Patton et al. (1977) using fragments from branch tips of Porites porites. Two replicate fragments from each branch were each extracted with two changes of Bloors solution (ethanol:ethoxyethane; 3:1) at room temperature (27°C) over 48 hours. Fragments were dried and their surface areas determined by weighing aluminium foil which had been cut and fitted to the polyp-bearing surface (10 replicates per fragment). Five controls containing no coral fragment were processed with each experimental group.

The Bloors extract from each fragment was concentrated to 5 ml under a stream of air at < 50°C, diluted with 3 ml of distilled water and extracted with two 5 ml changes of petroleum ether (b.p. 40 - 60°C) at room temperature (27°C) over 48 hours. The petroleum ether extracts were concentrated to 5 ml under air at < 50°C, centrifuged and duplicate 1 ml aliquots dried to a residue over P_2O_5 in pre-weighed aluminium planchets and weighed to the nearest 10 µg on a Mettler H6 balance. The mean of the duplicate residues from each fragment was corrected for the blank value and expressed as mg lipid.cm^{-2}, and the unit area lipid content of each branch tip was derived from the mean lipid content of its two fragments.

In order to see whether lipid reserves in Porites porites were depleted under conditions of low light and high sedimentation or enhanced in high light and low sedimentation conditions, the lipid content was compared after a period of rough weather and also after a period of calm weather. One branch from each of 5 colonies was collected from each site on 18 November 1985 after a week of rough weather and also on 27 January 1986 after a week of calm weather. The light intensity over the preceeding week was not measured.

In a later controlled laboratory experiment the lipid content of Porites porites was determined before and after exposure to a known irradiance to see whether the predicted energy surplus/deficit (from Chapter 4) agreed with the observed changes in lipid content. Six nubbins were prepared from each of 5 colonies (total 30 nubbins) for use in 6 treatments in an attempt to reduce between treatment variation caused by between replicate variation. Nubbins were collected on 9 September 1985 after having recovered for two weeks in situ and one nubbin from each of the five colonies was immediately sacrificed for the determination of lipid content on day 0. One nubbin from each of the 5 colonies was also placed in a darkened aquarium receiving seawater filtered through a net with a 50 μm pore size. These were sacrificed for lipid determinations after 5 days. The remaining 20 nubbins were placed in 4 cm depth of (filtered) seawater (50 um net) in a 5 x 4 array with 5 rows normal to the inflow of the seawater, and the position of nubbins in rows determined by random numbers. One nubbin from each colony was present in each column and no more than one nubbin from each colony in each row. All nubbins received 83 $\mu E.m^{-2}.s^{-1}$ (measured with a Li Cor LI 192S sensor) from an overhead bank of 6 x 15W Westinghouse Daylight fluorescent tubes which

were on continuously for 9 days (except for 10 hours on day 1). One column of nubbins was sacrificed for lipid determination after each of approximately 2, 4, 6 or 8 days accumulative exposure to 83 $\mu E.m^{-2}.s^{-1}$, and lipid content compared between treatments. Changes in lipid content were converted to Joules using the mean energy content of fat (39.5 $KJ.g^{-1}$; Brafield and Llewellyn, 1982) and were compared to the predicted energy production and consumption calculated from the 'representative' P/I relationship (Figure 11) and the energy budgets presented in Chapter 4.

6.4.3. Results

A preliminary lipid extraction showed that the second extraction of the fragments with Bloors solution increased the lipid yield by a mean of 10.0% (95% range 8.3% to 11.9%, n = 7) whilst a third extraction of the bulked Bloors solution with petroleum ether increase the lipid yield by less then 0.6% (95% range 0.3% to 1.0%, n = 7). Additional extraction with either Bloors solution or petroleum ether were unnecessary. The polyp bearing surface of fragments was typically 2 - 3 cm^2.

The lipid content of Porites porites after rough weather and after calm weather at each site are shown in Table 13 together with the results of t-test comparisons. The mean lipid contents were not significantly different after rough or calm weather at each site or after calm weather between sites, but were significantly different between sites after rough weather. The overall mean lipid contents for all the data from both rough and calm conditions at each site were 4.11 $\pm$ 0.79 mg $lipid.cm^{-2}$ ($\pm$ 95% confidence limits, WFR site) and 2.85 $\pm$ 0.51 mg $lipid.cm^{-2}$ ($\pm$ 95% confidence limits, CP site) which were significantly different.

COLONY	CALM		ROUGH	
	WFR	CP	WFR	CP
1	2.63	2.99	6.21	2.32
2	4.90	3.23	3.49	3.68
3	4.42	2.98	3.66	1.98
4	4.54	2.34	3.58	2.33
5	2.74	4.22	4.93	2.57
Mean	3.85	3.15	4.37	2.58
S.D.	1.08	0.68	1.18	0.65

Comparisons:

Calm WFR vs Calm CP	t = 1.2265,	N.S.
Calm WFR vs Rough WFR	t = 0.7269,	N.S.
Rough WFR vs Rough CP	t = 2.9711,	P < 0.02
Calm CP vs Rough CP	t = 1.3549,	N.S.

Table 13. Porites porites from the West Fore Reef (WFR) and the Columbus Park (CP) sites: lipid content (mg lipid.cm^{-2})at both sites after 1 week of calm weather and after 1 week of rough weather. The lipid content of each colony is the mean of two replicates which are in turn the mean lipid content of two fragments. Statistical comparisons were carried out by the t-test, t values and the probability (P) for a significant difference are shown. N.S. = not significantly different at P = 0.05.

The specimens exposed to approximately 2, 4, 6, or 8 days of light received 53.08, 101.17, 149.33 and 197.17 hours of light with a total of 10.08 hours of darkness (because of a power cut). The mean lipid content between the start and the four light treatments and also between replicates were significantly different (Table 14). The mean lipid content after 2, 4, or 8, days in the light were significantly higher than the initial lipid content (SNK test, Table 14).

The mean lipid content after 5 days in darkness was not significantly different from the initial value (Table 14).

6.4.4. Discussion

The overall mean lipid contents of Porites porites are equivalent to 22.1% (WFR site, with 18.59 mg dry tissue.cm^{-2}) and 18.4% (CP site, with 15.51 mg.dry tissue.cm^{-2}) of the dry tissue biomass. These are lower than the equivalent figures of 33% for tropical anemones (Bergmann et al., 1956) and 34% for the coral Pocillopora capitata (Patton et al., 1977) and may be the result of a mass of deep, metabolically inactive tissue with a low lipid content in P. porites (cf. Chapter 4.9.2.1, where the same argument is used to explain the low tissue-specific respiration rate). If lipid contents greater than about 5% of the dry tissue biomass of marine invertebrates represents energy reserves rather than structural components (Giese, 1966), P. porites has 17.1% (WFR site) and 13.4% (CP site) of the dry tissue as lipid reserves. These are equivalent to lipid reserves of 125.6 J.cm^{-2} (WFR site) and 82.1 J.cm^{-2} (CP site) which are consistent with the tissue energy contents determined by wet oxidation (WFR site: 300.8 J.cm^{-2}; CP site 223.3 J.cm^{-2}; derived from Table 4) and the suggestion in Chapter 4.9.1 that the high ash content at the WFR site may be due to lipid volatilisation. With a daily energy consumption of 350 J.g^{-1}

		DAYS IN LIGHT				5 DAYS
COLONY	START	2	4	6	8	DARK
A	3.55	4.64	3.64	4.64	5.07	3.00
B	5.18	6.87	6.94	4.91	7.46	5.14
C	4.78	5.82	6.37	4.79	5.81	5.69
D	4.57	5.97	5.32	5.00	6.81	5.56
E	3.94	4.17	4.47	4.31	5.25	3.68
Mean	4.40	5.49	5.35	4.73	6.08	4.61
S.D.	0.66	1.09	1.35	0.27	1.03	1.21

Table 14. Porites porites from the West Fore Reef site: lipid content (mg lipid.cm^{-2}) at the start and after approximately 2, 4, 6 or 8 days of exposure to 83 μE.m^{-2}.s^{-1} and 5 days in darkness. The lipid content of each colony is the mean of two replicates which are in turn the mean lipid content of two fragments. The lipid content from the start and after 2, 4, 6 and 8 days of light and also between replicates were significantly different (two way ANOVA):

$$F_{(\text{Treatments})4,16} = 7.800 \quad P < 0.01$$

$$F_{(\text{Replicates})4,16} = 12.353 \quad P < 0.001$$

The means which are not significantly different are joined by lines (SNK test, with the error mean square from the two way ANOVA, P = 0.05).

Comparisons of lipid content from start and after 5 days in darkness (t-test):

t = 0.3407, d.f. = 8, P = 0.05: not significantly different

dry tissue (= 6.51 $J.cm^{-2}$, WFR site) and 250 $J.g^{-1}$ dry tissue (= 3.88 $J.cm^{-2}$, CP site) (from Figure 14), the reserves are sufficient to meet the colony energy demands for 19 days (WFR site) or 21 days (CP site) with no external source of energy.

The significant difference in overall mean lipid content of Porites porites between sites is the result of between-site differences after rough but not calm weather. Rough weather results in an increased sedimentation rate which would require greater sediment shedding activity by the corals. This requires mucus (Hubbard and Pocock, 1972) which contains muco-lipid (Krupp, 1982). Greater sediment shedding activities at the CP site might result in lipid loss as a biochemical component of mucus. In addition, if the energy demand for mechanical sediment shedding is supplied by an increased daytime respiration rate (Chapter 6.2.4) using translocated glycerol as the substrate, it is possible that there would be less photosynthetically fixed carbon remaining to synthesise new lipid since more would be catabolised as glycerol.

Porites porites from the WFR site exposed to 83 $\mu E.m^{-2}.s^{-1}$ for 24 hours a day and with a daily energy consumption of 350 $J.g^{-1}$ dry tissue (from Figure 14) would have a daily surplus of 139.5 $J.g^{-1}$ dry tissue = 2.59 $J.cm^{-2}$ (at 18.59 mg dry tissue.cm^{-2}), equivalent to 66 μg lipid.cm^{-2} (using the 'representative' P/I curves in Figure 11 and the mean respiration rate from Table 4). The mean lipid content significantly increased from the dark value after 8 days exposure to 83 $\mu E.m^{-2}.s^{-1}$ and similarly after 2d and 4d but not after 6d (Table 14). The observed increases in lipid content are greater than the predicted values (Table 15; except after 6 days in the light), and are more similar to the predicted increase in lipid content calculated assuming that all the gross photosynthetically fixed energy is channeled into lipid (Table 15).

	DAYS			
	2	4	6	8
OBSERVED	+1.09 *	+0.95 *	+0.33	+1.68 *
PREDICTED A	+0.08	+0.21	+0.35	+0.48
PREDICTED B	+0.51	+0.97	+1.43	+1.89

Table 15. Increase in lipid content (mg lipid.cm^{-2}) of P. porites from the West Fore Reef site after approximately 2, 4, 6 and 8 days exposure to 83 uE.m^{-2}.s^{-1}. The observed values are the increase in the mean lipid lipid content from the mean start lipid content (Table 14). The mean lipid content after 2, 4, and 8 days were significantly higher than the mean start lipid content (marked with *, SNK test, $P < 0.05$, see Table 14).

Predicted A : predicted increase in lipid content using the exact exposure to light (including the 10.08 hrs of darkness) and the energy budget in Chapter 4.

Predicted B : predicted increase in lipid content if the entire gross productivity is channeled into lipid synthesis.

If the daily *in situ* energy expenditure (from Figure 14) remains the same in continuous darkness, *Porites porites* from the WFR site would require 5 x 350 = 1750 $J.g^{-1}$ dry tissue during 5 days of darkness, equivalent to 0.82 mg $lipid.cm^{-2}$. Lipid reserves in *P. porites* did not decrease during 5 days in total darkness suggesting that lipid was not catabolised.

Although between treatment differences caused by between replicate variation was reduced by using 6 nubbins from the same 5 colonies for each treatment, the variation between colonies was still significant and reduced the resolution of the experiment. As the predicted and observed changes in lipid content are small (Table 15) compared to the between replicate variance (Table 14), the results should be interpreted with caution. However the high lipid content in *Porites porites* and the general increase in lipid reserves during illumination are consistent with a lipid based energy economy in corals (Patton *et al.*, 1977). Although surplus photosynthetically fixed energy (PFE) can be stored as lipid, the increase in lipid content was greater than anticipated, lipid reserves were not utilised during darkness, and *P. porites* had a higher lipid content at the WFR site where it had a smaller daily surplus of PFE than at the CP site. However, some of the apparent ambiguities in these results are similar to the observations made by Szmant-Froelich (1981) on the temperate coral *Astrangia danae*. She found that the proportion of photosynthetically fixed carbon diverted to lipid synthesis increased in well fed individuals, and she went on to show (Szmant-Froelich and Pilson, 1984) that the same coral appeared to preferentially catabolise the protein from their food for energy and stored the absorbed lipids.

The lack of a detectable lipid catabolism in Porites porites maintained in total darkness in seawater filtered through a net with a 50 µm pore size was very surprising. Lipid catabolism during starvation conditions has been shown for the symbiotic anemone Anthopleura elegantissima (Fitt and Pardy, 1981) and the temperate coral Astrangia danae (Szmant-Froelich and Pilson, 1980), and a good argument has been developed for the importance of lipid in the energy economy of algal-cnidarian symbioses (Patton et al., 1977; Patton and Burris, 1983; Kellogg and Patton, 1983; Battey and Patton, 1984).

The catabolism of translocated glycerol during the day, as described in Chapter 6.2.4. to explain the elevated daytime respiration rate, would alter the quantity of photosynthetically fixed carbon remaining for lipid storage. A similar effect might also occur if additional heterotrophic inputs were available (cf. Szmant-Froelich, 1981). In the present study both the aquarium and reef water contained unquantified amounts of zooplankton, bacteria, DOM etc. (including zooplankton < 50 µm) which have been shown to be used as a food source by various corals (see references in Chapter 1.2). The use of an, as yet unidentified, heterotrophic source of energy may explain the conservation of lipid reserves in the dark, the enhancement of lipid storage in the light and the higher lipid reserves at the WFR site.

The results of the analysis of lipid content in Porites porites were confounded by the high variance between replicates. However, the daily surplus of PFE in P. porites can probably be stored as lipid instead of being lost from the colony. The amount of PFE available for lipid storage may be altered by respiring a variable proportion of the

PFE as glycerol and by obtaining additional energy from heterotrophic sources. This topic clearly warrants further research, in particular to increase the resolution of the analysis, to identify the metabolic fate of lipid and also to quantify the alternative sources of heterotrophic nutrition.

CHAPTER 7 SUMMARY DISCUSSION

The biology of algal-cnidarian symbioses was reviewed in Chapter 1. The significance of autotrophy and heterotrophy in the nutritional strategy of corals has been a key research topic for over 60 years. Most recent studies have taken an integrated approach to this question by producing 'complete' energy or nutrient budgets (Davies, 1984; Falkowski et al., 1984; Muscatine et al., 1984; Szmant-Froelich and Pilson, 1984). These have typically involved a small number of measurements over a short time course and the input and utilisation of energy/nutrients have usually been balanced by subtraction.

In the present study energy budgets were calculated for the reef coral Porites porites at 10 m depth in two different environments. The prolonged observation period provided an opportunity to measure a greater number of energy requiring processes over a longer time period with a good expectation of balancing the energy budgets without recourse to subtraction. It was hoped that for the first time differences in the derivation, allocation and use of energy within the colony could be shown for the same species of coral in two different environments.

Study sites on the West Fore Reef (WFR) and at Columbus Park (CP) were chosen because they represented different environments. The CP site received significantly less light, had a marginally significant higher sedimentation rate and perhaps a higher nitrate concentration than the WFR site (Chapter 2). Porites porites occurred at both sites although it was less abundant and had a more spindly morphology at the CP site.

The energy budgets at both sites are broadly similar and Porites porites is autotrophic at 10 m depth on an 'ideal' day (Figure 14) and on almost every day of the year regardless of water clarity or daily surface IntPAR (Figure 15). There is no requirement for energy from zooplankton capture. This agrees with the model of Porter (1976) which predicted that the zooplankton capturing ability of corals was proportional to polyp diameter, whilst photosynthesis was maximised by a high surface area to volume ratio (SA:V). He further suggested that competition amongst Caribbean reef corals for limiting energy resources has lead to niche separation based on autotrophic vs heterotrophic ability. The Poritidae were predicted to show a tendency to autotrophy because of their high SA:V ratio and small polyps. Porter (1985) found support for his 1976 model in the Faviid coral Montastrea annularis which has larger polyps than members of the Poritidae and was unable to photosynthetically fix sufficient carbon to meet its demands at depths greater than 10 m.

In the present study the colony respiratory energy expenditure accounted for more than 85% of the total daily energy expenditure at both sites (Figure 14). The application of the CZAR methodology (Muscatine et al., 1981; see Chapter 1.2) or the use of simple P:R ratios (Chapter 1.2) would therefore have also shown that Porites porites is essentially autotrophic. However, the energy budget methodology provides information on the individual components of the energy budget which gives a better insight to the overall nutritional strategy of the coral and allows between site comparisons.

A major difference between Porites porites growing at the two sites is the photoadaptation to the reduced PAR regime at the CP site. This involves changes in the P/I response at the CP site (Figure 11) to ensure that the gross daily productivity is higher than at the WFR

site (Figure 14). Alpha is greater and I_k is lower at the CP site (Table 7) than at the WFR site. Although the mean colony P_{max} was similar at both sites (Table 7), it was reached *in situ* at the CP site but was unobtainable at the WFR site.

The changes in the P/I response of *Porites porites* at the CP site are similar to photoadaptive responses to shade in other corals (see Chapter 4.9.2.1), which suggests that the reduced PAR at the CP site has a similar effect. The photoadaptive mechanism is unclear in *P. porites* but does not involve changes in either pigment content or numbers of zooxanthellae as in other corals (see Chapter 4.9.1). Instead it is suggested that a reduction in the unit area tissue content (Table 4) of *P. porites* at the CP site occurs together with a thinning of the tissue layer, which results in a redistribution of the zooxanthellae into superficial tissue layers. This would reduce the shading of the algae. Since colony P_{max} can only be reached when all the zooxanthellae are at their saturating irradiance, a reduction in algal shading could account for the more pronounced plateau in productivity (Figure 11) and attainable P_{max} at the CP site. In addition, changes in the photosynthetic efficiency and pigment distribution within the zooxanthellae (*sensu* Dubinsky *et al.*, 1984) may also be important in photoadaptation at the CP site.

Although the largest use of photosynthetically fixed energy (PFE) in *Porites porites* at both sites was for colony respiration, both the magnitude and the proportion of PFE expended during respiration was reduced at the CP site compared to the WFR site (Figure 14). This is probably analogous to the depth- and shade-dependent reduction in colony respiration rate found in other corals (Chapter 4.9.2.1). The net result of a reduced respiratory energy expenditure is to leave more energy available for other processes which may be important for the survival of *P. porites* at the CP site.

For the first time *in vitro* measurements of the respiration rate of freshly isolated zooxanthellae have been incorporated into energy budgets for the same coral that the zooxanthellae were isolated from. This method has been critisised (Chapter 4.9.2.1), but the frequently used alternative of predicting algal respiration rate (Muscatine and Porter, 1977; Chapter 4.9.2.1) has not been experimentally verified. However, as the respiration rate of aposymbiontic *Porites porites* plus the respiration rate of zooxanthellae in an equivalent sized symbiotic colony of *P. porites* approximates the respiration rate of symbiotic colonies (Chapter 4.9.2.1), the *in vitro* respiration rate is probably the best estimate of the *in situ* zooxanthellae respiration rate.

Measurements of zooxanthellae respiration rate in *Porites porites* at both sites show that the reduced colony respiration rate of *P. porites* at the CP site is entirely a function of the animal tissue alone (Figure 14). Although the unit area tissue content was lower at the CP site, since the algal biomass was not measured, it is not possible to determine how much of the reduction in animal respiration is due to a reduction in animal tissue biomass and how much is due to a reduction in tissue specific respiration rates. The lower respiration rate of *P. porites* at the CP site may represent a reduced energy expenditure on cellular synthesis as suggested by Davies (1980) to explain the similar depth dependent reduction in respiration rate in Caribbean corals. Although this is supported by the lower growth rates of *P. porites* at the CP site (Table 8), the observations on the elevated daytime respiration rate may also have some relevance.

The respiration rate of *Porites porites* from both sites increased after exposure to light (Chapter 6.2.4). The respiration rate of freshly isolated zooxanthellae from *P. porites* was not enhanced by

light (Chapter 6.2.4) and the elevated post-illumination respiration rate of symbiotic colonies must therefore be a function of the host tissue alone. In the present study the elevated post-illumination respiration rate of P. porites was taken as the best estimate of the respiration rate in the light. As a working model it is suggested that light enhancement of metabolism leads to an increased daytime energy expenditure which is manifest as a higher daytime respiration rate of the host tissue. Drawing on the previously documented importance of glycerol in the translocation of carbon to the host (see Chapter 1.2; and Battey and Patton, 1984) and more recently the demonstration of the accumulation of glycerol in the host tissue of Condylactis gigantea during respiratory inhibition by cyanide (Battey and Patton, in press) it is suggested that glycerol is the substrate for the elevated daytime respiration.

The greatest increase in the post-illumination respiration rate was found in Porites porites from the the CP site (Figure 16) where specimens also had the lowest dark respiration (as measured after overnight darkness; Table 7). Conversely specimens from the WFR site had a higher dark respiration rate (Table 7) but showed a smaller increase in respiration rate after a light period (Figure 16).

Some of the ambiguities in these results can be explained by suggesting that the differences in the dark respiration rate and the differences in the post illumination respiration rate re present the same effect. A high overnight energy expenditure would result in a high dark respiration, which might leave little scope for a further light dependent increase in energy expenditure. The increase in the post-illumination respiration rate would then be small. This agrees with the results obtained for Porites porites at the WFR site. Conversely, a low overnight energy expenditure would result in a low

dark respiration, but there may then be a greater scope for a light dependent increase in energy expenditure. There would then be a large increase in the post-illumination respiration rate. This agrees with the results obtained for Porites porites at the CP site. This could clearly represent an important differential energy utilisation by P. porites at the two sites.

The significance of an elevated post-illumination respiration rate in relation to the energy budgets and the different environmental conditions at the two sites cannot be fully evaluated until the the effects of an increased respiration rate on the determinations of P/I curves are resolved. More importantly, the processes that are possibly enhanced by light and which could account for the proposed differential energy expenditure at the two sites need to be identified. However, the present energy budgets together with the current literature provide at least two potential answers to these questions which could provide fruitful areas for future research.

Firstly, Porites porites expends the greatest amount of energy on tissue growth at the WFR site (Figure 14), where it also has the greatest mass accretion of $CaCO_3$ (Table 8), which is the end result of calcification. Calcification in corals is enhanced in light (Pearse and Muscatine, 1971; and Chapter 1.2), but slowly decreases at the end of a light period rather than stopping instantaneously (Chalker, 1977). The effects of light on calcification have some similarities to the effects of light on the respiration rate of P. porites. The colony respiratory energy expenditure as measured in the present study should include at least some of the energy requirements of calcification since calcification probably proceeded in the respirometry chamber. However, the intriguing possibility exists that both the higher dark respiration rate of P. porites at the WFR site and also the elevated daytime respiration rate at both sites represents the energy

requirements of calcification. To date the energetics of calcification in any scleractinian have never been measured. The relationship between calcification and respiration clearly offers an exciting new avenue for research.

Secondly, the uptake of some mineral nutrients by corals is light dependent (Muscatine, 1980b; also Chapter 1.2) and requires energy where ions are transported across membranes by active transport. The higher daytime energy expenditure of Porites porites may represent the cost of mineral nutrient uptake. If this is correct, the proportionately higher daytime energy expenditure of P. porites at the CP site may reflect the slightly different nutrient regime at this location.

The pooled growth rates for Porites porites (Table 8) obscure differential time- and size- dependent effects at each site (Chapter 4.4.2). These suggest that linear and radial branch extension occur at the same rate at the WFR site but that branch extension is favoured over radial increase at the CP site. Although this has little direct implication for the energy budgets, it may have greater ecological importance in ensuring that the living tissues remain above the accumulating sediments. In addition nubbins at both sites showed signs of a reduced growth rate towards the end of the observation period suggesting that the energy allocated to growth may be overestimated. As branches of P. porites growing in situ had similar amounts of living tissue to experimental nubbins they may show a similar size- or age- specific reduction in growth rates, and the lower rates may therefore be more representative of in situ growth.

Paradoxically, even with an apparent surplus of energy on nearly every day of the year (Figure 15), Porites porites at both sites has an almost insignificant expenditure on growth and reproduction. Conversely, Conover (1978) showed in a summary of 14 aquatic

invertebrates that on average 21% of the assimilated energy was used for growth and 15% for reproduction. Davies (1984) explained a similar low utilisation of energy as tissue growth in Pocillopora eydouxi by suggesting that corals may have a surplus of photosynthetically derived compounds which have to be released as mucus, whilst their growth is limited by the availability of nitrogenous compounds. Although nutrient limitation in P. porites finds some circumstantial support in the present study, the magnitude and fate of the apparent surplus energy requires reappraisal in the light of new findings.

The suggestion that a large proportion of the daily surplus energy is lost from corals as mucus (Davies, 1984) is supported by the measurement of substantial loses of photosynthetically fixed carbon from corals (Cooksey and Cooksey, 1972) as coral mucus (Crossland et al., 1980). It is also consistent with the overt release of coral mucus as flocs and slime and the realisation of the potential trophic importance of coral mucus in the marine environment (Benson and Lee, 1975). However, this scenario has a number of inconsistencies. Mucus contains a wide assortment of macromolecular components (see Chapter 4.9.2.5) which represents considerable anabolism of the initial products of photosynthesis (eg. glucose). Nitrogen may become incorporated into these macromolecules and is then lost with the mucus, and yet nitrogen has repeatedly been shown to be limiting in the tropical marine environment (Muscatine, 1980b). In addition the energy content of pure mucus is low (Krupp, 1982) which is contrary to the early emphasis on the trophic significance of mucus (Benson and Lee, 1975), whilst the significant lipid content of mucus (Crossland et al., 1980) may have been due to contamination (Krupp, 1982). It seems surprising that corals should synthesise a complex molecular mixture to lose carbon and energy when the end product has a low

energy content, and when a more direct route exists from the zooxanthellae to the environment as low molecular weight compounds, which contain little or no nitrogen (eg. glycerol).

In the crucial experiment of Crossland et al (1980) (cited by Davies (1984) to support his theory for the route of excess energy), branch tips (up to 3.5 cm long) of Acropora acuminata were incubated in 5 ml plastic syringes and 40% of the net photosynthetically fixed carbon was recovered as "mucus" from the incubation water by adsorption onto celite. Celite is a siliceous compound (SiO_2) which adsorbs many polar organic molecules by hydrogen bonding onto silanol groups (SiOH) which form in water (Iler, 1979). Although Crossland et al. (1980) collected mucus, its composition may have been unrepresentative of mucus released in situ because of possible stress involved in the incubation process, whilst low molecular weight polar compounds including glycerol and amino acids would also have been adsorbed by the celite. These would have been indistinguishable from the labelled mucus polysaccharides. The loss of about 50% of the photosynthetically fixed carbon from Siderastrea siderea and Montastrea annularis (Cooksey and Cooksey, 1972) and 50% from shade adapted Stylophora pistillata (Muscatine et al., 1984) may also be due to low molecular weight compounds rather than macromolecular mucus.

The release of soluble or particulate macromolecular mucus from Porites porites was not detected in the present study although a large surplus of energy had been predicted by subtraction (Figure 14). Whilst it remains likely that at least some of the surplus energy may be lost as low molecular weight compounds, the alternative hypothesis that surplus energy was lost as mucus tunics (Chapter 4.9.2.5; also Edmunds and Davies, 1986) was refuted by their low energy content (Chapter 6.3.3). However, mucus tunics may have a more important effect on the energy budgets if they result in a decrease in

photosynthesis. The selective advantage of mucus tunics would have to out-weigh this handicap, and the proposed retention of gametes may be sufficiently important. Clearly the effect of tunics on the annual productivity needs to be fully investigated.

The magnitude of the daily surplus of energy in Porites porites as predicted from the methodology in Chapter 4 may be substantially reduced by an elevated daytime respiration rate, mucus tunics or lipid storage as described in Chapter 6. In particular, the elevated daytime respiration rate may account for a major portion of the apparent surplus of energy, although this requires further work before the full significance can be calculated.

By combining the energy budget studies on Porites porites with concurrent studies of lipid content in the same species it has been possible to show that the daily surplus of energy can be stored as lipid. However, lipid cannot be stored indefinitely and must be utilised at some stage. In Chapter 5 it was suggested that the ability to survive a run of 'bad' days with low surface daily IntPAR and low transmission of PAR to 10 m depth could be important in determining the survival of P. porites at the two sites. Lipid reserves could supply the energy requirements on these days. Although calculations showed that P. porites at both sites has sufficient lipid reserves to survive more than 19 days with no external source of energy (Chapter 6.4.4), during 1983-84 there were only 9 consecutive days with insufficient daily surface IntPAR for full autotrophy under the most stringent conditions of energy demands and turbidity (at the WFR site, transmission = 18.3%). The important 'starvation' experiment carried out by maintaining P. porites in total darkness to approximate 'bad' days showed that lipid was not catabolised under these conditions, even though a decrease in lipid content was predicted.

The recorded increase in lipid content in P. porites, under conditions which were predicted to supply surplus energy, can only be reconciled with the apparent absence of lipid metabolism during starvation by identifying both alternative uses for the accumulating lipid together with an alternative energy source during starvation. The loss of lipid as the muco-lipid component of mucus used during sediment shedding offers one potential use for lipid. The high sedimentation rate recorded at the CP site may therefore result in a significant loss of lipid whilst shedding sediments in addition to the increased energy expenditure involved in the process. This would go someway to explaining the contradictory observation that P. porites at the CP site has a higher daily surplus of energy but a lower lipid content than at the WFR site.

The autotrophic input to corals can only supply the carbon requirements of the colony and other essential nutrients must be obtained from alternative sources. The survival of Porites porites during a period of darkness in filtered seawater without the use of lipid energy reserves, together with the greater than anticipated accumulation of lipid during light incubation (Table 15) suggests that P. porites can obtain energy and nutrients from the sea water.

Both Franzisket (1970) and Johannes (1974) carried out similar experiments to show that hermatypic corals could grow in the light in filtered seawater (FSW, 1 µm) and Franzisket further showed that corals atrophied or died during 60 days of darkness in FSW (1 µm). These authors interpreted their results to emphasise the autotrophic ability of corals. However, their results also imply that particulate food greater than 1 µm in size was unnecessary for growth in the light. Franzisket's results can also be interpreted to suggest that

the organic material remaining in 1 μm FSW was inadequate to support growth in the dark, although this effect may be more complex because of the absence of light-promoted nutrient uptake in the dark incubations.

In the lipid content experiments in the present study, Porites porites was maintained in seawater filtered through a net with a 50 μm pore size which is considerably larger than the filter used by Franzisket (1970) and Johannes (1974). It is posible that the particulate material which remains in 50 μm FSW (which would include bacteria) can provide a source of energy and nutrients to ensure the survival of P. porites in darkness. The removal of this fraction in the dark experiments of Franzisket (1970) may have lead to the atrophy and death of his corals.

This is clearly a speculative explanation for the ambiguities between the results of the lipid content experiments in the present study and the results of Franzisket (1970) and Johannes (1974). However, it is supported by the apparent digestion of bacteria by corals (Sorokin, 1973; Chapter 1.2) and the use of DOM (Lewis and Smith, 1971; Chapter 1.2) and the cognate observations of Goreau et al (1981) that larval and juvenile Porites porites atrophied and/or died when maintained in "membrane filtered" seawater in the light. This area of coral nutrition clearly requires further research.

The original objectives of the study were firstly to produce balanced energy budgets without recourse to subtraction for Porites porites growing in two environments, and secondly to use the budgets to identify between-site differences in energy derivation, allocation and use. The energy budgets developed in Chapter 4 have a large surplus of energy determined by subtraction. However, the topics

investigated in Chapter 6 show that the 'surplus' energy may be stored or utilised for previously unidentified functions. Any truly surplus energy may be lost as low molecular weight compounds rather than as mucus as previously supposed.

The second objective of the study has resulted in energy budgets for Porites porites which show that this species can be autotrophic on nearly every day of the year at 10 m depth and at two quantitatively different sites. However, the apportioning of energy within the colony differs between sites and can be related to the environmental conditions.

Adaptations at a site with a low irradiance, a high sedimentation rate and a slightly enhanced nutrient regime has involved changes in the photosynthesis/irradiance responses, together with a reduction in animal respiration rate and preferential linear branch growth. The animal respiration rate is enhanced by light at both sites and represents a previously unaccounted for energy expenditure. Between-site differences in this effect suggest that different processes may be responsible for the increased energy expenditure at each site.

Although the present study shows that Porites porites can adapt to a reduced irradiance and high sedimentation rate to maintain an autotrophic status, this may not be true over its entire range of environments. In deeper water or extremely shaded locations P. porites may be more dependent on heterotrophic sources of nutrition.

Throughout this study it has been assumed that the zooplankton input to Porites porites is negligible. This was based on the absence of visible zooplankters in the guts of a large number of polyps (Chapter 4.5). By concentrating on the autotrophic input, P. porites has been shown to be essentially autotrophic in terms of energy. This agrees with the prediction made by Porter (1976) and a number of previous studies which have also shown corals to be essentially

autotrophic eg. Davies (1984), Kawaguti (1937) and Muscatine et al. (1984). However, when corals have a large surplus of photosynthetically fixed carbon as in the present study (Figure 14), and when they show ability to adapt to maintain their autotrophic status under adverse conditions (as at the CP site), it would seem unlikely that their distribution, growth and success can be explained by energetics alone. Circumstantial evidence for the use of DOM and or particulate material less than 50 μm in size as a food source by P. porites has been obtained in the present study (Chapter 6). The possible role of infrequent zooplankton capture in supplying inorganic nutrients, vitamins or essential amino acids has been noted elsewhere (Johannes et al., 1970). In spite of the difficulties in quantifying and determining the significance of the heterotrophic inputs available to scleractinians, it seems likely that the next major step forward in scleractinian nutrition will concern the supply of nutrients other than carbon or energy.

Although corals have never been quantitatively shown to be the "superbly efficient and voracious carnivores" as described by Goreau et al. (1971), future research may show that whilst heterotrophy contributes only a small proportion of the colonies energy demands, heterotrophy assumes greater importance than autotrophy by supplying non carbon nutrients to the corals.

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APPENDIX I

Appendix I, Table 1. Porites porites at the West Fore Reef site: net photosynthesis vs irradiance data which were used to calculate best-fit hyperbolic tangents for each nubbins as described in Chapter 3.7. For each of 1 - 10 specimens the dry tissue content (mg) and the net photosynthesis ($\mu l O_2 . g^{-1}$ dry tissue.min^{-1}) at each of 10 irradiances (I, $\mu E . m^{-2} . s^{-1}$), together with dark respiration (at I = 0.0) are shown. A net oxygen uptake is indicated by a negative sign, release of oxygen by a positive sign. Dashes indicate where the data points were unreliable or unobtained. The mean, the standard deviations and sample sizes for the dry tissue content and for the net photosynthesis at each irradiance are shown in the three columns at the right hand side of the table. The photosynthetic characteristics from the best fit curves are given in the last 4 rows. The symbols I_k ($\mu E . m^{-2} . s^{-1}$), Alpha ($\mu l O_2 . g^{-1}$ dry tissue.$min^{-1} . \mu E^{-1} . m^2 . s$), P^{net}_{max} ($\mu l O_2 . g^{-1}$ dry tissue.min^{-1}) and r are explained in the methods (Chapter 3.7) The values of I_k, alpha and P^{net}_{max} beneath the 'mean' column are the photsynthetic characteristics for the 'representative' P/I curve (see Figure 11) calculated for the data in the 'mean' column.

SPECIMEN	1	2	3	4	5	6	7	8	9	10	MEAN	S.D.	N
DRY TISSUE	314	478	226	287	322	329	277	300	365	403	330	71	10
I													
0.0	-13.62	-8.70	-10.61	-9.74	-9.02	-6.32	-11.49	-23.45	-6.75	-7.11	-10.68	5.02	10
28.5	-5.88	-5.46	-1.46	-3.81	-3.60	-4.17	-3.00	-8.48	-2.09	-4.14	-4.21	2.01	10
50.0	-2.77	-3.88	+3.26	+2.21	-0.71	+0.45	+4.34	-0.67	+3.13	-1.85	+0.28	2.81	10
61.0	+1.11	-2.55	+5.08	+2.97	+1.83	+2.44	+6.41	+1.76	+4.85	-0.14	+2.38	2.64	10
103.0	+1.19	-0.67	+15.01	+10.50	+12.08	+10.66	+17.26	+9.18	+11.08	+5.39	+9.17	5.68	10
171.0	+5.74	+3.75	+27.56	+18.33	+18.72	+15.13	+24.01	+20.39	+20.40	+10.72	+16.48	7.68	10
198.0	+7.82	+6.66	+32.27	+24.21	+27.07	+25.19	+35.70	+23.26	+25.54	+14.39	+22.21	9.67	10
235.0	+7.82	+7.14	+32.27	+20.78	+34.15	+30.23	+48.69	+27.79	+25.81	+19.29	+25.40	12.46	10
285.0	+7.82	+9.50	+36.97	+28.13	+21.69	+36.79	+31.06	+41.24	+37.75	+24.86	+27.58	11.71	10
300.0	+7.82	+12.64	+39.06	+30.79	+23.53	+29.39	+50.85	+47.94	+37.75	+30.60	+31.04	13.84	10
330.0	—	+14.11	+39.06	+30.08	+24.24	+45.96	+50.85	+47.94	+37.75	—	+36.25	12.69	8
I_k	111	610	197	223	147	1070	250	520	407	1020	334		
Alpha	0.16	0.07	0.27	0.19	0.26	0.15	0.27	0.22	0.17	0.12	0.17		
p^{net}_{max}	+9.20	+35.00	+43.90	+35.10	+28.00	+148.70	+57.70	+99.70	+62.50	+111.80	+47.91		
r	0.945	0.990	0.997	0.991	0.958	0.981	0.964	0.985	0.995	0.989	0.994		

Appendix I, Table 1

Appendix I, Table 2. Porites porites at the Columbus Park site: net photosynthesis vs irradiance data which were used to calculate best-fit hyperbolic tangents for each nubbin as described in Chapter 3.7. For each of 1 - 10 specimens the dry tissue content (mg) and the net photosynthesis ($\mu lO_2.g^{-1}$ dry tissue.min^{-1}) at each of 11 irradiances (I, $\mu E.m^{-2}.s^{-1}$), together with dark respiration (at I, 0.0) are shown. A net oxygen uptake is shown by a negative sign, release of oxygen by a positive sign. Dashes indicate where the data points were unreliable or unobtained. The mean, the standard deviations and sample sizes for the dry tissue content and the net photosynthesis at each irradiance are shown in the three columns at the right hand side of the table. The photosynthetic characteristics from the best fit curves are given in the last 4 rows. The symbols I_k ($\mu E.m^{-2}.s^{-1}$), Alpha ($\mu lO_2.g^{-1}$ dry tissue.min^{-1}.$\mu E^{-1}.m^2.s$), P^{net}_{max} ($\mu lO_2.g^{-1}$ dry tissue.min^{-1}) and r are explained in the methods (Chapter 3.7). The values for I_k, alpha and P^{net}_{max} beneath the 'mean' column are the photosynthetic characteristics for the 'representative' P/I curve (see Figure 11) calculated for the data in the 'mean' column.

SPECIMEN	1	2	3	4	5	6	7	8	9	10	MEAN	S.D.	N
DRY TISSUE	215	182	175	389	165	159	158	188	204	158	199.3	69.51	10
I													
0.0	-4.11	-7.76	-10.81	-4.52	-10.15	-7.30	-7.56	-5.47	-6.26	-11.31	-7.53	2.55	10
25.0	+1.20	-2.41	-4.55	-0.54	-6.79	+1.13	+1.06	+1.37	+0.79	+2.76	-0.60	3.04	10
45.0	+5.94	+8.12	+1.17	+2.31	+1.45	+9.86	+9.80	+7.59	+4.91	+11.17	+6.23	3.67	10
54.0	+7.52	+13.90	+7.52	+5.44	+1.79	+13.14	+14.91	+11.58	+8.15	+13.98	+9.79	4.36	10
95.0	+16.92	+26.32	+19.73	+9.78	+19.03	+12.38	+23.35	+15.95	+15.46	+23.01	+18.19	5.14	10
140.0	+22.21	+44.58	+36.97	+14.04	+29.76	+32.83	+30.59	+28.16	+23.82	+30.09	+29.31	8.31	10
180.0	+30.15	+53.85	+52.63	+21.54	+39.52	+39.97	+36.09	+28.59	+26.02	+33.13	+36.15	10.69	10
195.0	+38.06	+45.38	+62.03	+21.54	+61.03	+45.76	+37.85	+33.79	+35.19	+33.13	+41.38	12.60	10
240.0	+36.58	+53.09	+75.70	+19.78	+66.03	+45.76	+60.44	+38.11	+37.04	+41.63	+47.42	16.53	10
275.0	+36.58	+58.09	+75.70	---	+66.03	+45.76	+60.44	+38.11	+45.22	+49.61	+52.84	13.14	9
300.0	+36.58	+70.79	+75.70	+22.17	+66.03	+45.76	+60.44	+38.11	+44.32	+49.61	+50.95	16.98	10
430.0	+43.66	---	---	+22.17	---	---	+60.44	+38.11	+45.30	+49.61	+43.22	12.74	5
I_k	195	197	300	148	304	180	238	160	232	191	174		
Alpha	0.25	0.41	0.42	0.16	0.37	0.33	0.32	0.29	0.24	0.30	0.35		
p^{net}_{max}	+44.1	+71.7	+111.6	+23.4	+99.7	+52.7	+69.0	+39.7	+50.1	+51.3	+51.9		
r	0.991	0.986	0.993	0.989	0.984	0.982	0.981	0.994	0.992	0.985	0.986		

Appendix I, Table 2

SPECIMEN	DAY 0	DAY 21	DAY 42	DAY 63
1	4.046	4.457	4.960	5.458
2	6.507	7.193	7.974	8.570
3	8.664	9.446	10.106	10.380
4	5.455	5.911	6.444	6.935
5	—	8.868	9.740	10.540
6	4.708	5.019	5.485	5.821
7	4.907	5.202	5.664	5.950
8	4.270	4.780	5.398	5.854
9	8.037	8.896	9.995	10.890
10	5.562	6.107	6.853	7.343
11	6.815	7.784	8.756	9.671
12	10.354	11.353	12.362	13.327
13	7.736	8.264	8.904	9.453
14	6.551	7.067	7.555	7.861

Appendix I, Table 3. Porites porites at the West Fore reef site. Skeletal weight (g) of nubbins used for the measurement of growth over a total of 63 days. The skeletal weights were obtained from buoyant weighed nubbins and the dry tissue content obtained from the relationship:

$$y = 0.7437x + 1.9034$$

where $y = \log_{10}$(mg dry tissue)

$x = \log_{10}$(g skeleton)

The weight of specimen 5 on day 0 was not measured as this was obtained from a previous group of nubbins which had been on the reef about 7 days when the rest of the group were at day 0. The data from specimen 5 (for day 21, 42, 63) were used in calculations of the mean growth rates over the whole period but was omitted from the ANOVA analyses.

SPECIMEN	DAY 0	DAY 23	DAY 44	DAY 64	DAY 99
1	8.762	9.106	9.577	9.674	10.002
2	4.414	4.898	5.315	5.494	5.755
3	7.026	7.511	7.950	8.060	8.361
4	6.019	6.390	6.726	6.981	7.535
5	7.020	7.202	7.452	7.717	8.108
6	5.568	6.113	6.450	6.572	6.885
7	5.457	6.057	6.440	6.662	6.950
8	5.495	5.789	6.091	6.255	6.499
9	4.408	4.838	5.187	5.361	5.675
10	4.741	5.200	5.527	5.691	5.856
11	4.713	5.074	5.410	5.577	5.845
12	7.843	8.253	8.558	8.650	8.865

Appendix I, Table 4. Porites porites at the Columbus Park site. Skeletal weights (g) of nubbins used for measurement of growth over a total of 99 days. These skeletal weights were obtained from buoyant weighed nubbins and the dry tissue content was obtained from the relationship:

$$y = 1.1145x + 1.5547$$

where $y = \log_{10}(\text{mg dry tissue})$

$x = \log_{10}(\text{g skeleton})$

	DAYS								
	10.5			31.5			52.5		
SPEC	DT	TSTG	TSSG	DT	TSTG	TSSG	DT	TSTG	TSSG
1	245	2.7	79.9	261	3.1	91.8	278	2.9	85.3
2	333	3.4	98.1	358	3.5	103.9	382	2.6	74.3
3	408	3.0	91.3	433	2.5	72.6	449	1.0	29.1
4	294	2.4	73.9	310	2.8	81.9	328	2.5	71.3
5	*	*	*	417	3.3	99.6	445	3.0	85.6
6	266	2.0	55.7	279	2.7	79.5	293	1.8	54.6
7	272	1.8	51.7	285	2.7	77.2	298	1.4	45.7
8	254	3.4	95.6	274	3.7	107.4	292	2.5	74.4
9	388	3.7	105.4	422	4.2	124.0	455	3.1	42.6
10	299	3.0	86.8	321	3.7	110.7	342	2.4	68.2
11	349	4.5	132.2	382	4.1	121.2	414	3.6	105.3
12	469	3.5	101.4	503	3.2	95.5	537	2.9	85.6
13	372	2.3	67.6	392	2.7	77.7	413	2.2	63.3
14	332	2.4	74.0	349	2.3	66.6	362	1.3	40.3

Appendix I, Table 5. Daily tissue-specific growth rates for P. porites at the West Fore Reef site for the median day of each measurement period (first = 10.5 days, second = 31.5 days, third = 52.5 days). For each of 14 specimens (SPEC) the dry tissue content (DT, mg) is the mean of the dry tissue content of nubbins at the start and end of each measurement period. TSTG = tissue-specific tissue growth ($mg.g^{-1}$dry $tissue.d^{-1}$), TSSG = tissue-specific skeletal growth ($mg.g^{-1}$dry $tissue.d^{-1}$). * = data not comparable for this period, see Appendix I, Table 3.

	DAYS											
	12			33.5			54			81.5		
SPEC	DT	TSIG	TSSG	DT	TSIG	TSSG	DT	TSIG	TSSG	DT	TSIG	TSSG
1	412	1.9	36.3	433	2.6	51.8	448	0.6	10.8	459	1.1	20.4
2	200	5.0	105.5	221	4.3	89.9	236	1.9	38.0	246	1.4	30.3
3	327	3.2	64.5	350	3.1	59.7	365	0.7	15.1	375	1.1	23.0
4	274	2.9	58.9	292	2.8	54.9	307	2.1	41.6	327	2.5	48.4
5	320	1.2	24.8	330	1.7	36.1	343	2.0	38.6	360	1.6	31.0
6	257	4.6	92.4	278	2.7	57.7	289	1.0	21.1	300	1.5	29.8
7	253	5.0	103.3	277	3.3	66.0	292	1.9	38.1	304	1.3	27.1
8	247	2.5	51.8	262	2.7	55.0	273	1.5	30.0	283	1.2	24.6
9	198	4.6	94.7	217	3.7	76.8	229	1.8	38.0	241	1.8	37.3
10	214	4.5	93.3	233	3.3	66.8	245	1.6	33.5	253	0.9	18.6
11	211	3.5	74.6	227	3.4	70.5	240	1.9	34.9	251	1.5	30.6
12	367	2.5	48.6	385	2.0	37.7	395	0.5	11.7	403	0.7	15.3

Appendix I, Table 6. Daily tissue-specific growth rates for P. porites at the Columbus Park site for the median day of each measurement period (first = 12 days, second = 33.5 days, third = 54 days, fourth = 81.5 days). For each of 12 specimens the dry tissue content (DT, mg) is the mean of the dry tissue content of nubbins at the start and end of each measurement period. TSIG = tissue-specific growth ($mg.g^{-1}$dry $tissue.d^{-1}$), TSSG = tissue-specific skeletal growth ($mg.g^{-1}$dry $tissue.d^{-1}$).

	WFR		CP	
DATE	NOS. FECUND	NOS. WITH PLANULAE	NOS. FECUND	NOS. WITH PLANULAE
13-11-84	0	0	0	0
21-11-84	0	0	0	0
27-11-84	1	0	4	0
03-12-84	0	0	16	16
11-12-84	22	7	8	8
18-12-84	2	0	35	3
31-12-84	16	4	32	8
06-01-85	12	2	23	14
13-01-85	32	4	8	2
20-01-85	20	5	13	1
27-01-85	35	17	20	11
03-02-85	20	7	23	7
12-02-85	22	3	19	5
17-02-85	38	14	12	7
26-02-85	38	27	27	6
03-03-85	38	26	29	24
12-03-85	26	0	13	2
19-03-85	36	7	31	8

Appendix I, Table 7. Reproductive data for Porites porites at both the West Fore Reef (WFR) and Columbus Park (CP) sites. The number of fecund polyps and the number of polyps containing mature planulae are shown for each sampling period. 40 polyps were examined at each sampling period.

EXPERIMENTAL				CONTROL		
REPLICATE	R1	R2	% ELEVATION	REPLICATE	R1	R2
1	11.64	12.81	10.1	1	7.04	7.68
2	5.18	8.98	73.4	2	10.95	8.46
3	8.92	10.28	15.3	3	7.18	7.45
4	8.06	11.61	44.1	4	8.78	8.54
5	7.31	8.36	14.4	5	8.40	7.68
6	7.99	14.90	86.5	6	7.69	8.02
				7	7.28	7.69
MEAN	8.18	11.16	39.3%	8	7.08	8.96
S.D.	2.11	2.46	(8.2% to 76.4%)	9	5.88	6.56
				10	8.89	8.09
				MEAN	7.92	7.91
				S.D.	1.40	0.67

Appendix I, Table 8. Porites porites from the West Fore Reef site: comparisons of the respiration rate ($\mu l O_2 . g^{-1}$ dry tissue.min^{-1}) before (R1) and after (R2) a 3 hour exposure to light (experimental treatment) or to darkness (control treatment). The mean and 95% range is shown for the percentage data and is calculated from arcsine transformed data.

REPLICATE	EXPOSURE TO LIGHT (MINUTES)				
	0	10	20	40	80
1	4.84	4.78	6.79	7.10	8.68
2	6.27	6.78	7.15	8.88	9.35
3	7.12	6.55	7.29	8.69	10.11
4	5.89	6.77	8.92	8.04	8.73
5	5.65	8.41	8.67	9.39	10.07
S.D.	0.84	1.29	0.96	0.88	0.69
MEAN	5.95	6.66	7.76	8.42	9.39

Appendix I, Table 9. Porites porites at the West Fore Reef site: elevated respiration rate ($\mu l O_2 . g^{-1}$ dry tissue.min^{-1}) after exposure to 140 $\mu E . m^{-2} . s^{-1}$ for 0, 10, 20, 40 and 80 minutes. Respiration rates were significantly different between replicates and between treatments, two way ANOVA:

$$F_{(treatments)4,16} = 20.61, \quad P < 0.001$$

$$F_{(replicates)4,16} = 6.01, \quad P < 0.01$$

The means for each treatment which are not significantly different (SNK test, using the error mean square from the two way ANOVA, P = 0.05) are underlined.

REPLICATE	EXPOSURE TO LIGHT (MINUTES)				
	0	10	20	40	80
1	9.43	9.71	13.05	15.30	15.07
2	5.96	6.96	8.91	12.15	13.14
3	6.99	8.46	8.63	11.24	13.31*
4	5.95	7.62	9.02	12.95	14.80
5	6.47	7.62	10.08	12.76	13.40
MEAN	6.96	8.07	9.94	12.88	13.94
S.D.	1.45	1.06	1.83	1.51	0.91

Appendix I, Table 10. Porites porites at the Columbus Park site: elevated respiration rate ($\mu l O_2 . g^{-1}$ dry tissue.min^{-1}) after exposure to 140 $\mu E . m^{-2} . s^{-1}$ for 0, 10, 20, 40 and 80 minutes. *: estimation of a missing value used in ANOVA (Sokal and Rohlf, 1969). Respiration rates were significantly different between replicates and between treatments, two way ANOVA;

$$F_{(treatments)4,15} = 82.74, \quad P < 0.001$$

$$F_{(replicates)4,15} = 7.60, \quad P < 0.01$$

All the means are significantly different from each other (SNK test using the error mean square from the two way ANOVA, $P < 0.05$).

APPENDIX II

Modelling surface PAR throughout a day from recordings of daily surface integrated photosynthetically active radiation (IntPAR)

In order to calculate both the daily productivity of P. porites for the range of daily light conditions experienced over a whole year at Discovery Bay, and the annual productivity (Chapter 5), recordings of daily photosynthetically active radiation (PAR) over a year are required. The only data available are in the form of daily integrated PARs (IntPAR) recorded by Porter (1985). Since photosynthesis can only be calculated from instantaneous PAR (Chapter 5.2), it was therefore necessary to predict the daily surface PAR curve corresponding to the recorded daily surface IntPAR values. This was then used to predict the PAR at 10 m depth and hence the in situ productivity at each site as described in Chapter 5.2.

A generalised sine curve was used to model the surface PAR based on the equation:

$$y = \text{Sin } ax \qquad 1.$$

where a is a constant.

The recordings of daily surface IntPAR values were assumed to have occurred on a 12 hour day with a sine wave distribution of daily surface PAR and a maximum irradiance ($E.m^{-2}.h^{-1}$) defined as I_{max}. To specifically model surface PAR throughout a day, equation 1 was modified to:

$$I = I_{max} \times \text{Sin}[(3.142 \times T)/D] \qquad 2.$$

where I = irradiance ($E.m^{-2}.h^{-1}$) at time T (hours after sunrise), D = daylength (12 hours) and (3.142 x T)/D changes the time of day into radians.

The integral of equation 2 between T = 0 and T = 12 gives the area beneath the sine curve which is equivalent to the daily surface IntPAR.

The integral of the generalised sine curve (equation 1) is:

$$\int \text{Sin } ax.dx = -a^{-1}\text{Cos } ax + C$$

where C is the integration constant. Therefore:

$$\int_{T=0}^{T=12} I_{max} \times \text{Sin}[(3.142 \times T)/D]\ dT =$$

$$I_{max}\{(-3.142/D)^{-1} \times \text{Cos}[(3.142xT)/D) \times T\}_{T=0}^{T=12}$$

and finally, since IntPAR is the area under the sine curve and if D = 12 hours:

$$\text{IntPAR} = 7.6384 \times I_{max}$$

hence:

$$I_{max} = 0.1309 \times \text{IntPAR} \qquad 3.$$

By substituting a specific value for daily surface IntPAR in equation 3 it is possible to obtain a value for the corresponding unknown I_{max}. By substituting this value of I_{max} in equation 2, a unique sine curve is defined which has an area beneath the curve between T = 0 and T = 12 hours exactly equivalent to the specific value of surface IntPAR used to obtain the I_{max}. Curves of this form were used to predict the daily surface PAR which were than used to calculate the productivity at 10 m depth as described in Chapter 5.2.