The role of sediments in epilithic algal communities on coral reefs

Thesis submitted by

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Abstract

Sediments comprise a mobile, physical component of all reef habitats. Forereef sediments can become trapped within epilithic algal communities (EACs) of hard reef substrata, however, the mechanisms of this process and the role of sediments in modifying EACs is poorly known. Sediment loads on reef substrata can vary naturally and increase from human-induced sedimentation. It is important to understand effects of sediments on EACs, as the EAC plays a significant role in primary production for reef ecosystems.

A pump-operated sampling device was developed to quantitatively collect the mobile sediments that accumulate within EACs of hard substrata. Using this method, sediments were collected from EAC-covered substrata at Lizard Island, in the northern Great Barrier Reef (GBR), Australia. Replicate sediment samples were collected from four forereef habitat zones; the reef base, crest, fore-flat and mid-flat. Sediment distribution followed a predicted pattern, from hydrodynamic forces, of low loads on the crest and higher loads at the reef base and with leeward distance from the crest. The grain-size composition of sediments was even on the crest, but became sorted with leeward distance.

The areas covered by algal forms (crustose, globular, turfing and macroalgae) and the mean heights of EACs from which sediments were collected were measured. Sediment distribution was strongly, positively correlated with the heights of EACs among and within habitat zones. Sediment load was also correlated, but to a lesser extent, to the area covered by algal forms within the sampling units; turfing and crustose forms were related to higher and lower sediment accumulation respectively. Spatial variations in sediment loads were still significant when significant effects of EAC heights were accounted for in an ANCOVA, showing that

other factors (e.g. hydrodynamic forces) significantly modify sediment distribution on these substrata.

New procedures for analysis of total organic carbon, nitrogen and phosphorus were developed and tested to alleviate problems of decarbonation of carbonates mixed with reef material. Total organic carbon, nitrogen and phosphorus were determined for both detritus (removed from EACs with sediment) and EACs (collected after sediment and detritus were removed). The biomass of EACs and detritus was variable at all spatial scales examined and both were positively correlated to sediment load. Algal biomass was significantly higher than that of detritus closer to the crest, while detrital biomass tended to be higher at the reef base. Although crest detritus was consistently low in terms of biomass per unit of substratum, it contributes a much greater fraction of the particulate mass when compared with the other zones. A similar pattern for algae (with high biomass:sediment load on the crest) suggests that crests on this reef should be favoured by sediment-avoiding herbivores and detritivores. The C:N ratios of algal tissue and detritus, as a predictor of food quality, were variable within but not among habitats. Phosphorus content of algae and detritus tended to increase with leeward distance from the crest, which supports the possibility of transfer of phosphate between algae and detritus and/or reef sediments. A trend of higher nitrogen and phosphorus content of detritus compared to algae suggests that detritus is of higher nutritional value on forereefs than algal tissue.

A month-long field experiment examined the effects of cleared sediments on the growth and nutritive quality of EACs on coral tiles while partitioning the effects of herbivory with exclusion cages. EACs in the open were grazed to low biomass in all three sediment treatments. The final biomass of EACs within cages (as a measure of net algal growth), however, was significantly lower with increased sediment load. The magnitude of this effect depended on the site. Experiments using different types of cage controls supported these findings. C:N ratios of algal tissue were lower with

high sediment loads, however, this appeared to be due to lower rates of carbon fixation. Nocturnal invertebrates were more abundant within EACs with lower sediment loads in open and caged treatments, indicating that sediments influenced their foraging preferences more than algal biomass or quality.

A model involving interactions among sediments, EACs and herbivores is proposed, and explains the contradictory information on the effects of sediments on algal growth from observational and experimental work. In view of the findings, sediment loading is expected to have deleterious effects on algal-based food chains, but sediments may provide a local refuge from herbivory which permits high algal standing stocks on reefs.

Preface

Sediments comprise a significant proportion of the physical structure of coral reefs (Darwin 1842, Davies 1983). This is particularly marked in continental shelf reefs and atoll reefs, where sediment infilling of leeward areas produce extensive lagoonal habitats. Sediments on coral reefs may include inorganic grains derived from the land (e.g. siliceous sand and silt) but are usually dominated by reef-derived particles (e.g. foraminifera, *Halimeda*, and eroded coral and coralline algae). A considerable number of studies have examined the influence of sediments on invertebrate community structure in lagoonal habitats on coral reefs (see Gray 1974, Riddle 1988, Jones *et al.* 1992, Millet and Guelorget 1994). In contrast, we know little of the role of sediments on hard reef substrata, where sediments are deposited in layers thin enough to permit the growth of algal and coral communities. These mobile sediments can vary in load on substrata both temporally and spatially, and are often used as a physical feature to characterise reef habitats.

Human activities such as coastal development, dredging, trawling and deforestation of water catchments, can lead to increased amounts of sediments suspended in waters surrounding coral reefs. Deposition of these sediments onto reef substrata can pose a serious threat to biota when these elevate the existing load of reef-derived sediments. In many cases, human-induced sedimentation can lead to shifts in coral reef communities, especially with respect to the corals themselves (reviewed by Rogers 1990, Brown *et al.* 1990, McClanahan and Obura 1997). Reviews on disturbances to coral reef systems have viewed sedimentation as the most common and serious human-induced threat to coral reefs worldwide (Hatcher *et al.* 1989, Grigg and Dollar 1990).

In view of the concern of reef sedimentation, a vast number of experimental and observational studies have been carried out to determine the effects of sediments on corals and coral communities (reviewed by Rogers 1990). Effects on corals are variable, depending on the species and the magnitude of the disturbance, but are commonly deleterious, such as reduced calcification, growth, reproductive potential, productivity, recruitment and survivorship. Some studies, however, have shown that certain coral species are affected little by sedimentation events (e.g. Sheppard 1980, Chansang *et al.* 1992), hence we cannot assume that responses of all reef biota to sediment loading will be negative.

In contrast to the focus on corals, few studies have investigated the response of epilithic algae to sediment loading. This is alarming, in view of the significance of epilithic algal communities (EACs) in the trophodynamics of coral reef ecosystems. For instance, EACs are considered to be the main contributors to autochthonous (within the system) primary production on coral reefs (Wanders 1976, Klumpp and McKinnon 1989, 1992), and with respect to coralline algae, are important in reef growth by cementing carbonates (reviewed by Littler and Littler 1984). Studies have also shown also that EACs are the main dietary targets of reef herbivores (reviewed by Steneck 1988 and Choat 1991) and are thought to provide the base constituent of coral reef detritus (Hatcher 1983b, Kinsey 1985, Alongi 1988, Hansen *et al.* 1992). Deleterious effects on the growth of epilithic algae from sediment loading would therefore be expected to flow on to higher trophic levels of reef food chains, thus affecting the system at a broad scale.

EACs often present a carpeted texture to coral reef surfaces. Algal mats within soft-bottom, lagoonal habitats on coral reefs have been shown to trap and accumulate sediments due to the intertwined nature of algal filaments (Scoffin 1970, Neumann *et al.* 1970). In a similar way, EACs of hard forereef substrata also appear to trap and accumulate sediments.

Through this process, EACs may be able to affect sediment distributions on these substrata and mediate the effects of sediments on neighbouring biota (see Walker and Ormond 1982, Kennelly 1983). There is little information, however, on the characteristics of EACs which govern the extent of sediment accumulation or of the scale in which EACs might affect sediment distributions on reef substrata. Sediments accumulated within EACs are likely also to alter the state in which algae are available for consumption by herbivores, and may in turn affect the ability of EACs to maintain high rates of productivity. The spatial extent at which these modify EACs as a food resource could likewise affect grazing by herbivores, however, there is little information also on the likely patterns by which these occur on coral reefs.

The term 'EAC' (*sensu* Hatcher and Larkum 1983, Scott and Russ 1987) refers here to all diminutive algae growing on dead coral reef substrata, including filamentous and fleshy algae, immature macrophytes and crustose corallines. It is not considered (*sensu* Hatcher 1981, 1983a) to include organic detritus; a component that can now be sampled separately. These EACs are diverse assemblages, with representatives from Chlorophyta, Cyanophyta, Rhodophyta and Phaeophyta, with species integrated at a fine scale. This makes studies *in situ* on growth, metabolism or productivity of benthic algal assemblages at species or even functional group level difficult, hence such processes are more conveniently studied at the community level (Steneck 1988). Identification of algae at the level of broad functional groupings (defined later) is the resolution used for much of the present project. This approach does not undermine the importance of taxon-specific responses of interactions with sediments, but seeks to examine relationships with sediments in a broader context.

The term 'grazers', as considered by Hatcher (1983a), is used here to mean those animals that remove algal tissue as a primary source (by volume) of their diet. This is for convenience, and is not meant to undermine the importance of functional classifications of herbivores, such

as grazers vs browsers (Horn 1989) or excavators vs scrapers (for scarids; Bellwood and Choat 1990).

The broad objectives of this project were firstly to develop methods for assessing sediment load in EACs, secondly to examine the spatial patterns of sediment distribution within EACs and the way in which these modify epilithic food resources, and finally to determine the direct effects of sediments on EAC growth and nutritive quality. This dissertation is set out as a series of five separate studies (chapters) to address these objectives, with a final overview to summarise the main findings and bring together this information into broader contexts of coral reef ecology and management .

Chapter 1 describes a submersible apparatus and procedure for quantitatively sampling EAC-bound sediments from small units of substratum. This study tests the efficiency of sediment collection from EACs of natural substrata in terms of the proportion of the load (by weight) and the grain size composition of sediments removed.

Chapter 2 describes procedures for analysis of organic carbon, total nitrogen and total phosphorus in biological material mixed with reef carbonates. These cost-effective methods were required for estimating the biomass and nutrient content of algae and detritus in later studies (Chapters 4 and 5). A new method for organic carbon analysis in a LECO auto-analyser is tested to ensure that decarbonation of reef carbonates is alleviated. The appropriateness of combusting samples (ash-free dry weight method) to determine biomass of material mixed with reef carbonates is evaluated. Precision analysis of established, colorimetric analyses for measuring the nitrogen and phosphorus content of material is determined as an indirect test that chemical reactions with carbonates in samples are controlled with the modified procedures.

Chapter 3 uses the sampling device (Chapter 1) to investigate quantitative and qualitative patterns in the distribution of EAC-bound sediments on substrata within a forereef in the Northern GBR. It aimed also to use measurements of the physical structure of EACs, from which the sediments were collected, to reveal correlative relationships with sediment loads within and amongst forereef habitat zones. This approach is used to infer the extent to which physical characteristics of EACs affect sediment accumulation at these spatial scales.

Chapter 4 uses the sampling device (Chapter 1) to collect the algae and detritus from the same area of substrata (above). Analyses of algal and detrital biomass allows the trophic-functional role of sediments and the comparative role of detritus within EACs to be investigated. Correlative relationships are used to examine potential nutrient dynamics among algae, detritus and sediments using the measurements of sediment load and the nitrogen and phosphorus content in detritus and algae. These quantitative data on the distribution of algae and detritus amongst forereef zones are placed within the context of published accounts of spatial patterns of foraging in reef herbivores and detritivores.

Chapter 5 aimed to determine the direct effects of reef sediments on EACs through a multi-factorial field experiment that partitions the effects of herbivory on EACs of carbonate tiles using exclusion cages. Responses of epilithic algae to sediment load and grazing, in terms of growth and nitrogen uptake, are inferred from analysis of organic carbon and nitrogen content of algal tissue after a 1 month period of exposure to treatments. Quantitative censuses of invertebrates and roving herbivorous fishes are used to address the causes of differences in EAC biomass among experimental factors and the potential for sediments to affect grazing. Preliminary experiments are presented also, which established the sediment manipulation rates and test the potential artifacts of exclusion cages on algal growth.

Chapter 1

A direct method for assessing sediment load in epilithic algal communities

1.1. Introduction

Mobile sediments within coral reef environments can be deleterious to corals (Rogers 1990), and their deposition onto reef surfaces may directly affect other benthic biota. Epilithic algal communities (EACs) commonly cover significant proportions of coral reef surfaces (Morrissey 1980, Pichon and Morrissey 1981), and can trap sediments which may deleteriously affect neighbouring biota such as corals (Walker and Ormond 1982). Furthermore, sediments can remain in coral reef systems for long periods (Chansang *et al.* 1992) and via resuspension events, may be transported through other biotopes. The ability to measure sediment loads on hard reef surfaces, such as EAC-covered substrata, where they are directly influencing reef biota, is therefore important for assessing sediment stresses (*sensu* Grime 1979) on coral reefs.

The principal methodology used to assess sedimentation on coral reefs has been the deployment of sediment traps (Koop and Larkum 1988, Rogers 1990). Sediment traps collect suspended sediment over a given time; these values are interpreted as the gross downward flux rates of particles in the water column. Within this context, sediment traps have been invaluable as research tools for documenting gross sediment inputs to reef systems. Problems can arise, however, when sediment trap data are extended to infer accrual rates of sediments to reef substrata (Cortés and Risk 1985), since a sediment trap does not approximate the nature in which particles are bound to the benthos (Gardner 1980). Moreover, the technique does not provide

any information about the amount of sediment deposited on natural substrata, in contact with sessile biota.

Ideally, studies should incorporate direct sampling of accumulated sediments on reef substrata to provide baseline assessments of the natural load and supplement information on sedimentation rates during disturbances. This chapter outlines a portable apparatus and sampling technique which allows a diver to collect sediments on reef surfaces, and a test of its efficiency at removing sediments held within EACs of natural coral reef substrata. This rapid method permits the measurement of the instantaneous (net) load, rather than the sedimentation rate, of terrigenous and reef-derived sediments on algae-covered substrata.

1.2. Materials and Methods

The sediment sampler (Fig. 1.1) is a submersible apparatus which uses a bilge pump to vacuum particulate material from substrata. It can be viewed as four connected components; a brush to loosen bound sediments from algae, a filter to retain coarse sediments, a pump which produces an intake current, and a collection bag to retain water and fine sediments. The electric rotary bilge pump (Whale Superline 99) is powered by a 12V dryfit battery and associated electronics contained within a waterproof housing. An adjustable timer and current regulator circuit, which maintains a constant voltage (10.5V), standardises the water flow speed and duration for each sample. A voltmeter mounted within the housing can be checked periodically, to indicate when the battery power is insufficient to run the current regulator.

The sediment filter used for sampling is contained within a 250 ml plastic sample vial, which has two tapered fittings attached to the lid. The filter houses an intake hose which is fitted through the centre of five perforated PVC baffles stacked 10 mm apart within the vial, with a 200 μm

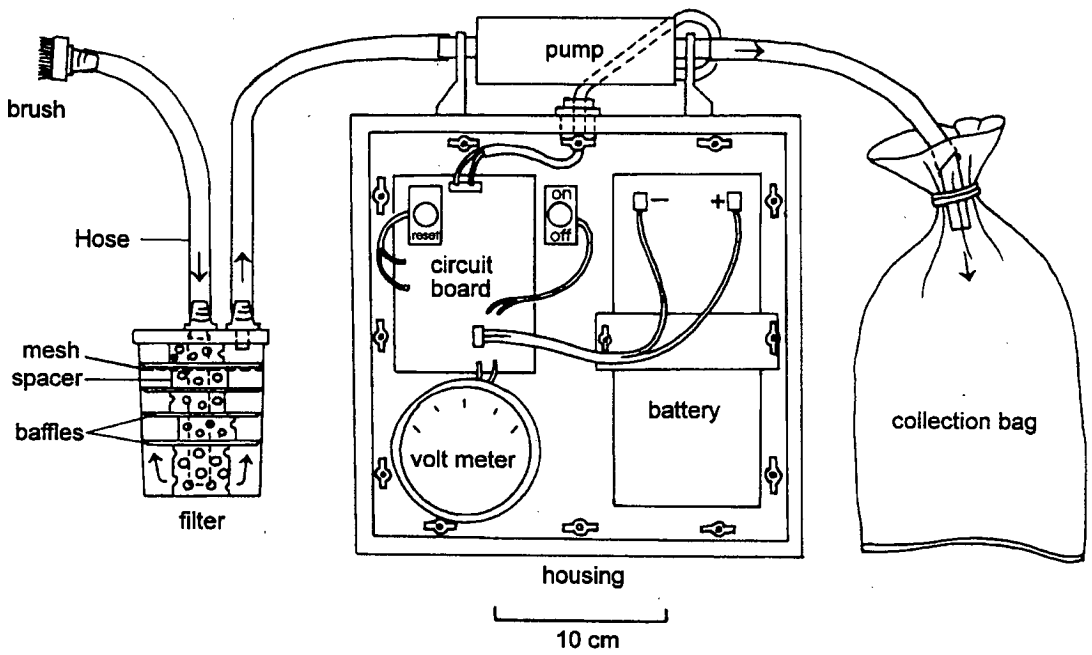


Fig. 1.1. Diagram of the sediment sampling apparatus. Collection bag drawn at approximately 0.5x. *Dashed lines* indicate hidden features, *arrows* show direction of current flow.

nylon mesh screen below the uppermost baffle. The central hose carries water and particulate material to the bottom of the vial, and as they pass through the filter, the perforated baffles impede turbulence, and retain the coarse sediments.

A brush (25 mm diam.) with soft, nylon bristles around the perimeter, is attached to the intake hose. The brush attachment has a central opening (20 mm diameter) which results in an intake current speed of about 28 cm s^{-1} at the opening. A circular sampling ring of 6 mm thick PVC is pinned to the substrata to outline a 100 square cm (1 dm^2) sampling area and partition the enclosed sediments from those on neighbouring surfaces. The brush is applied to the substratum within the sampling unit and, once the pump is switched on, it is used to brush/dab the algae (or other epilithic biota) to release bound sediments which are immediately vacuumed through the filter. Fine sediment grains and water (5.4 l) pass through the bilge pump and fill a plastic collection bag (530 x 300 mm, 100 gauge). Upon completion of each sample, the hoses are disconnected, and the entire sediment filter is inserted into the collection bag and sealed with an elastic band.

A sampling period of 60 s appears to be ample time to remove all available sediment from a 1dm^2 area of algae-covered substrata and fills the collection bag to near capacity. Each sample takes around 5 min to collect, with multiple sampling possible if the diver is equipped with additional filters and collection bags. The filter operates efficiently (without clogging) for samples with up to about 50 g of sediment. In the laboratory, filters are disassembled and rinsed in the water in the collection bags. The resulting (total) sediment sample is settled in containers, and processed to yield standardised samples of the total sediment load per unit area of substratum.

A laboratory-based experiment was carried out to test the efficiency of the sediment sampler at removing sediments from algae-covered substrata (i.e. the percentage of available sediment actually collected). Six unattached

pieces of flat, coral reef substrata, covered with epilithic algae and associated sediments, were collected from a subtidal reef flat at Lizard Island (14°42'S, 145°27'E), Great Barrier Reef. The substrata were placed carefully (to minimise disruption of algal-bound sediments) into 80 l containers filled with filtered seawater. For each piece of substratum, the sampling ring was pinned to the flattest section, and the *in-situ* sediments were sampled, employing the same procedure and duration as outlined. The sampling unit was left in the same position, and sampling of the 'residual' sediments was repeated four more times. On the final sample, the substratum was also scraped lightly with a perspex spatula while vacuuming the sediment, to dislodge and collect any sediments which may have been bound by basal cells and rhizoids of the algae. This yielded six discrete, sequential samples, all taken from the same 1 dm^2 area.

Each sample was placed in a cylinder (50 cm high, 150 mm diam.) with a funnel at the bottom to concentrate the sediments during a three hour period (ample time to settle out all grains greater than 10 μm) (see Dyer 1986). Following draining and decanting of excess water, the settled sediments were emptied into collection vials. The sediments were then treated with three consecutive washes of 10% sodium hypochlorite ($NaHClO_4$; to remove particulate organic material, following Hammond (1981)), followed by five washes with filtered tapwater, with a 1 day settling period between each.

Each of the sediment samples was then oven-dried at 60° C, weighed to the nearest 0.1 mg and dry-sieved through a connected series of small (50 mm diam.) mesh sieves (2000, 1000, 500, 250, 125, and 63 μm). Sieves were shaken for 2 to 3 min to ensure complete separation of grain size fractions, which were then weighed to the nearest 0.1 mg. Proportional data on the yields of sediment from the efficiency test were arcsine transformed to improve homogeneity of variances and normality of data distributions. The null hypothesis that yields were not dependent on the amount of sediment

present (total yield) was tested using a linear regression of efficiency on total sediment yield.

1.3. Results

The experiment demonstrated that the sampling procedure is efficient at collecting sediments held within EACs, with an average of 90.9% (± 3.1% 95% CI) of the total sediment mass being recovered in an initial 60 second sample (Fig. 1.2). Sealing the sampling ring to the substratum was a potential problem, and it is likely that 'residual' sediments included some which subsequently leaked under the ring into the sampling area after the initial sample (which would result in underestimating the actual efficiency). Extending the sampling period to 2 min would improve this yield only by about 3.8 percent. The low variance associated with efficiency estimates indicates a high level of precision for replicated sampling. There was no significant trend in the efficiency of collection on total available sediment load (Fig. 1.3; $t_{0.05(1),4} = 2.10$, $p = 0.104$) within the range tested (6.52 to 14.04 g), indicating that the procedure should be equally suitable over a wide range of sediment loads.

The apparatus is capable of retrieving fine, silt-sized particles as well as coarse sand grains. Graphical representation of the differences in grain size composition between the initial and residual sediments (Fig. 1.4) shows that the first sample is very similar to that of the residual fraction collected in the 5 subsequent sampling cycles. The apparatus and sampling technique appear therefore, to collect samples which are also representative with respect to the relative proportion of grain fractions of all available sediments.

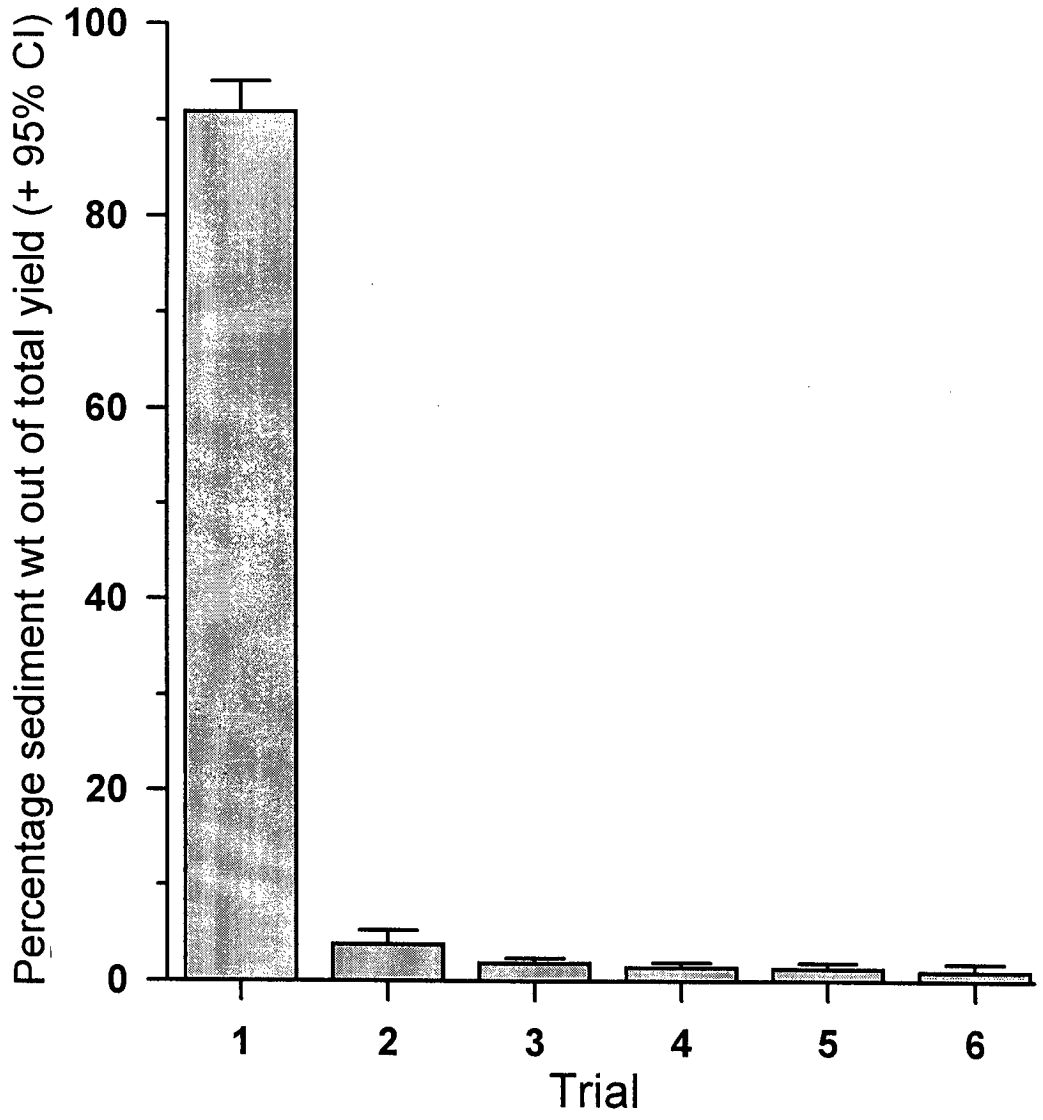


Fig. 1.2. Efficiency of sampling on natural substrata. Histogram of percentage weight of sediments collected in consecutive sampling trials out of the total (summed) weight collected. Number of substrata sampled for each trial = 6.

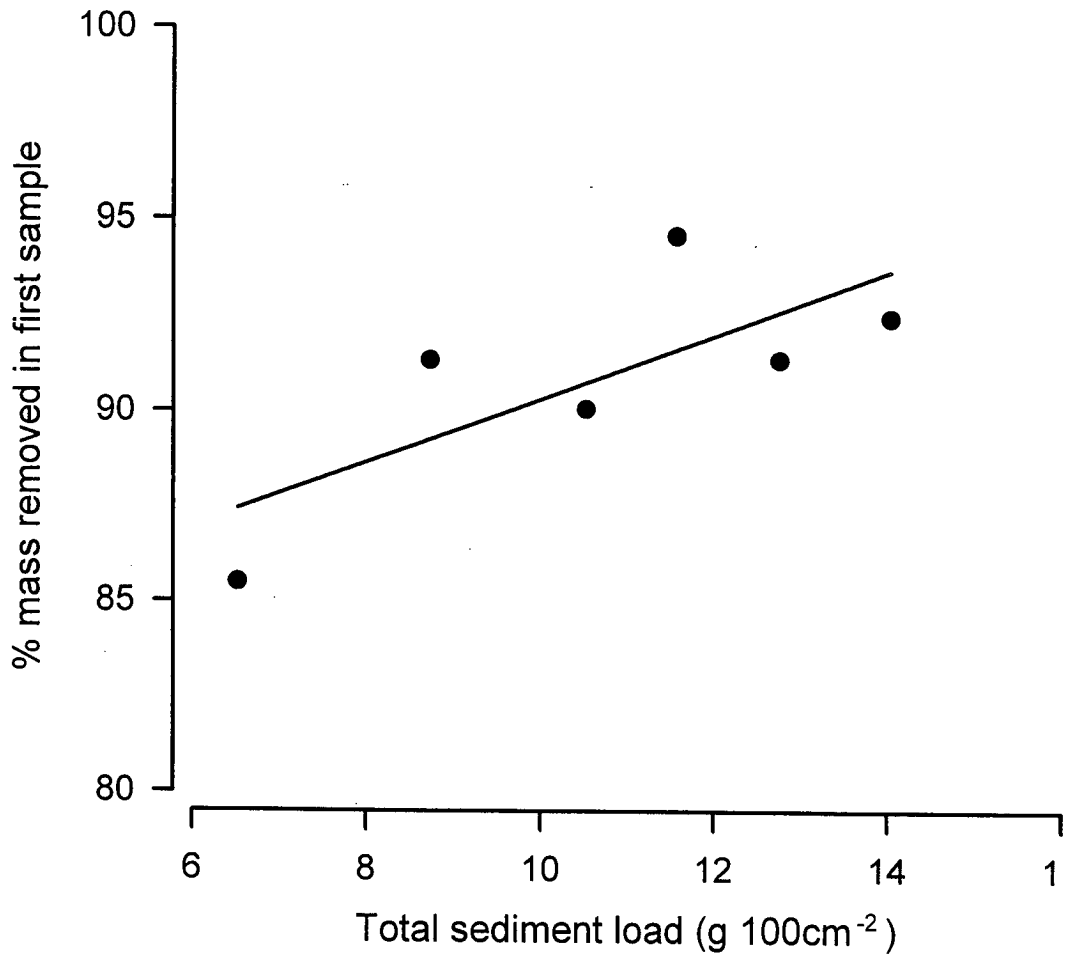


Fig. 1.3. Scatterplot of efficiency of sediment collection (% yield in first 60 s) vs the sediment load of the sample. Trend of increasing efficiency was not significant (t = 2.1, p = 0.104).

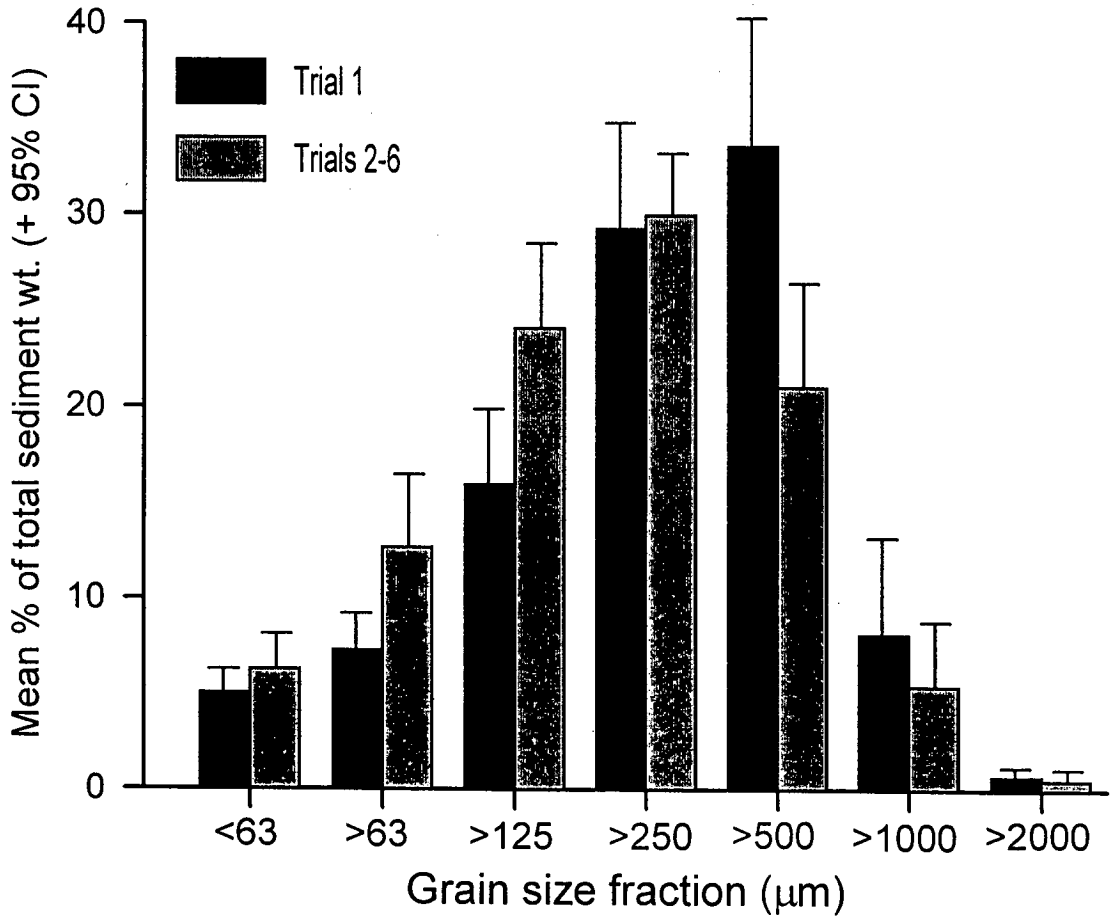


Fig. 1.4. Histogram comparing grain size class composition of sediments collected from initial (60 sec) samples with those of the (combined) 'residual' sediments. For each bar, n = 6.

1.4. Discussion

Sampling using this procedure permits quantification of the load (net amount) and grain size composition of sediments which have accumulated within EACs on coral reefs. The results illustrate an accuracy of over 90% in collecting sediments from coral reef substrata underwater. This type of methodology presents an alternative approach to sediment traps in measuring the influence of sediments on reefs. It allows sediments, both biogenic and imported, to be quantified directly, from areas where they are actively affecting reef biota. Cortés and Risk (1985) emphasised that the flux of material into sediment traps is a measure of gross, but not net, sedimentation rates. They argued that reefal areas with high wave energy and a relatively cemented substratum might engender a situation where suspended sediments pass over the reef, resulting in little material actually being delivered to the reef surface. Substrata with a high percentage cover of crustose coralline algae have been shown to accumulate less sediment than substrata dominated by turfing forms within a coral reef (Chapter 3). In such cases, direct sampling eliminates potential biases associated with techniques which assume that sedimentation rates will reflect accumulation rates on reef substrata.

The methodology may be applied not only to baseline assessments, but also to determine the precise changes in load and composition of these sediments through time. It should be noted, however that estimates of sediment load per unit area will depend on the substrata sampled, as those with epilithic algae, for example, will probably retain more sediments than surfaces such as live coral. The technique fulfils requirements proposed by Dahl (1977) for monitoring systems, in that it is rapid, simple (in terms of construction and operation), and is repeatable and standardised. It also has the advantage of being non-destructive, with no visible damage to EACs. This sediment sampler differs from other pump-operated suction devices, designed primarily for collecting benthic invertebrates (e.g. Smith 1973, Taylor *et al.*

1995), in that its components facilitate collection of all sizes of particulate materials from the substratum. In this context, it may also serve as a useful tool for sampling the interstitial microfauna and detritus held within EACs.

Chapter 2

Quantifying organic carbon, nitrogen and phosphorus content of material from coral reefs

2.1. Introduction

This study was carried out to establish accurate and cost effective procedures for determining the biomass and relative nutrient content of samples of organic material (namely algae and detritus) from coral reefs. Analysis of organic content is a common way to evaluate the biomass of biological and geological material from ecological systems. Determination of ash-free dry weight (AFDW; also termed 'loss on ignition') is among the simplest of available procedures, in which the amount of combustible organic material in a sample is determined by subtraction of the weight of 'ash' (material remaining after combustion) from the initial dry weight. In cases where inorganic components such as sediments are involved, bias in this method can arise from variable thermal instability of carbonate mineral phases at ashing temperatures (450-600° C); some of the CO_2 may be lost from the mineral phase and not exclusively from the oxidative decomposition of organic matter (Morse and Mackenzie 1990). A number of geological studies (Dean 1974, Telek and Marshall 1974, Hirota and Szyper 1975) have reported negligible dissociation of carbonate (reagent grade) at 500° C. On the basis of these findings, recent studies on coral reefs have applied AFDW determinations at this temperature to suspended solids, benthic sediments, epilithic algae and stomach contents of herbivores; all of which contain biogenic carbonates.

The suitability of AFDW determinations of recent material from coral reefs is unknown. In most shallow marine environments, particularly coral

reefs, carbonates are typically of a complex mineralogy (Chave 1962) and can contain considerable proportions of unstable mineral phases, such as high-magnesium calcite that may begin to decarbonate below standard ashing temperatures. This study aimed to evaluate this potential error by conducting ashing trials of coral reef sediments over a range of temperatures and comparing the results with those from a new procedure for organic carbon analysis using a LECO auto-analyser. This is a simpler procedure for induction furnace analysis than those recently described by Cutter and Radford-Knoery (1991) and Nieuwenhuize *et al.* (1994) as it deals with carbonate interference by using as single-step acid-treatment of samples in reusable vessels to alleviate carbonate interference prior to analysis. The procedure presented by Sandstrom *et al.* (1986) for determination of organic carbon was also considered, but requires a specialised analyser (Beckman Tocamaster) and the analyses proved too costly to warrant its use in this project.

In addition to assessing biomass, ecological studies also use analyses of critical nutrients to assess nutritional quality of food sources and metabolic processes of plant communities. Nitrogen and phosphorus are two basic nutrients commonly used in such investigations. Nitrogen and phosphorus are key elements for growth of coral reef algae (see reviews by Atkinson 1988, D'Elia and Wiebe 1990, Furnas 1992). Nitrogen is used by algae for producing metabolic cofactors and amino and nucleic acids (Furnas 1992) and is a major element of proteinaceous material (Roman 1983). Algae also require phosphorus for intracellular production of nitrogenase (Fogg 1974), energy metabolism (ATP) and the production of nucleic acids and phospholipids (Furnas 1992). Nitrogen and phosphorus are needed, for these purposes also, for growth and metabolism in herbivores and detritivores.

Cost-efficient procedures for quantifying nitrogen and phospohorus content of biological material were needed for studies on reef algae and detritus (Chapters 4 and 5). Nitrogen and phosphorus analyses of biological material have been described by Baethgen and Alley (1989) and Anderson

and Ingram (1989; adapted from Murphy and Riley 1967) respectively. These procedures were designed primarily for analysing terrestrial plant material and soils, and begin with a wet oxidative digestion of the material with acid. Although these procedures do not suffer from interference from decarbonation of $CaCO_3$, these digestions needed to be modified to account for reactions with carbonates in biological samples from coral reefs. Incomplete digestion of samples would result in variable estimates between replicate analyses. These modifications to oxidative digestions are outlined here also, with tests of the replicate precision of analyses on samples of reef algae and detritus that are mixed with carbonates.

2.2. Materials and methods

2.2.1. *Organic content analysis*

Carbonate sediment samples (n = 4) were collected from a reef flat at Lizard Island (14°42'S, 145°28'E), Great Barrier Reef. These were cleared of organic material by soaking in three series of 10% bleach ($NaHClO_4$) followed by five series of 1μm filtered tapwater, with minimum soak periods of 12 hr. The samples were then oven-dried at 60° C, and stored in a desiccator with silica gel. Duplicate aliquots (approx. 1 g) from each sediment sample were weighed into pre-fired (650° C) and desiccated crucibles to the nearest 0.1 mg. These were combusted in a calibrated Carbolite® muffle furnace for 16 hrs in separate trials at 400, 450, 500, 550, 600 and 650° C, then were cooled in a desiccator for several hours before being reweighed to determine the ash-free content. Duplicate empty crucibles were also fired during each temperature trial and showed negligible weight loss of the vessels. Change in appearance of sediments (superficially and within grains) that were combusted at the standard ashing temperature of 500° C was checked with light microscopy. The contribution by weight of siliceous sediments in each sample was determined after carbonate dissolution in hydrochloric acid (HCl).

A LECO SC444-DR elemental analyser was used to quantify organic carbon content of triplicate aliquots of the same sediment samples. To permit acidification of samples, vessels (2 ml capacity troughs) were constructed from heat resistant HSQ quartz glass tubing (Heraeus Quarzglas) and were fitted into standard furnace boats. Aliquots (50 mg) of each sample were weighed to the nearest 0.1 mg in pre-fired vessels. These were then wetted with a few drops of deionised water and treated with 2 N AR hydrochloric acid, a few drops at a time, until the glass vessels were near full; this is enough HCl to liberate all CO_2 from 200 mg of carbonate material. The samples were then oven dried for 12 hrs at 70° C, then analysed in the LECO analyser. This machine combusts samples in a furnace at 1200° C and detects the amount of evolved CO_2 by infra-red spectroscopy, which is then converted to proportion of carbon using the initial sample weight. The glass vessels were rinsed in HCl and deionised water to allow multiple use, and have an estimated half life of about 50 analyses.

An experiment was carried out to assess the suitability of this procedure for analysis of organic carbon of biological material; it tested whether: a) organic carbon is affected by the acid treatment, b) interference from inorganic carbon is eliminated, and c) the procedure adds any organic carbon. Laboratory cultured *Enteromorpha flexuosa* (Chlorophyta), a non-calcified filamentous marine alga, was used as the biological material to be tested. Fresh algae were rinsed thoroughly in distilled water, oven dried at 60° C, and ground to a homogenous powder using a mortar and pestle. Aliquots (n = 6) of algae with and without $CaCO_3$ (AR grade), $CaCO_3$ alone, and empty vessels were treated with acid and analysed as outlined above, as were aliquots of untreated algae and $CaCO_3$. Additionally, samples of epilithic algae (n = 120) and detritus (n = 60) were also collected from Lizard Island (Chapters 4 and 5), ground to a fine powder and analysed in triplicate using the above method. These field samples varied in the type of organic material and in the proportion of carbonate material present, providing a suitable range

of samples to assess the within-sample precision of organic carbon analyses using this procedure.

2.2.2. *Nitrogen and Phosphorus analyses*

Nitrogen and phosphorus content of algae and detritus were deterimined using colorimetric determinations of digested material described by Baethgen and Alley (1989) and Anderson and Ingram (1989). These entire analyses start with the wet oxidation of the sample material with sulphuric acid and hydrogen peroxide, and a selenium catalyst. This simple digestion has a broader utility compared with the standard Kjedahl digestion because one rapid digest can be used for determinations of both nitrogen and phosphorus. The digest brings nutrients into solution completely, and volatilisation of nitrogen and phosphorus compounds does not appear to occur (Allen 1974, Anderson and Ingram 1989).

The digestion mixture consists of:

1. Concentrated sulphuric acid (H_2SO_4; AR grade)
2. Hydrogen peroxide (H_2O_2), 30%
3. Selenium Kjedahl catalyst tablets, containing 0.05 g Se and 1 g $NaSO_4$

The digestion mixture is formulated by adding 350 ml of H_2O_2 to a boiling flask containing 10 Se catalyst tablets. These are mixed well, then 420 ml of H_2SO_4 is added slowly while cooling in an ice bath. The mixture is then refrigerated at $<5°$ C and is stable for 4 weeks.

Algae and detritus, from coral reef substrata and carbonate tiles (see Chapters 4 and 5), were freeze dried and ground to a fine powder. These samples contained considerable amounts ($>50\%$ by weight) of inorganic reef carbonates, and as a result, the heating schedule of digestions was

extended and repeated rinses of the tubes to wash down frothed material were added to the standard procedure.

Duplicate aliquots (0.1 to 0.4 g) of algal (n = 64) and detrital samples (n = 16) were weighed into digestion tubes (75 ml). This material was washed down in each tube with 1-2 ml of double distilled (DD) H_2O, then 4.4 ml of the digestion mixture is added. The mixture was allowed to react for 1 hr, and was checked regularly to ensure that samples did not froth over; the following procedures are modifications to accommodate this frothing. After the reaction ceased, material on the inside of the tubes was rinsed again with 1-5 ml of DD H_2O. The digestion tubes were then heated in a block digester to 100° C, and the samples boiled for 1-2 hrs. Material that frothed onto the inside of the tubes was repeatedly rinsed down with DD H_2O until reactions ceased, then the heat was increased slowly to 365° C, and this digestion continued for another 30 min. The digest and tubes are allowed to cool to room temperature before being placed in an ice bath. The digestion mixture in each tube was then made up to 75 ml with DD H_2O and mixed well by inverting the digestion tubes several times. Blank samples (of digest only) as well as nitrogen (ammonium sulfate solution) and phosphorus (KH_2PO_4 solution) standards were also treated using the same procedure.

Nitrogen content was determined using the salicylate-hypochlorite method of Baethgen and Alley (1989), which allows faster throughput of samples compared to the traditional distillation and titration method. It involves reactions of 0.1 ml of each digested sample with two reagents, separately. Phosphorus content was determined using an adaptation of Murphy and Riley's (1967) single solution method (Anderson and Ingram 1989). This involves reaction of 1 ml of each digested sample with ascorbic acid solution and a molybdate reagent. Reacted solutions for nitrogen and phosphorus were then analysed colorimetrically using an atomic absorption spectrophotometer (Varian, DMS 90) at 655 and 880 nm respectively.

Concentrations of total N of samples were finally determined by plotting sample absorbances against linear functions from absorbances of standard solutions using Tablecurve® (Jandel Scientific) software.

2.3. Results

2.3.1. *Organic content analysis*

AFDW determinations (Fig. 2.1) indicate that decarbonation of washed coral reef sediments begins at low ashing temperatures, and dramatically accelerates between 550 and 600° C. The average proportional weight loss of sediments was 3-4% for furnace temperatures up to 550° C, but increased to 10.1% (± 0.1% SE) at 600° C and 40.3% (± 1.9% SE) at 650° C. Following ashing at 500° C most of the dominant sediment particles, such as those from coral, calcareous algae and foraminiferans, changed, both superficially and within grains, from off-white to dark grey in colour. This indicates that mineral decarbonation, rather than the combustion of a residual organic layer on sediments, was attributing to the weight loss upon ashing. This observation however, was not consistent amongst all particles, as some, such as those from bivalve shells and echinoid tests showed little signs of mineral decarbonation, indicating that thermal stability varies amongst the carbonates of different coral reef organisms. Siliceous minerals can bias the accuracy of AFDW determinations via the loss of lattice OH-water (Dean 1974), but siliceous particles were a negligible component by weight (mean = 0.48% ±0.06% SE) of all sediment samples.

LECO analyses (Fig. 2.2) showed that detected values of organic carbon of acid treated algae samples were not significantly different from those of samples with added $CaCO_3$ or to control (untreated) samples (one-way ANOVA; $F=0.24$, $p=0.79$). This demonstrates that interference of carbonates is avoided with the acid treatment, with negligible loss (e.g.

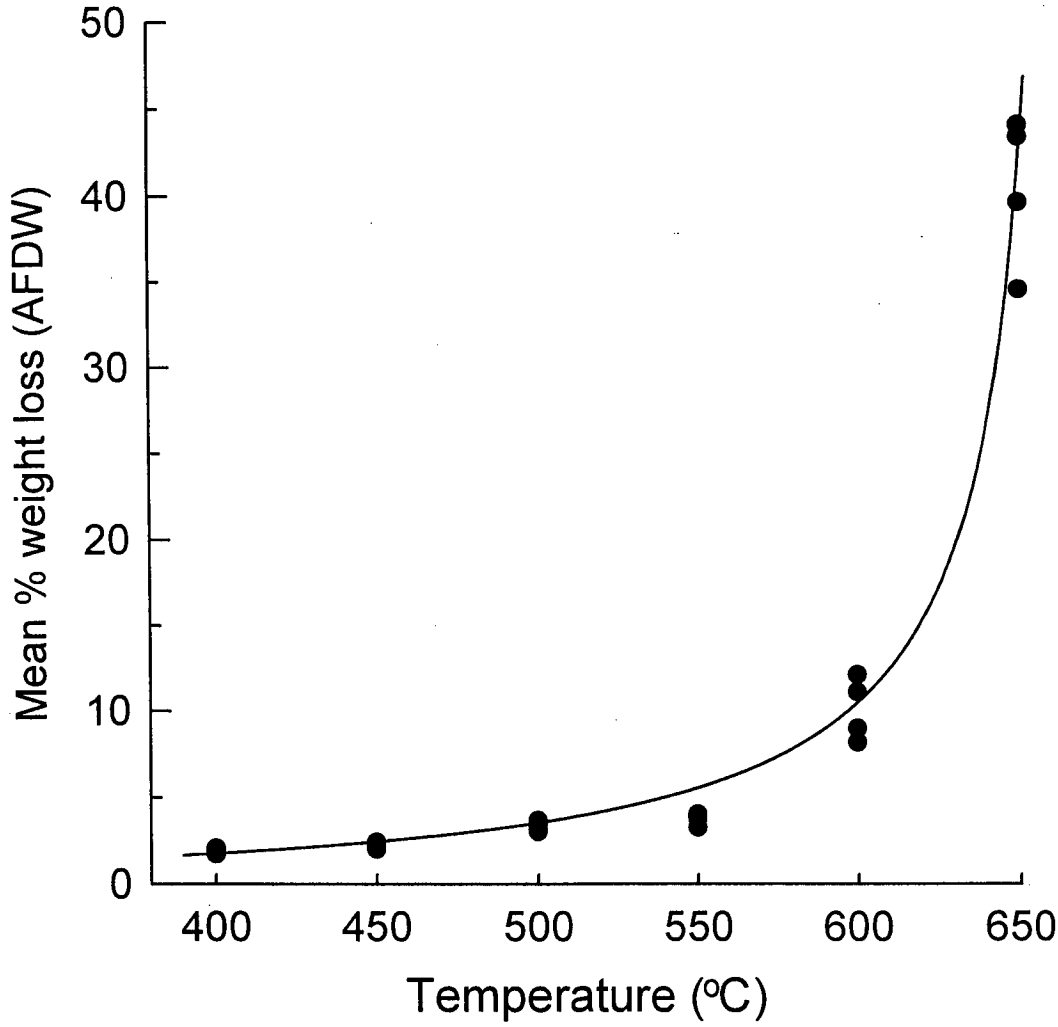


Fig. 2.1. Plot of mean percentage weight loss (AFDW) of duplicate, bleach-washed, coral reef sediment samples at different furnace temperatures. Curve of best fit ($y = x/(-0.84x + 561)$; $r^2 = 0.981$) indicates early decomposition of carbonate material and increasing thermal instability at successively higher ashing temperatures.

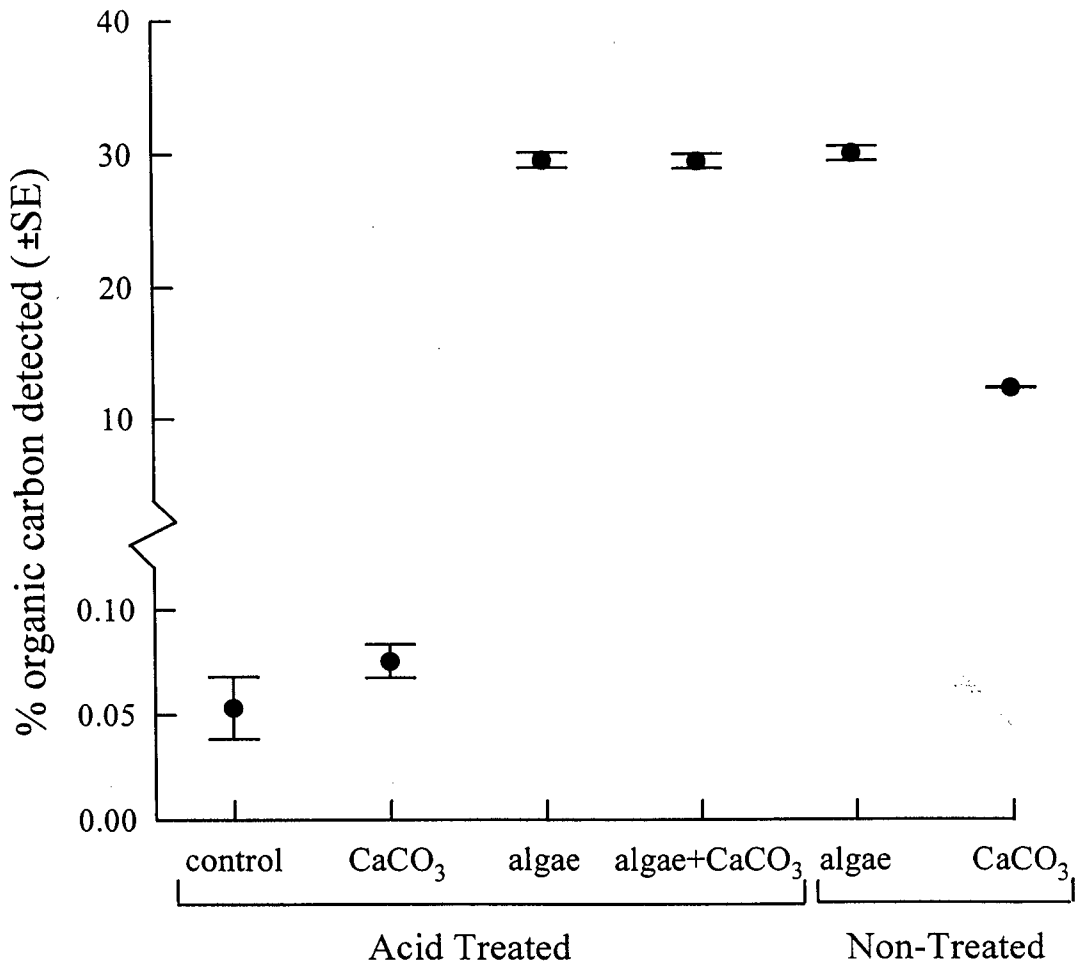


Figure 2.2. Graph of mean percentage content of total organic carbon of test materials using the LECO elemental analyser, with and without an acid treatment prior to analysis. Control treatment shows content of organic carbon detected in the acid-only treatment after drying. Values for reagent grade $CaCO_3$ represent the proportional amount of carbon detected (from carbonate dissociation), while values for algae represent the proportional amount of organic carbon in algal tissue.

volatilisation) of organic carbon. Accuracy of the analyser was confirmed by the carbon analyses of untreated reagent $CaCO_3$, which varied less than 2% (relative) from the predicted value of 12%. Analyses of acid treated $CaCO_3$ showed that the acidification is capable of eliminating at least 99.4% of the interference from carbonates. Acid-only controls indicate that acid introduced carbon can be considered negligible, as this accounted for less than 0.2% of that detected in test algal samples.

Average precision (SE/mean) of this procedure for organic carbon analyses was 2.3% for 180 carbonate-mixed biological samples from a coral reef, ranging from 0.34% to 16.01% organic carbon. The average organic carbon content of these samples was 3.25%, with an average standard error for triplicate samples of ± 0.05%, which is the detection limit of the instrument (LECO 1992). As a trend, the precision improved (relative error decreased) with increasing organic carbon content of samples (Fig. 2.3). A log-curve best explained this trend, indicating a multiplicative loss in precision with decreasing organic carbon content.

Comparison of values provided by the two methods (AFDW vs organic carbon analysis) using coral reef sediments reveals that AFDW determinations are markedly overestimating organic matter content. Although both methods indicate that a small amount of organic matter remained after bleach-washing, the AFDW values of sediments combusted at 500° C were more than an order of magnitude higher than LECO values (Table 2.1). One must consider, however that AFDW measurements are for bulk combustible organic matter (C,H,N,S,O), whereas the LECO analyser provides values for elemental carbon. Organic carbon values were therefore divided by the mean proportion of organic carbon out of the weight of detritus within sediments from Lizard Island (0.36; Chapter 4) to convert these to estimates of crude organic matter. Each of these 'corrected' values, which are now inflated to a comparable unit of measurement, are still at least six times lower than the AFDW determinations of aliquots of the same samples (Table 2.1). This

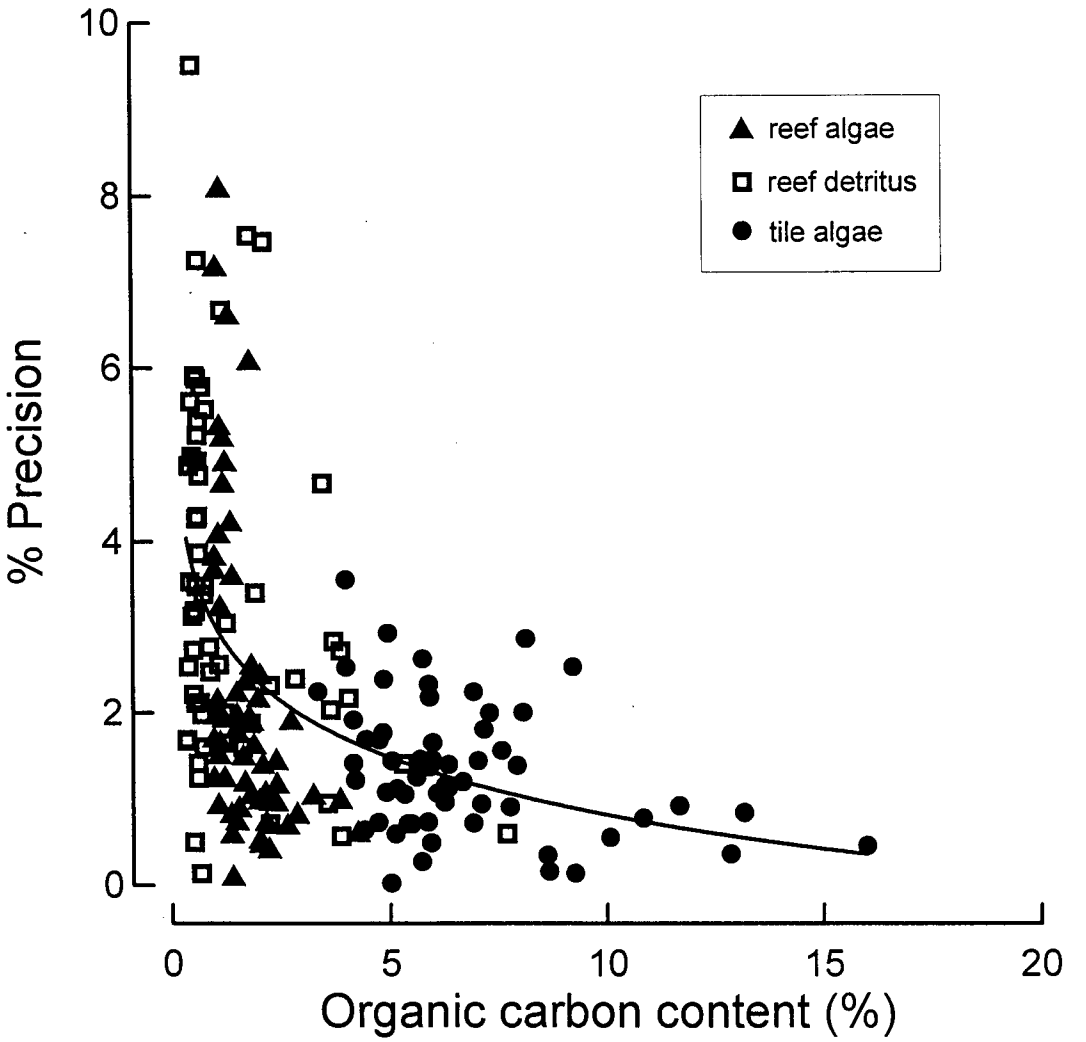


Fig. 2.3. Plot of mean values of percentage precision ((SE/mean) x 100) vs organic carbon content of triplicate analyses (LECO) of samples of reef algae, detritus and algae grown on tiles, following acid dissolution. Curve of best fit ($y = -0.0097.\log(x) + 0.004$; $r^2 = 0.26$) indicates better precision (smaller relative error) with increasing organic carbon content.

demonstrates that other components in the sediment samples, such as thermally unstable carbonate minerals, decomposed at the ashing temperature to produce an error of about 3 percent of the sample weight.

Table 2.1. Mean values (± SE) of percentage bulk combustible organic matter (%AFDW at 500° C), organic carbon (acid treatment and LECO analyses), and bulk organic matter (see text) of reef sediments.

Sample	% AFDW	% organic carbon (LECO)	% organic matter (corrected)
1	3.052 (± 0.006)	0.169 (± 0.005)	0.468 (± 0.009)
2	3.489 (± 0.138)	0.164 (± 0.014)	0.456 (± 0.024)
3	3.679 (± 0.005)	0.167 (± 0.005)	0.466 (± 0.010)
4	3.143 (± 0.086)	0.188 (± 0.024)	0.523 (± 0.043)

2.3.2. *Nitrogen and phosphorus analysis*

The modifications to the wet oxidation procedures enabled algal and detrital samples to be digested without overflow of material from reactions with carbonate sediments. Precision (SE/mean) of duplicate nitrogen and phosphorus determinations using the modified digestion procedures (Table 2.2) show that, on average, these determinations had a precision (SE/mean) of less than 0.05, over a range of sample concentrations.

Table 2.2. Repeatability of nitrogen and phosphorus analyses. Average precision tests on duplicate analyses of reef algae (n = 64) and detritus (n = 16), indicating range of nutrient concentrations in the samples used.

	Nitrogen		Phosphorus	
Material	Av. Precision (% ± SD)	Concentration Range (%)	Av. Precision (% ± SD)	Concentration Range (%)
Algae*	2.8 (±2.6)	0.14 - 1.53	4.1 (± 6.8)	0.02 - 0.08
Detritus*	4.0 (±2.9)	0.054 - 0.52	4.2 (±3.4)	0.03 - 0.05

* Note that these samples contained a large proportion of reef carbonates.

2.4. Discussion

This study indicates that decarbonation of thermally unstable carbonate sediment particles can bias AFDW determinations in samples containing coral reef sediments. It appears that the bias is detectable at temperatures as low as 400° C, which is consistent with reports that the initial step in the decarbonation reaction for magnesium calcites can occur at 250° C (Morse and Mackenzie 1990). The marked escalation in weight loss of the sediments around 600° C is probably due to decarbonation of phases such as calcite which, although reports are inconsistent, has been shown to decarbonate at this temperature (Hirota and Szyper 1975).

Skeletal carbonates of calcifying organisms can be composed of a combination of minerals, such as calcite, aragonite and a spectrum of high-magnesium calcites (Chave 1962). It is not surprising that mollusc shells, which are composed of aragonite and calcite (Chave 1962, Milliman 1974), appeared unaffected after ashing at 500° C. Conversely, sediment grains such as those of calcareous algae and benthic foraminiferans are reported to have relatively large amounts of magnesium in the calcite making up the test

(Chave 1962, Ross 1977), and were amongst those types which appeared most thermally affected.

The relative error in combusting biogenic sediments at the previously proposed ashing temperature of 500° C shows that AFDW are of limited value for quantifying organic matter from tropical coral reefs. Biogenic carbonates often comprise an overwhelming fraction, by dry weight, of biological samples from coral reefs compared to the organic material. In these cases, the relative error in AFDW determinations is likely to be high, confounding our understanding of the status of organic material in these ecosystems. Applying correction factors for the decarbonation of carbonate (Telek and Marshall 1974) should be avoided for coral reef samples, as this depends on the composition of carbonate minerals which is likely to vary considerably amongst spatially and temporally distinct samples.

In cases where auto-analysers are not available, incorporating an acid dissolution prior to ashing samples may eliminate the interference of reef carbonates for AFDW determinations. Acidification of samples should be followed by a drying step in the same vessel, to retain acid-soluble organic carbon (Roberts *et al.* 1973). This would however, require weight determinations of the hygroscopic residues which are potentially inaccurate because these hydrate and gain weight rapidly. A check should also be made to ensure that all organic material to be tested is combusted at the desired temperature, as there is a suggestion that some organic material may resist combustion at standard ashing temperatures (Froelich 1980, Krom and Berner 1983). Given these precautions, AFDW determinations could be more reliable for assessing bulk combustible organic material. For determinations of organic carbon of sediments, benthic algae, or detritus from coral reefs, the method presented for acidification and analysis of samples (10-100 mg) using a LECO elemental analyser provides an accurate procedure in which the interference from carbonate minerals is alleviated.

Results of the determinations of nitrogen and phosphorus content of reef algae and detritus revealed that, on average, the standard error of analyses was less than 5% of the mean nutrient content. These were therefore considered sufficiently replicable for studies looking at broad differences (e.g. >10%) amongst different samples, and appropriate for studies in Chapters 4 and 5 given the large sample sizes and wide range of values obtained. These analyses, however, may not be suitable for studies where small changes in the nitrogen and phosphorus content (i.e. of a few percent) are being investigated.

Chapter 3

Distribution of sediments associated with epilithic algae on a forereef in the northern GBR

3.1. Introduction

Sediments are a ubiquitous feature of the substrata of coral reef habitats. They are composed of carbonate particles, such as fragments of coral, coralline algae, and invertebrate tests, together with siliceous particles originating from organisms such as sponges and diatoms or eroded from coastal areas. On platform reefs of the Great Barrier Reef (GBR), biogenic sediments are thought to be originate chiefly within the forereef margin and transported to leeward habitats by water movement (Maxwell *et al.* 1964, Davies 1983). Sediments have been shown to accumulate within algal mats of soft-bottom lagoonal habitats (Scoffin 1970) and on temperate rocky platforms (Stewart 1983), and it is clear that epilithic algal communities (EACs) can also accumulate and stabilise sediments on hard reef substrata of coral reefs.

Shallow forereef zones can be viewed, on a unit area basis, as trophically dynamic regions of platform coral reefs of the GBR. In these zones, the production of organic material by EACs is often high (Hatcher 1981, Polunin and Klumpp 1992), and is coupled with high rates of secondary production due to intense grazing by invertebrates (Klumpp *et al.* 1988, Polunin and Klumpp 1992) and fishes (Hatcher 1981, Russ 1984, Polunin and Klumpp 1992). At Lizard Island, in the northern GBR, windward crests and slopes have been shown to contain prolific assemblages of sessile invertebrates, especially corals (Pichon and Morrissey 1981, Nelson 1992), which are spatially interspersed with EACs.

The nature and distribution of sediments are important characteristics of forereef habitats on coral reefs because of the effects these have on benthic communities. The sediment load (accumulated mass) on substrata, for example, can strongly affect the settlement and survivorship of corals (reviewed by Rogers 1990, Babcock and Davies 1991, Wittenberg and Hunte 1992). Within forereef EACs, sediment load may also affect the feeding biology of herbivores which must contend with this inorganic component during grazing (Choat 1991). Additionally, grain size composition of sediments has been shown to influence the community structure and diversity of mobile benthic invertebrates (Gray 1974, Jones 1984, Diaz and Erséus 1994). Knowledge of the patterns of sediment distribution and the way in which these are associated with EACs on hard forereef substrata is currently lacking.

From a physical perspective, sediment distribution on coral reefs is thought to be governed by hydrodynamic processes (Suhayda and Roberts 1977, Davies 1983), but it may be influenced also by sessile reef biota via modification of reef surfaces at local-scales. Epilithic algal communities (EACs) on reefs of the GBR are widespread and ubiquitous (Price and Scott 1992, McCook *et al. in press*) and present a carpeted texture to forereef surfaces. Carpenter and Williams (1993) recently demonstrated, on a Caribbean forereef, that the canopy heights of EACs reduce flow speeds of water near reef surfaces. Physical characteristics of EACs relate to boundary layer characteristics, and thus may also relate to sediment deposition and retention on reef surfaces.

This study examines EACs and sediment loads amongst zones across a windward reef in the northern GBR with two main objectives. Firstly, to determine the patterns of sediment distribution amongst these forereef zones, and secondly to investigate the relationships between sediment load and physical characteristics of EACs, namely canopy height and algal types. The intention here was to ascertain whether EACs could mediate sediment

distribution and thus the influence of sediments on benthic reef biota in these productive zones.

3.2. Materials and methods

3.2.1. *Study site*

Field work was conducted on the exposed, subtidal reef between Bird Islets and South Island (14°42'S, 145°28'E), adjacent to Lizard Island, approx. 30 km from the mainland coast in the northern Great Barrier Reef (Fig. 3.1). This location receives little input of terrigenous sediments, which are restricted to the mainland coast in this region (Torgersen *et al.* 1983). The front margin of this reef is aligned in a SW-NE direction and is thus exposed directly to the dominant SE trade winds and receives frequent periods of moderate wave energy. The site is characterised by numerous, large 'bommies' (carbonate pinnacles) rising from a depth of approximately 10 m, 10-30 m in front of the contiguous crest and reef platform. The physiography and hydrometeorology of this site has been described previously in detail by Pichon and Morrissey (1981). The geomorphology, wave energy and leeward relief of the study reef are typical of the windward margins of midshelf platform reefs described by Price and Scott (1992) to comprise the majority of reefs on the Great Barrier Reef.

Three transects were laid haphazardly 70 to 120 m apart along the reef in areas with adequate algal cover (approx. >40%) and not fragmented by spur and groove ('gutter') structures, and were aligned perpendicular to the crest. The transects started from the reef base immediately in front of the crest, and extended back towards the inter-island lagoon. Barnes *et al.* (1975) showed that water movement along similar transects on this reef was in a leeward (NE) direction during both flooding and ebbing tides, therefore, the present transects were expected to parallel the dominant axis of current

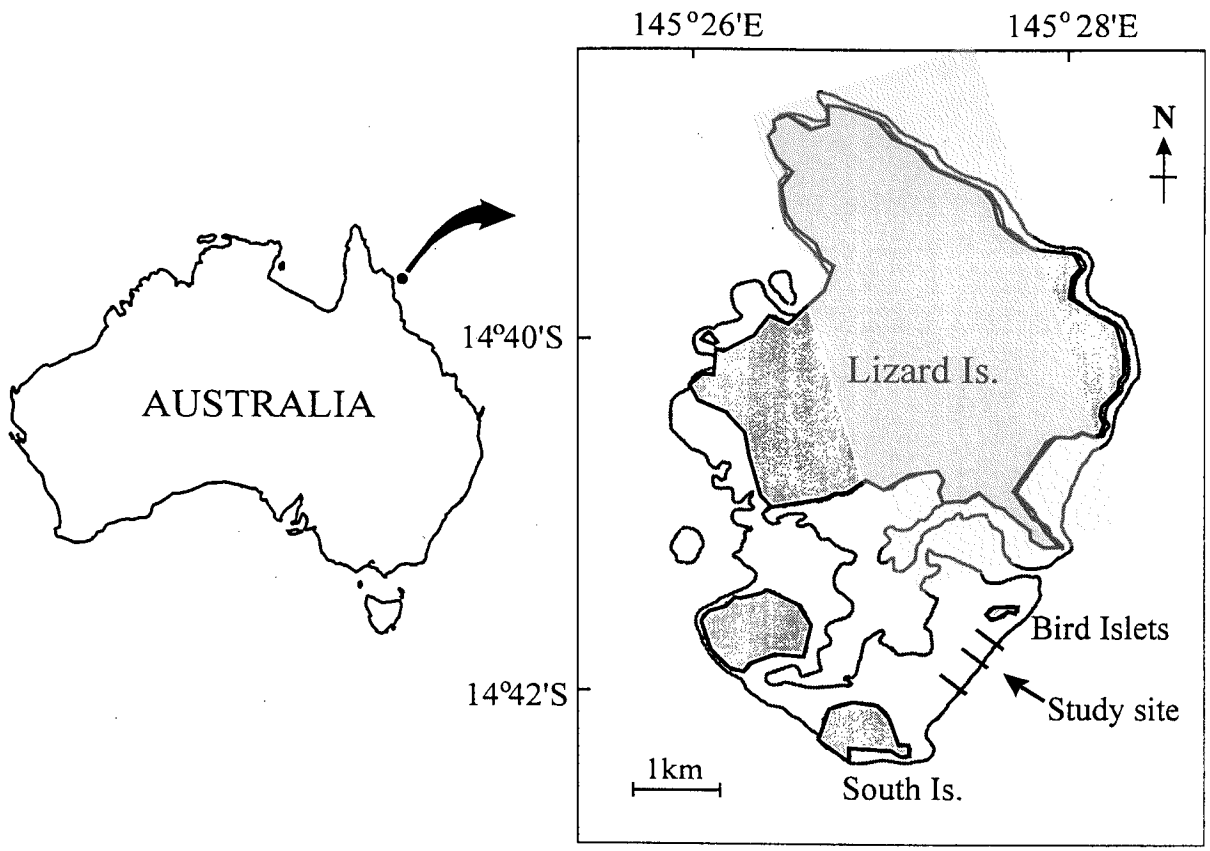


Fig. 3.1. Map indicating the location of Lizard Island and the three transects within the forereef section of the platform reef between Bird Islets and South Island. See text and Fig. 3.2 for location of habitat zones within each transect.

flow across the reef. Four habitat zones were nominated along each transect: the 'reef base' at 4-6 m depth, the 'crest', the 'fore-flat' (10 m behind the reef crest), and the 'mid-flat' (30 m behind the crest); see reef profile in Figure 3.2. Sampling areas for zones along each transect were delineated as 8 square metre areas of substrata, hereafter referred to as 'plots', which were permanently marked out, 2 m long and extending 2 m either side of the transect line.

3.2.2. *Data collection*

Sediment samples and measurements of the substratum and algae within each of the twelve plots were taken daily on SCUBA, between 0800 and 1330 hrs on ten days (i.e. for each variable, total n = 120) during a 16 day period in October 1994. This sampling effort was predicated on pilot sampling of sediments from sites at Lizard Island that suggested that 10 replicates should yield a sampling precision (SE/mean) of 0.15 to 0.20. The sampling order was rotated periodically and, to maintain standardisation of techniques, all sampling was carried out by the author throughout the study. Sampling was interrupted for six days during the middle of the study period due to rough weather (wind speed 15 - 25 knots, swell approximately 1 m).

Within each plot, samples (n = 10) were taken from EACs on areas which were: 1) flat ($<15^{\circ}$ from horizontal), 2) free of obvious pits for sediment retention, and 3) free of macrophytes higher than 20 mm. A sampling ring (5 mm high) covering 100 square cm (1 dm^2) was pinned down to the first random area of substratum encountered within the 2 x 4 m plot which met these requirements. Sediments within the sampling unit were collected using the apparatus and methodology described in Chapter 1, which allows EAC-bound sediments to be vacuumed and retained without removing the attached algae. Each sediment sample consisted of fine particles contained in a plastic collection bag and coarse particles trapped within a pre-

filter. Each area of substratum with its associated EAC was then photographed using a Nikonos V camera with a macro lens.

Estimates of canopy heights of the EACs, from which sediments were extracted, were obtained from means of the heights above the substrata of 20 randomly selected algae within the sampling unit areas. This was achieved by firstly overlaying a second ring, bearing a grid of strings with randomly positioned knots, over the initial sampling ring. The height above the substratum of the alga under each knot was then measured using a naval compass. For each alga measured, the point of one arm of the compass was placed on the substratum at its base and the other arm (with pencil tip) was adjusted to the uppermost part. The distance between arm tips (= height above substratum of the alga) was then recorded (by marking with pencil tip against a reference line) on underwater paper and later measured to the nearest mm. The standard deviation of these individual measurements of algae within each sampling unit was on average 39% of the mean, reflecting high variability in algal length at this fine scale. Average precision (SE/mean) of these samples was 0.09 which shows that the 20 measurements provided a precise estimate of the mean EAC height above substratum within sampling units. Tags were nailed to the centres of the sampled areas of substratum to prevent re-sampling on subsequent days.

In the laboratory, sediments needed to be separated from the seawater of the samples. Sediments in the pre-filters and collection bags were combined and this total sample was filtered through two successive mesh screens, 63 and 20 μm, and rinsed briefly with freshwater. Visible invertebrates were removed from the samples, then the two screen fractions were scraped into a labelled sample vial and were frozen and later freeze dried.

For samples collected on the last five days, sediment splits from the 63 μm and 20 μm screens were retained separately. This provided a test of

the proportionate efficiency of these mesh sizes at retaining sediments. Once these sediment splits were freeze dried and fully processed (see below), this test revealed that the 63 μm screens were highly efficient, as they also collected 66.79% (± 2.16% SE) of all sediments less than 63 μm through the compacting effect of sediments during sieving. Tertiary filtering of the filtrate (using GF/C glass fibre filters) from four sediment samples (one from each zone) also showed that the use of 63 μm and 20 μm screens successfully collected 99.86% (± 0.11% SE) by weight of all sediments collected in field samples.

Each of the freeze dried sediment samples from the first 5 days were weighed and placed into a plastic trough, where they were spread out evenly and separated into four sections. One portion was selected randomly, weighed and retained for a separate study, examining the detritus mixed with the sediments (Chapter 4). For each sediment sample, the remaining three portions to be used for sediment analysis were combined and weighed. These 'sub-samples' and the sediment samples from the final 5 days (total n = 120) were treated with 10% sodium hypochlorite (bleach; $NaHClO_4$), as described in Chapter 1, to remove organic material. The sub-samples were oven-dried at 60° C, freeze dried again, weighed and dry-sieved through a connected series of small (50 mm diameter) mesh sieves (2000 to 63 μm). Sieves were shaken for 2 to 3 minutes to ensure complete separation of grain size classes, which were then weighed to the nearest 0.1 mg. For each of the sediment sub-samples, the sample weight was multiplied by a correction constant, calculated by dividing the initial sample weight by the weight of the three combined sub-samples before bleach-washing, to provide an estimate of the total bleach-washed sediment weight.

In situ removal of sediments from EACs acted also to reveal the algae within sampling units for puposes of identification into broad functional groups with respect to perceived sediment trapping abilities. Published functional groupings of algae, shown to be ecologically useful, have been

based on anatomical and morphological characteristics of algal genera (Steneck and Watling 1982, Steneck and Dethier 1994). It was not possible to categorise algae into these published functional groupings because the genera of algae could often not be accurately identified (by I.R. Price) from slide photographs and because anatomical investigations of the algae within these EACs, which are highly speciose (Price et al. 1976), were beyond the logistics of this study. Further, filamentous and corticated (small branched) algae occurred often intertwined, precluding delineation of surface area coverage for these algal types separately.

Slide photographs of each sampled area were examined, and each identifiable portion (>3 mm^2) within the sampling unit was grouped as:

Algae: 1) crustose - non-geniculate coralline or fleshy algae in an encrusting mono layer (eg. *Peyssonnelia, Porolithon, Spongites*)

2) domed - single or compound with rounded or domed shape; not branching (eg. *Codium, Colpomenia, Dictyosphaeria, Ventricaria*)

3) filamentous and small branched - filamentous algae, macroalgae with thin branches, corticated macroalgae or blue-green algae; erect or stoloniferous (eg. *Amphiroa, Caulerpa, Ceramium, Dictyota, Enteromorpha, Gelidiella, Herposiphonia, Jania, Lyngbya, Polysiphonia, Pterocladia, Valoniopsis*)

4) broad macroalgae - erect, leathery macroalgae and broad articulated calcareous algae; broad branches or segments wider than 3 mm (eg. *Halimeda, Sargassum, Turbinaria*)

Other: 5) bare substrata

6) invertebrates (e.g. sponge, coral recruit, echinoid)

To determine the percentage cover of algae within these categories, areas on the projected images covered by each group were delineated, traced

onto paper and digitised using a Houston Instruments Hi-Pad and with Sigmascan® software (Jandel Scientific V3).

To avoid confusion, the term 'turf algae' has been avoided here because of the variable nature by which it has been defined. For instance, Hay (1981) defined 'turfs' morphologically as algae that have relatively tall branches (> 5 mm) packed closely together, while Scott and Russ (1987) refer to 'algal turfs' as "aggregates of small filamentous and fleshy algae with developmental stages of larger algae". Further, and more commonly, 'turfing' algae are recognised as an assemblage of diminutive algae, primarily unicellular and filamentous forms (Borowitzka *et al.* 1978, Rogers and Salesky 1981, Carpenter 1986, Steneck 1988, Williams and Carpenter 1990, Klumpp and McKinnon 1992). The 'filamentous and small branched' group of the present study includes these latter defined 'turfing' algae along with small fleshy macroalgae, and thus is closest to the 'algal turfs' of Scott and Russ (1987). The functional groupings of algae used here are relatively broad, and algal types which could be considered functionally separate have had to be pooled for logistic reasons discussed. This approach may preclude the detection of patterns of distribution of algal types and/or correlations with sediment retention.

3.2.3. *Statistical Analyses*

EAC canopy height and sediment load data were log(x + 1) transformed (see Underwood 1981), which homogenised variances (Cochran's test) and normalised distributions for parametric analysis. Differences in mean sediment loads amongst zones (fixed factor) and transects (random factor) were tested using a 2-way ANCOVA, employing an unconstrained model, with EAC canopy height as the co-variate. The assumption of parallelism (colinearity) was confirmed by non-significance of tests of interaction between the covariate and the two factors (zone and transect) and their interaction.

Multiple comparisons following the ANCOVA were not carried out due to non-independence of adjusted means (Day and Quinn 1989).

The relationships between EAC canopy height and sediment load within zones and for all data combined were assessed using correlation analysis on $\log(x+1)$ transformed data. The percentage cover of each functional group of algae within EACs were also correlated with the $\log(x+1)$ transformed sediment load data for each zone. Correlation coefficients are used here as a measure of the intensity of association between two variables (Zar 1984) and are presented without probability values to avoid compounding type I error rates of hypothesis tests.

A multivariate analysis of variance (MANOVA) was carried out (SPSS 6.1, SPSS Inc.) to test for differences in grain size composition (percentage dry weight of each size fraction) of sediments amongst zones and transects. Data on $\log(x+1)$ transformed percentage weight of grain size fractions were used as variables analysed simultaneously. Canonical discriminant analysis (CDA) was then used to identify which plot(s) had sediments with significantly different grain size compositions, and which grain sizes were important in the differences among plots. Data on the percentage of <63 μm sediments displayed strong interdependencies with >63 μm (63 - 125 μm) sediments, and would have yielded similar structure coefficients for the CDA. This variable was thus considered redundant with respect to partitioning variance for between-group centroid separation, and was omitted from the analysis.

3.3. Results

Sediment loads varied markedly amongst habitat zones along the reef profiles examined (Fig. 3.2a). The ANCOVA test showed that EAC canopy height had a significant effect on sediment loads and that significant spatial variations in

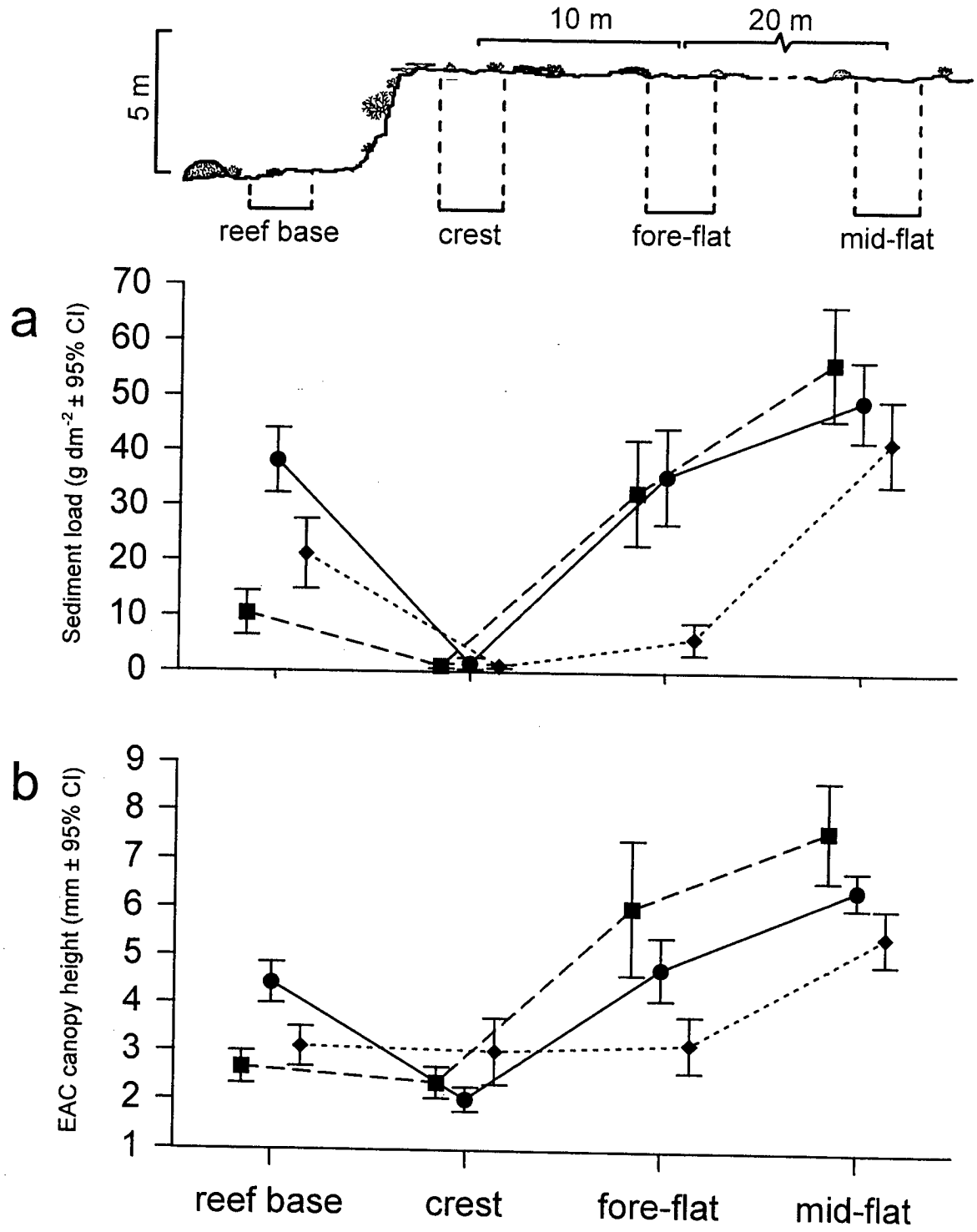


Figure 3.2. Spatial profiles along transects of (a) mean sediment loads (n = 10), and (b) mean EAC canopy heights (n = 10) for each zone. Lines represent the changes in these variables amongst successive zones along each transect (*dashed* = T1, *solid* = T2, *dotted* = T3). Schematic representation (above) of a 'typical' transect illustrates the cross-section reef profile at the study site, and the relative positions of sampling plots within each zone. Vertical scale is the approximate depth with respect to MLW.

mean sediment loads occurred even when these were adjusted for the effects of EAC canopy height (Table 3.1). While differences in sediment loads amongst zones were significantly variable amongst transects (significant zone x transect interaction), trends along this hydrodynamic gradient in broad terms are worth noting (Fig. 3.2). For instance, mean sediment loads at the reef base were quite variable amongst transects (10-38 g dm^{-2}), but are within the upper and lower bounds of those of upper platform zones (Fig. 3.2a). On all crest plots, in contrast, the average sediment loads (1-2 g dm^{-2}) were the lowest of any of the zones. The homogenous distribution of sediments on crest substrata is revealed by the relatively low local (within plot) variability.

Table 3.1. Results of mixed-model ANCOVA of differences in mean sediment loads amongst zones and transects with EAC canopy height as the covariate. Continuous data were log (x + 1) transformed.

Source	SS	d.f.	MS	*F*	*p*
zone	6.20	3	2.07	10.59	0.013
transect	.69	2	.34	1.79	0.264
zone x transect	1.28	6	.21	11.88	< 0.001
EAC canopy height	.75	1	.75	41.76	< 0.001
residual	1.91	107	.02		

As a trend, mean sediment load increased in successively leeward zones from the crest(Fig. 3.2a). Spatial profiles of mean sediment load along transects were variable however, demonstrating that these incremental changes in sediment load were not simply a function of distance from the crest. The layers of sediments on substrata within mid-flat plots were the greatest of any of the zones examined, with mean loads ranging from 40-56 g dm^{-2}. Sediment loads within fore-flat and mid-flat EACs were highly variable within plots, reflecting a high degree of patchiness at a local (within-plot) scale.

Spatial patterns in the mean canopy heights of EACs along transects (Fig. 3.2b) were very similar to those described for sediment loads. (Note that these values are means of the *mean* heights above the substratum of algae within sampling units.) The relatedness of these variables at the scale of this study reef is indicated also by a significant positive correlation (Pearson's correlation coefficient $r = 0.83$; $p < 0.001$) for data of all zones combined (Fig. 3.3). At a reduced scale, this relationship was strong within each zone except the reef crest, where the positive correlation detected between these variables was weak (Table 3.3; see also Fig. 3.3). It is worth noting that the crest on transect 3 contained a territory of the surgeonfish *Acanthurus lineatus* (Linneaus); a herbivore which can modify the algal community in its territory (Robertson *et al.* 1979). The algae in this crest plot were taller, on average, compared with algae elsewhere in this zone, but these EACs held similarly low sediment loads.The significant interaction in the ANCOVA test, which accounted for the effects of algal canopy heights, indicates that other factors influenced the relationship between sediment loads and EAC canopy heights at a local scale.

While the sampling design was not explicitly designed to examine the temporal dynamics of sediment loads and EAC canopy heights, the occurrence of rough weather, that interrupted sampling, allows pre/post comparisons around this event to be made. Figure 3.4 illustrates that mean sediment loads and EAC canopy heights of most plots (9 out of 12) exhibited decreases after the rough weather. Note that proportional changes in these variables were comparable in magnitude within zones except the crest. On average, sediment loads on crest substrata were reduced by 45% (±16% SE) while their EAC canopy heights remained relatively static over this period, decreasing by only 7% (±1% SE).

Sediments within EACs amongst the four habitat zones studied predominantly had coarse sand (500-1000 μm) as the modal grain size, although their overall composition was different (Fig. 3.5). The MANOVA test

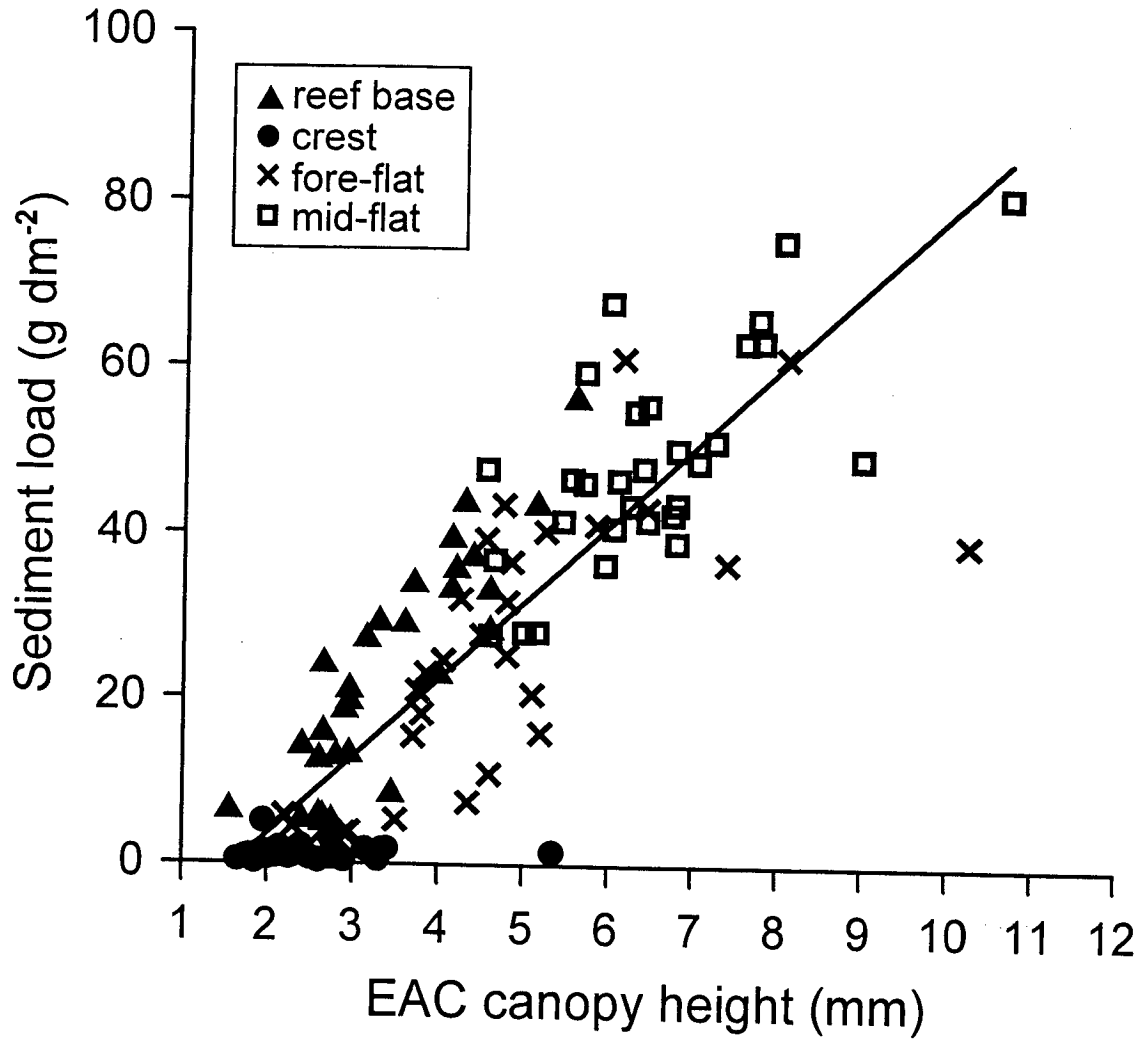


Fig. 3.3. Scatterplot of paired measurements of sediment load vs. canopy height of EAC's within the four habitat zones. Line of best fit represents the correlative trend for the combined data (r = 0.83; p < 0.001; n = 120).

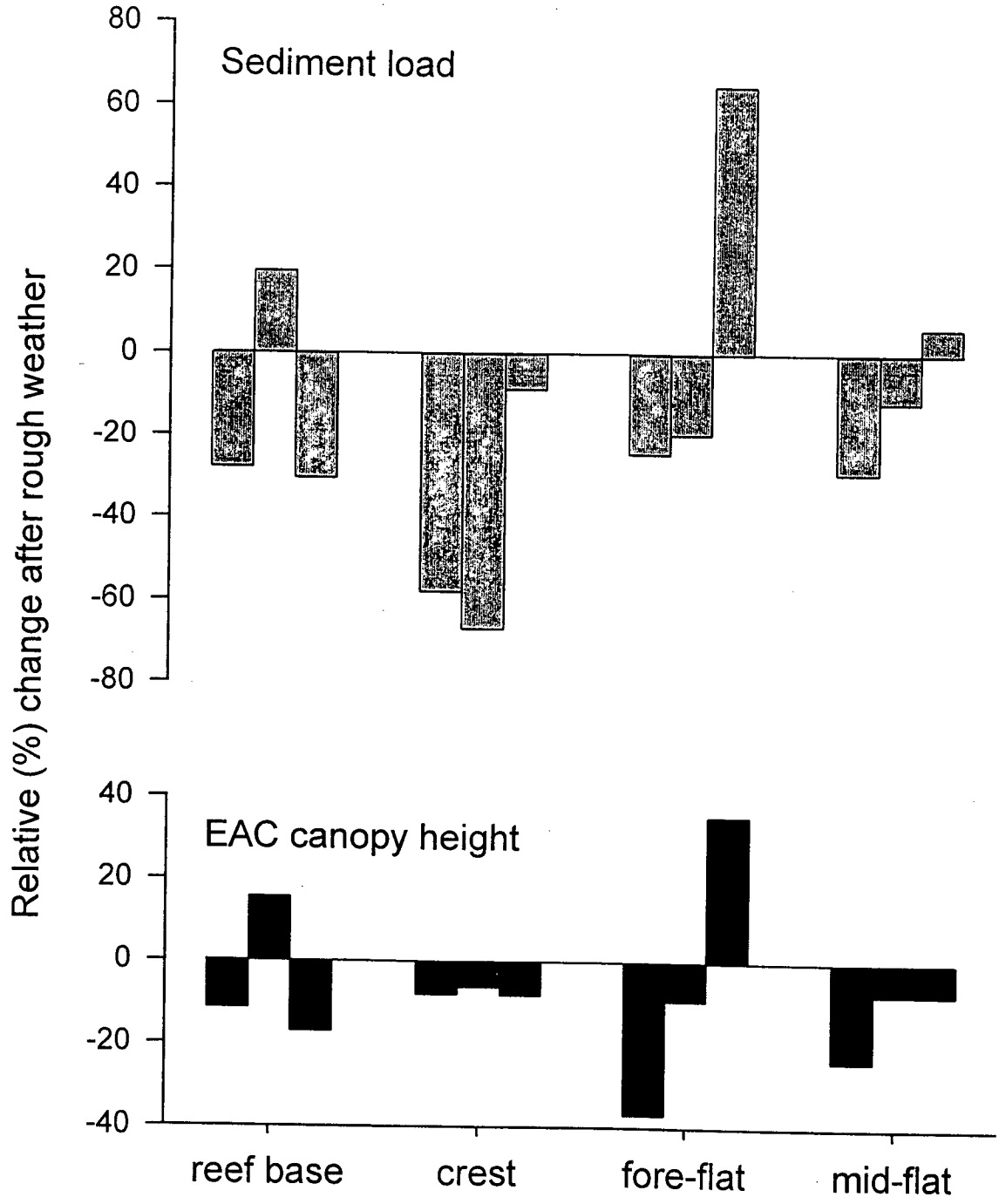


Figure 3.4. Bar graph of the changes in mean sediment loads and canopy heights of EACs after rough weather. Bars indicate the percentage difference of the means after this event (n = 6) compared to those before (n = 4), for each transect across the four zones; negative values represent reduced means.

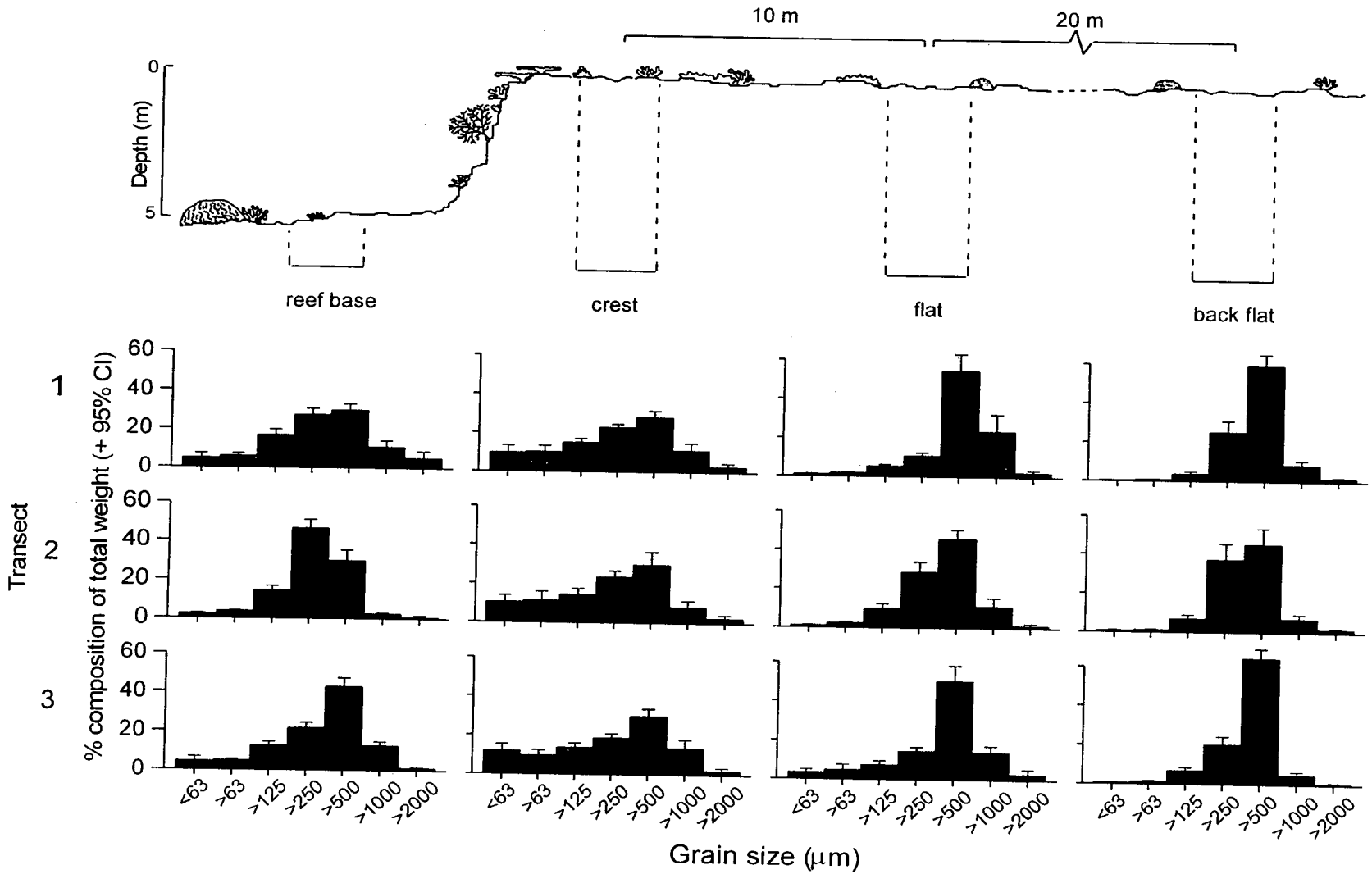


Fig. 3.5. Spatial patterns in the mean proportional contributions of grain sizes of sediments collected within the three transects across the four habitat zones (n = 10 for each bar).

on mean grain size composition detected a significant zone x transect interaction (Pillai's Trace $F_{36, 648} = 7.159$; $p < 0.001$). While this shows that changes in sediment composition amongst zones were not the same amongst all transects, spatial trends in broad terms were apparent. For example, crest sediments were poorly sorted (contained even proportions of grain sizes), and differed from those of other zones primarily in displaying higher proportions of fine sand and silt sized (0-125 μm) grains (Fig. 3.6). Their composition appears to be highly consistent amongst different positions along this front reef crest compared with sediments amongst plots in other reef zones (Figs. 3.5 and 3.6). As a trend, sediment composition became well sorted with distance from the crest. In contrast to the crest, sediment grains <125 μm in size made up a smaller proportion of the sediment load on fore-flat plots, and even smaller contribution to sediments within mid-flat EACs (Fig 3.5). Mid-flat sediments were composed predominantly of medium and coarse sand, i.e. 250-100 μm grains (Figs. 3.5 and 3.6). Sediments within EACs at the reef base were generally poorly sorted, although not to the extent of the crest sediments, and were highly variable in composition amongst transects (Figs. 3.5 and 3.6).

In general terms, functional groups of algae within EACs were present in similar proportions, in terms of surface area coverage, amongst zones (Table 3.2). (It should be noted, that at a higher resolution, these communities appeared to vary greatly in species composition amongst zones.) Patchiness in the composition of functional groups of algae at within-habitat and within-plot scales is evident, however, in the variability in mean coverage amongst and within transects for most groups. Within the EACs defined by the sampling criteria, algae within the 'filamentous and small branched' group, on average, constituted the highest percentage area cover in all zones (mean, 75-88 %), followed by crustose forms (mean, 4-20 %).

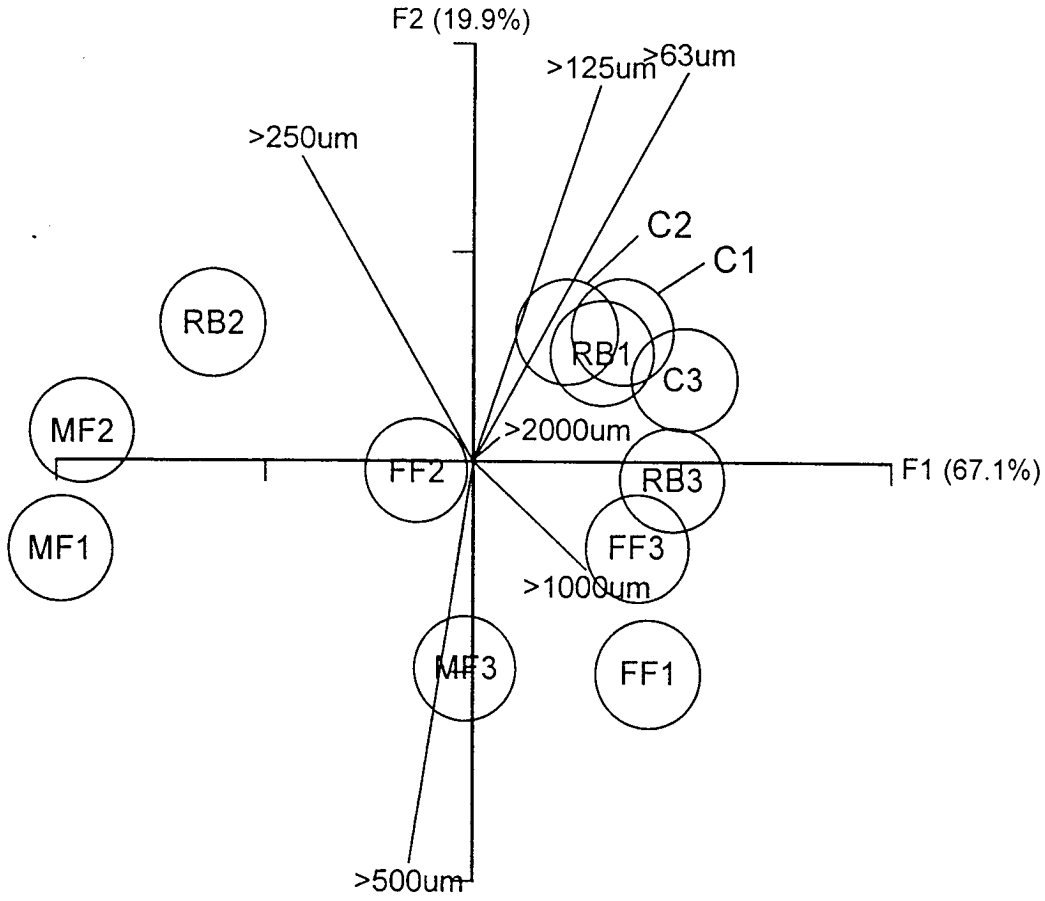


Fig. 3.6. Ordination of Canonical Discriminant Analysis (CDA) of the grain size composition of sediments collected from the three transects across the four habitat zones. Plot illustrates the first two axes (and their percentage variance contribution) of the CDA with approximate circular 95% confidence intervals around each group mean centroid of data from each of the four zones (RB = reef base, C = crest, FF = fore-flat, MF = mid-flat) along each transect (1-3). Lines indicate the structure coefficient vectors of the discriminating variables (grain sizes) with longer lines indicating stronger influence in separating mean group centroids.

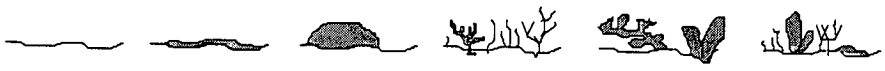
Table 3.2. Mean proportional surface area cover (± 1 SD) of bare substrata and algal functional groups within sampling units (n = 10 x 1 dm^2) from each zone on each of the three transects. Note that the sampling criteria excluded macroalgae > 20 mm tall.

zone	transect	bare	crustose	filamentous and small branched	domed	broad macroalgae
reef base	1	5.5 (± 2.4)	9.6 (± 6.0)	83.7 (± 6.5)	0.1 (± 0.5)	0.5 (± 0.8)
	2	9.1 (± 6.1)	4.3 (± 2.6)	86.1 (± 5.2)	0.2 (± 0.3)	0.2 (± 0.7)
	3	8.4 (± 3.9)	3.7 (± 2.9)	87.6 (± 4.2)	0.1 (± 0.1)	0
crest	1	7.7 (± 4.2)	8.9 (± 3.9)	83.1 (± 6.8)	0.3 (± 0.7)	0
	2	3.9 (± 2.3)	19.8 (± 6.0)	76.3 (± 5.9)	0	0.1 (± 0.3)
	3	6.0 (± 4.1)	6.9 (± 5.7)	85.5 (± 7.3)	1.1 (± 2.6)	0.2 (± 0.5)
fore-flat	1	5.0 (± 3.3)	6.9 (± 6.0)	80.5 (± 9.8)	3.0 (± 4.2)	4.4 (± 8.4)
	2	8.7 (± 4.1)	6.7 (± 4.8)	84.2 (± 6.5)	0.1 (± 0.5)	0.2 (± 0.5)
	3	8.3 (± 3.8)	14.0 (± 11.1)	76.6 (± 8.6)	0.5 (± 1.5)	0.5 (± 1.0)
mid-flat	1	9.7 (± 3.7)	7.8 (± 5.1)	80.2 (± 8.5)	1.6 (± 2.3)	0.4 (± 0.6)
	2	9.2 (± 2.6)	7.0 (± 3.1)	82.2 (± 6.6)	1.2 (± 2.1)	0.2 (± 0.4)
	3	11.4 (± 6.4)	12.7 (± 5.7)	74.9 (± 9.9)	0	0.9 (± 0.9)

Algal morphologies were correlated to sediment load within habitat zones in different ways (Table 3.3). High surface area cover of crustose forms appears to reduce the potential for EACs to trap sediments, as correlations with sediment load were negative in all zones except the crest. Conversely, the area covered by filamentous and small branched algae was positively correlated with sediment load on fore-flat and mid-flat habitats, indicating that algae within this functional group can increase sediment retention. This was not the case on substrata within the turbulent crest or deeper reef base, where coverage of filamentous and small branched algae was weakly correlated with sediment load. Algae within the 'domed' and 'broad macroalgae' groups were uncommon in the areas sampled, and were weakly correlated with sediment load in all reef zones ($r \leq 0.02$). Bare

patches covered relatively small percentages of substrata, and displayed weak correlations with sediment load within zones except at the reef base, where this relationship was notably positive.

Table 3.3. Summary of the relationships between sediment load (g dry wt dm^{-2}) and the percentage surface area cover of bare substrata, each functional group of algae, and canopy heights of EACs for each zone (transects pooled). Values are Pearson's correlation coefficients (*r*); *n* = 30 paired replicates for each correlation. Filamentous and small branched = F + SB; broad macroalgae = BM.



Zone	Bare	Crustose	Domed	F + SB	BM	Canopy Ht.
Reef base	.46	-.34	.20	-.07	-.07	.80
Crest	-.10	.04	.12	-.01	.17	.20
Fore-flat	-.27	-.40	.01	.47	.06	.82
Mid-flat	-.15	-.41	.20	.29	-.03	.70

3.4. Discussion

Sediment loads and the canopy heights of EACs varied markedly amongst forereef zones on this platform reef. These two variables were closely correlated at scales of the study reef and within habitat zones also, with the exception of the crest where sediment loads were low. Differences in sediment loads amongst zones were not attributed to the canopy heights of EACs alone, suggesting that other factors that vary spatially, namely hydrodynamic forces, also strongly affect the magnitude of accumulation on forereef substrata. Indeed, distribution patterns of sediments at the scale of a

reef are considered to be determined mainly by hydrodynamic forces from waves and tidal currents (e.g. Maxwell *et al.* 1964, Flood and Orme 1977, Suhayda and Roberts 1977, Davies 1983). The distribution of sediments within EACs of this platform reef followed a pattern based on these forces, noted by Pichon and Morrissey (1981), of minimal accumulation on the crest and increasing sediment load in zones with lower wave action and distance from the crest.

Epilithic algae on coral reefs are often present as compact assemblages of species of erect, and often branching, habit (Price and Scott 1992). These features predispose them to trap and accumulate particulates, and this should affect sediment distribution at local-scales. The study site was similar to most of the exposed reef fronts on midshelf reefs of the GBR (Price and Scott 1992), which experience strong wave and tidal current forces. While differences in these hydrodynamic forces at the scale of this study reef would explain the observed distribution of sediments, these forces do not easily explain the corresponding pattern of canopy heights of EACs.

In addition to local-scale effects of algal trapping on sediment loads, it is possible that patterns of EAC canopy height at the scale of this study reef reflect a benefit from sediments. For example, it could be argued that sediments may enhance the growth of epilithic algae through desorption of sediment-associated nutrients, namely phosphorus (Patriquin 1972, Entsch *et al.* 1983, Furnas 1992). High sediment loads have been considered, however, to decrease algal growth by smothering (Adey & Goertemiller 1987, Lawn & Prekker 1993). Alternatively, the heights of EACs are governed by the extent of cropping by herbivores, which is in turn influenced by the thickness of the sediment layer. Regulation of EAC canopy heights by herbivores seems quite plausible, given that their grazing strongly affects algal abundance on coral reefs (eg. Sammarco *et al.* 1974, Wanders 1977, Sammarco 1982, Hatcher & Larkum 1983, Hughes *et al.* 1987), and is generally most intense towards

the (low-sediment) forereef crests on platform reefs of the GBR (Hatcher 1981, Russ 1984, Polunin and Klumpp 1992).

Rough weather appeared to have an initial effect of resuspending and removing some sediments held within EACs. The cause of the concomitant trend of reduced algal heights after rough weather is, however, not so clear. While some filamentous and/or fleshy coral reef algae are considered to be adapted to areas subjected to strong currents or wave surge (Hay 1981, Hackney *et al.* 1989), there are physical limits to such adaptation. Sloughing of long algal filaments by wave action (see D'Elia & Wiebe 1990) or abrasion of algae by shifting sediments during rough weather here may have lead to a reduction in EAC canopy height. A further mechanism causing the reduced canopy heights of EACs may have been a response in the feeding behaviour of browsing herbivores, such as some acanthurids which nip exposed distal portions of algae (Purcell and Bellwood 1993). However, an assessment of this idea would require temporally replicated measurements of such responses to reductions in sediment layers, which are currently not available.

Although the results indicate that sediment loads are related to EAC canopy height, variability in sediment loads amongst and within habitat zones could not be attributed to this relationship alone. In particular, differences in sediment loads amongst habitat zones were still significant when effects of algal canopy height were partitioned in the ANCOVA. Forereef crests are zones usually exposed to high wave energy (Maxwell *et al.* 1964, Suhayda and Roberts 1977, Price and Scott 1992). Sediment loads on crest substrata may thus be influenced more by wave forces that override fine-scale boundary layer effects of EACs, resulting in weaker associations with algal heights.

It is interesting that the composition of EACs, on a surface area coverage basis, was roughly similar amongst zones (Table 3.2) despite

marked differences in EAC canopy heights. At the resolution of functional groupings used here, the composition of EACs could not explain patterns of sediment distribution amongst zones. This may reflect the broadness of the functional groups used, in view that community structure of algae using more detailed functional groupings has been demonstrated to vary amongst habitats of differing productivity and disturbance potentials (Steneck and Dethier 1994). If it had been possible to separate further the functional groups here, it is quite likely that significant differences in EAC composition amongst these forereef zones would have been revealed. For example, simple filamentous algae seemed to dominate the 'filamentous and small branched' group on the crest, with fleshy macroalgae becoming more abundant in leeward zones.

At the finer scale of within habitats, the findings did show that algal functional groups were related to sediment accumulation. Cortés and Risk (1985) hypothesised that areas with relatively cemented substrata would accumulate less sediment, which would simply pass over these areas. The present study supports this idea, as EACs with higher percentage cover of unbranched crustose (i.e. non-geniculate) algae tended to hold less sediment, with the converse occurring for algae within the 'filamentous and small branched' group, which are able to form a canopy, on both reef flat zones. Clearly, there is a confounding effect of algal shape on height; crustose forms are short, while filamentous and branching forms can be tall. In simple terms, only the canopy-formers can trap sediment, while those that are spatially simple and unbranched can not. These basic disparities in sediment trapping abilities may explain some of the variability in sediment loads at a within-zone scale in this study. It is likely that finer-scale functional groupings would have produced a more detailed understanding of relationships between algal morphology and sediment retention. Further, these relationships have been considered here in tems of surface area coverage only and do not consider the frond densities of algae. If relationships were considered also in terms of biomass, the relative importance of 'turf' algae (*sensu* Williams and Carpenter

1990) for sediment retention may have been emphasised (see Steneck 1997).

Bare, excavated areas of substrata also correlated positively with sediment loads at the reef base, but not within zones on the upper reef platform. This is expected, as accumulations of sediment on reefs are often the result of the filling in of hollows in the bedrock, except where current strength is high (Scoffin 1970) and supports the idea that substratum microtopography influences sediment retention, particularly in less turbulent zones.

In addition to spatial variations in sediment loads, the grain size composition of sediments varied also amongst zones. Modal grain size is commonly used to define distributional patterns of sediments on coral reefs (e.g. Maxwell *et al.* 1964, Flood and Orme 1977, Jones 1984). However, in the present study, the 500-1000 μm grain size was the modal class in eleven of the twelve plots sampled, despite significant variations in sediment grain compositions. These findings therefore caution that while a univariate approach may be convenient for distinguishing sediments where these cover a wide range of depositional environments, it does not seem appropriate for studies of sediment types on forereef habitats.

Grain size compositions of sediments on reefs are thought to be indicative of the hydrodynamic conditions acting within each zone (Maxwell *et al.* 1964, Flood and Orme 1977). In this context, crests are depicted as zones where fine sediments do not accumulate due to a regime of high wave energy (Maxwell *et al.* 1964, Roberts and Suhayda 1983). While sediment loads within EACs on the crest in the present study were always low, these sediments actually contained relatively high proportions of fine sediment grains. Similar findings have also been reported at Lizard Island using different sampling techniques (Bellwood 1996). These 'Type III' sediments (*sensu* Flood & Orme 1977) are more typical of protected leeward reef zones which

have lower resuspension rates. Multivariate ordination of grain size data showed crest sediments in the present study to be highly similar in composition between crest plots, suggesting that similar features which unify this zone, such as the filamentous nature of the algae, may be a key in understanding this contradictory finding. The pattern of increased sorting (uneven spread of grain sizes) of sediments across zones with leeward distance from the crest supports previous suggestions that silt-sized particles are removed (separated in suspension) from the pool of forereef sediments during bed-load transport in a leeward direction to less turbulent zones (Maxwell *et al.* 1964, Davies 1983, Bellwood 1996).

This study may help to predict and explain sediment distributions across similar forereef habitats, but should be extrapolated with caution given the variability in geomorphology and hydrodynamic regimes amongst coral reefs. For instance, it is possible that the results have an inherent island effect; the neighbouring islands and compressed nature of the zones of the reef platform may manifest sediment types and distribution that differ from those of non-island platform reefs of the GBR. Furthermore, Caribbean coral reefs with algal ridges (see Adey 1975, Steneck and Adey 1976, Connor and Adey 1977) may have sediment distributions quite dissimilar to those depicted here due to different hydrodynamic processes associated with these structural features and also the narrow tidal range. Indeed, one of the few studies of sediments on an upper platform reef by Garrett and co-workers (1971) at Bermuda showed mean grain size of sediments decreasing away from the crest. Had the transects in the present study been extended into the lagoon, this broader pattern for this GBR reef would probably have emerged (see also Maxwell *et al.*, 1964, Davies 1983).

In order to effectively forecast the magnitude and temporal scale of sedimentation on coral reefs, data on net inputs of sediment (e.g. from sediment traps) need to be integrated with information on existing (accumulated) loads. Koop and Larkum (1994) showed that measurements of

sediment supply to reef zones may poorly reflect the actual net load of sediments that are capable of being retained on substrata. Predictions of the susceptibility of habitat zones to sediment impacts based on the results of this study should also be tentative. For instance, while crest EACs were able to accumulate proportionally high contributions of fine sediment, these appeared to be ephemeral and loads were always low and are unlikely to be affected by slight increases in sedimentation rate due to the strong influence of wave action. Sediments within EACs of the reef base also had relatively high proportions of fine grains, and these zones may be more affected by fluxes of fine sediments because of lower turbulence levels and resuspension rates. Sedimentation impacts on reef biota associated with EACs are, therefore, likely to be greatest under calm weather conditions or in areas where EACs have the capacity to achieve tall canopies.

In summary, sediment loads on forereef substrata at this study reef were linked closely to the canopy heights of epilithic algal communities at the scale of within zones and within the study reef. Composition of EACs, based on functional groupings used here, appears also to affect sediment retention under certain circumstances at small scales. Local areas with high percentage cover of crustose algae were shown to accumulate less sediment than similar areas covered by intertwined filamentous and small branched forms. Finally, the potential of forereef zones to accumulate sediments can not be inferred from hydrodynamic information alone, as characteristics of benthic biota, such as EACs, appear to influence sediment dynamics at this scale.

Chapter 4

Sediments and the nature of algal and detrital food resources within forereef zones

4.1. Introduction

On tropical coral reefs, hard substrata that are not colonised by invertebrates are typically covered by highly productive epilithic algal communities (EACs). These communities have been shown to trap sediments (Chapter 3) and also accumulate detritus originating from triturated algae, dead animal tissue and sloughed mucous with a similar propensity. Consequently, algae consumed by reef herbivores generally contains an adherent complement of organic detritus and sediments (Choat 1991). Of ecological significance to consumers are the relative proportions of these three items within foraging areas, as herbivores must selectively feed on algae or incidentally ingest detritus and sediment, and conversely, detritivores must selectively procure detritus accumulated within EACs.

Processes that affect algal dynamics are important also to the detritus food chain on coral reefs. Although the grazing on epilithic algae is intense, a significant proportion of algal material removed by reef herbivores is not digested; assimilation efficiencies of algae are generally in the range of 35-45% for macro-invertebrates (see Klumpp and Pulfrich 1989) and 20-70% for fishes (Horn 1989, Bruggemann *et al.* 1994b, Galetto and Bellwood 1994). Thus, high grazing rates result in a continual production of triturated plant material. It is argued that this material, along with sloughed algae, forms the main constituent for the detritus pool on coral reefs (Hatcher 1983b, Kinsey 1985, Alongi 1988, Hansen *et al.* 1992).

An increasing perception among aquatic ecologists is that detrital food chains are key pathways for primary production to enter higher trophic orders (Pomeroy 1980, Hatcher 1983b, Mann 1988). Likewise, evidence from coral reefs has shown that detritus is utilised by a wide range of animals (Hatcher 1983b, Alongi 1988) and may be necessary for the transfer and recycling of energy and nutrients within these ecosystems (Koop and Larkum 1987). Most of this work, however, has been conducted within lagoonal habitats (e.g. Hammond 1983, Johnstone *et al.* 1990, Riddle *et al.* 1990, Hansen *et al.* 1992). In contrast, forereef zones have been largely neglected in quantitative research on detritus in spite of the fact that these often contain a high number of active bottom-feeders, especially herbivorous fishes (Hatcher 1981, Russ 1984). These productive zones are thought also to generate much of the detrital material for backreef habitats (Hatcher 1983b, Riddle *et al.* 1990, Polunin and Klumpp 1992). In a study using sediment traps at One Tree Reef in the southern GBR, Koop and Larkum (1987) concluded that forereef zones actually receive high inputs of detritus compared to backreef areas. There is currently little information to provide a basic understanding of forereef detritus in terms of its spatial distribution on substrata, relative contribution to the mass of particulates within EACs, and abundance in comparison to algal tissue. Such information would allow an appropriate assessment of food resource availability and broaden our perspective on detritus in reef trophodynamics.

Traditionally, detritus has been defined as non-living, particulate organic matter in various forms of decomposition (Bowen 1983, Mann 1988). However, in natural environments such as coral reef, this material is invariably colonised by suite of biota such as bacteria, fungi, microbes and microscopic invertebrates that act to breakdown further the detritus. Macro-consumers of benthic detritus on coral reefs generally consume large quantities of material and cannot separate the non-living fraction from that of the associated biota (Pomeroy 1980, Alongi 1988, Wotton 1994), and likewise, these components are difficult for the researcher to quantify

separately. For these reasons, the working definition of detritus as particulate organic material including the associated microscopic biota (*sensu* Hatcher 1983b) is arguably more appropriate for ecological studies and is the definition adopted in this dissertation.

While spatial variations in sediment loads have been shown to reflect the physical structure of EACs (Chapter 3), the relationship of sediments to algae and detritus with reference to their value as food resources on coral reefs is unknown. Specifically, it would be valuable to relate sediment loads to the biomass or nutritive quality of both algae and detritus amongst different forereef zones.

Nitrogen and phosphorus are essential elements for growth and metabolism in plants and animals (discussed in Chapter 2). Odum *et al.* (1979) noted that marine algae have negligible amounts of non-protein nitrogen, hence nitrogen content is an accurate indicator of protein content of algae and derivatives of algae, i.e. detritus. Nitrogen is considered to limit the growth of marine detritivores (Valiela 1984, D'Avanzo and Valiela 1990) and herbivores (Choat 1991), hence its ratio to carbon in food sources is an indicator of nutritional value. Differences in standing stock and nitrogen content of algae and detritus amongst zones are likely to strongly influence feeding and habitat preferences of herbivores and detritivores. This information would be useful for generating ideas about potential effects of sediments on reef food chains.

While consumers require phosphorus for metabolic functioning (ATP) and in nucleic acids, the lack of information about the selection for foods of high phosphorus content by reef consumers precludes the use of phosphorus content here as an indicator of food quality. However, information on phosphorus content in algae and detritus would be useful for examining spatial correlations for this element between these resources to stimulate

future testable hypotheses, and may serve in this study to indicate an element of growth limitation of algae.

This study aimed to collect associated samples of the total sediments, detritus and algae from discrete areas amongst forereef zones to permit correlative examinations of the way in which sediments relate naturally to algae and detritus. Given our limited knowledge of detritus on forereefs, the intention of this study is to also identify spatial patterns of the quantity and nutritive quality of detritus on forereef substrata and compare these with those of epilithic algae. This is in some respects a hypothesis generating exercise with respect to the relative importance of these food sources. That is, this information can indicate the apparent trade-offs, in terms of accessibility and nutritive quality of food resources, for forereef herbivores and detritivores. Although data on the distribution and feeding behaviour of herbivores and detritivores were not collected here, general trends from previous studies on these aspects on similar forereef areas on the Great Barrier Reef provides the basis for discussing the findings within this context.

4.2. Materials and methods

4.2.1. Data collection

The study was conducted on the windward, sub-tidal forereef between Bird Islets and South Island (14°42'S, 145°28'E), adjacent to Lizard Island, in the northern Great Barrier Reef (GBR; see Chapter 3 for details). Field work was conducted at the same time and used the same sampling design and schedule as that described in Chapter 3. To reiterate briefly, on each of 10 days within October 1994, sediments were collected from 1 dm^2 areas within each of 4 zones, defined along each of three transects aligned perpendicular to the reef crest margin. The substratum units (n = 120) were randomly selected from available areas in the defined plots which were flat, devoid of pits for

sediment retention, and were free of macro-algae of >20 mm height. These criteria provided a focus on algal assemblages which are the key primary producers (Wanders 1976, Klumpp and McKinnon 1989, 1992) and prime targets for the abundant herbivores and detritivorous fishes in these zones (Russ and St John 1988, Choat 1991). Sediments and detritus occur as mixed aggregates within EACs of coral reefs. These two components were vacuumed from EACs using a diver-operated device (Purcell 1996); each sample consisted of particulates (sediment + detritus) and about 5 l of seawater held within plastic bags.

Following collection of the resident sediment and detritus from each sampling area, the entire algal community was collected with the sediment sampler. This was achieved by scraping the sample substratum to a depth of 2 mm (approximated visually) with an angled steel tube, fitted to the intake hose. The detached algae were simultaneously sucked through a simple filter, containing a 220 μm mesh screen, fitted between the terminus and pump. This technique also collected a portion of the endolithic algae which constitute an important food resource for scraping herbivores (Bruggemann *et al.* 1994a). A cap was placed on the intake of algal filters, which were then retained on ice for a maximum of 4 hours prior to processing. Tags were nailed to the sampled areas to avoid re-sampling on subsequent days.

Upon return to the field station, the algae in each filter were briefly rinsed with freshwater to remove salt, then transferred to a labelled vial and frozen. Algal samples (n = 120) were subsequently freeze dried, weighed to the nearest 0.1 mg and ground to a fine powder in a tungsten-carbide ring mill.

Detritus and sediments were filtered out of field samples in the laboratory by passing each sample sequentially through a 63 μm and 20 μm mesh screen. All invertebrates distinguishable to the naked eye (>3 mm) were removed. These splits were then combined; this results in a filtering

efficiency of >99% for all particles (Chapter 3). The particulates were then rinsed with tapwater and transferred to vials. After freezing the samples, they were freeze dried and weighed to the nearest 0.1 mg. About one-quarter of each sample from the first five days (n = 60) was randomly portioned (see Chapter 3) to provide a sub-sample for detritus analysis. These detritus sub-samples were then homogenised to a fine powder in a tungsten-carbide ring mill and constitute the material used for organic carbon, nitrogen and phosphorus determinations. Sediments (in the remaining portion of samples) were cleared of organic material with bleach, dried, and weighed to the nearest 0.1 mg. Once corrected for the proportion of material removed for detritus analysis, these values are taken to represent 'sediment load' per dm^2 (see Chapter 3). Due to efficient removal of organic detritus during bleaching (see Chapter 2), the difference in weight before vs after this procedure is used here as a measure of the proportion (by weight) of crude detrital material. Samples of detritus and algae were stored at -20° C.

4.2.2. *Organic Carbon Analyses*

Direct determination of dry weight of algal and detrital material as a measure of biomass was not possible as these are usually mixed with carbonate particles which are necessarily ground with the samples. Organic carbon comprises approximately one-third by weight of coral reef algae and detritus (see Chapter 2) and is a commonly used index of biomass for algae and detritus (e.g. Moriarty 1982, Hansen *et al.* 1992, Klumpp and McKinnon 1992) due to its prevalence in structural components of cells. Studies on coral reef sediments (e.g. Entsch *et al.* 1983, Johnstone *et al.* 1990) have generally been unable to distinguish the relative proportions of detrital and mineral-bound nutrients. Most of the organic material associated with inorganic sediments occurs as coatings of detritus and bacteria on individual grains (Suess 1973), and is available for assimilation by consumers. The definition outlined by Hatcher (1983b) which considers detritus to include

these components and the associated microbial community is therefore used in this study.

Total organic carbon was determined for the ground algal and detrital samples by analysing triplicate aliquots (40-90 mg) in a LECO SC444-DR auto-analyser using the procedure described in Chapter 2, which alleviates interference from inorganic carbon (in carbonates) mixed with the samples. Analysis accuracy was confirmed daily using calibrated or registered LECO standard within the range of values to be tested; the machine was recalibrated if drift was >2%. Organic carbon values for samples were obtained by averaging triplicate estimates unless one deviated >5% (relative) from the other estimates, then the remaining duplicate values were averaged.

4.2.3. *Nitrogen and Phosphorus Analyses*

Nitrogen content of algae and detritus samples was determined using a micro-Kjeldahl digestion involving wet oxidation of the sample in catalysed hydrogen peroxide and sulphuric acid (see Chapter 2). Total nitrogen of sample aliquots was analysed following the salicylate-hypochlorite method of Baethgen & Alley (1989). Total phosphorus content of algae and detritus was analysed, after wet oxidation of the samples mentioned above, using an adaptation of Murphy and Riley's (1967) molybdate-ascorbic acid, single solution method (Anderson & Ingram 1989)(see Chapter 2).

Due to the inability to measure total organic material accurately (see above), total N and P content of algae and detritus were standardised using paired values of total organic carbon of the same units. In view of the fact that organic carbon-rich structural components such as lignin and cellulose are largely indigestible to marine herbivores (Horn 1989) and detritivores (Roman 1983), this standardisation provides a relative measure of the nutritional quality of algae and detritus.

4.2.4. *Statistical analyses*

Differences in the biomass and nutrient content of algae and detritus amongst zones and transects were tested using mixed-model (Model III) two-way ANOVA, with zone and transect considered as fixed and random factors respectively. An unconstrained model (the interaction MS is the denominator for *F*-ratios of main effects) was used in these tests. Homoscedasticity and distribution normality of data were verified using Cochran's test and box-plot analyses respectively; data of algal biomass and percentage crude detritus were log(x) and log(x + 1) transformed respectively (see Underwood 1981). Tukey's tests (α = 0.05) were used for unplanned comparisons amongst zones only, given that transect was a random factor in the design.

Linear correlation analyses were conducted to examine relationships between sediment load and the biomass of algae and detritus, and between the content of nitrogen and phosphorus in algae and detritus, as there was no clear case for considering any of these as dependant variables. Atomic (molar) N:C and P:C ratios were used (in preference to atomic C:N or C:P ratios) to provide intuitive illustrations of spatial patterns in the relative content of nitrogen and phosphorus (with respect to carbon) in algae and detritus. An algorithm generated in the software package S-PLUS® was used to calculate 80% confidence ellipses of individual points for each zone for relative nutrient content of algae and detritus. These ellipses delineate the 80% likelihood of a replicate sample having a relative nutrient content within the enclosed range of values, and hence represent the bounds of most (80%) of the data for each zone.

4.3. Results

4.3.1. *Food resource biomass*

The biomass of both algae and detritus per unit area were highly variable amongst the four zones on the study reef (Fig. 4.1a, b). Patterns of change in algal biomass along transects, i.e. amongst successive zones, were particularly incongruent (zone x transect interaction; $F_{6, 108} = 5.26$, $p < 0.001$) indicating high spatial variability at a between-transect scale (~ 100 m). Substrata on the reef base were covered by sparse EACs which were consistently low in average biomass amongst transects (109, 105 and 101 mg dm^{-2}); average EAC biomass was significantly lower compared to that on the fore-flat and mid-flat (~ 200-300 mg dm^{-2}), but not compared to the crest (Tukey's test). Overall, average algal biomass on reef crest substrata was lower than that within fore-flat or mid-flat zones, but this was not significant in the Tukey's test..

In contrast to algae, spatial changes in detrital biomass were more consistent amongst forereef zones (Fig. 4.1b), and were similar to those described for sediment loads in Chapter 3; detrital biomass decreased from the reef base to the crest, then increased in leeward zones. A significant zone x transect interaction ($F_{6, 48} = 6.02$, $p < 0.001$) was detected using a two-way ANOVA, demonstrating that the spatial changes in detrital biomass among zones were statistically different among transects. Average estimates of detrital biomass on the crest were lower than any other zone on all transects (~ 40-60 mg dm^{-2}), with this trend being significant for data pooled amongst transects (Tukey's test). The Tukey's test failed to detect significant differences in comparisons of mean detrital biomass amongst reef base, fore-flat and mid-flat zones. Average detrital biomass within mid-flat plots was 4 to 6 times higher than within crest plots.

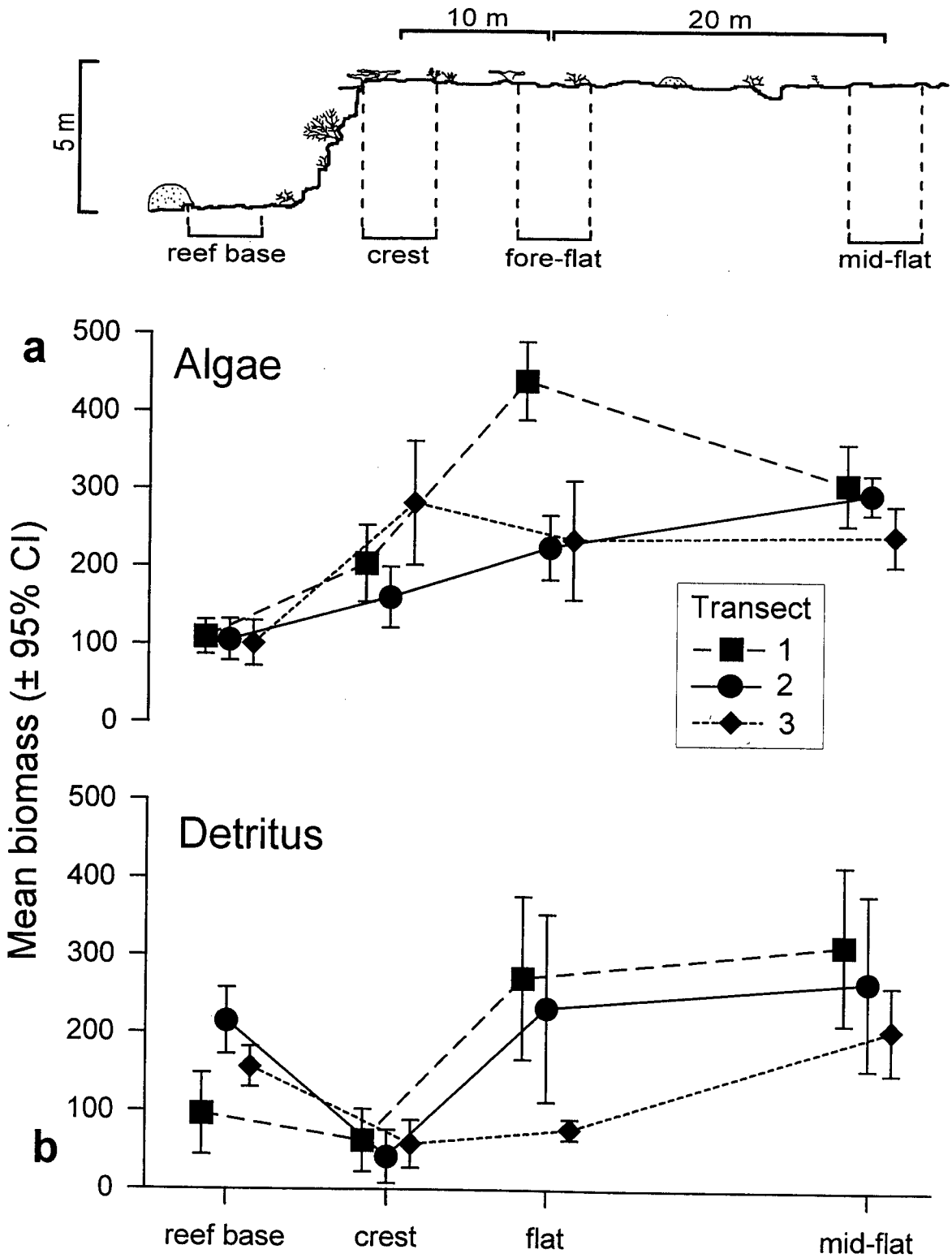


Fig. 4.1. Spatial patterns of mean biomass (mg organic carbon.dm^{-2}) of (a) algae, n = 10, and (b) detritus, n = 5, amongst successive forereef habitats along each of three transects. Schematic, cross-section profile of study reef indicating location of habitats is provided above.

To compare epilithic food resources, the biomass value of algae was divided by that of detritus to provide a ratio of relative abundance for each sample unit (Fig. 4.2). Assessing whether the confidence intervals of the ratio means include 1 is a factorial analogy to the paired t-test. This comparison shows that in about half of the plots, mainly on the fore-flat and mid-flat, mean biomass of epilithic algae was similar to that of the accumulated detritus, i.e. the algae:detritus ratio for biomass was not significantly different from 1. On the reef crest, mean biomass estimates of algae were many times greater than those for detritus, although the ratio between these two resources was highly variable within this zone (Fig. 4.2). With increasing detritus accumulation on substrata with distance from the crest, algal and detrital food resources become increasingly comparable. On reef base substrata, in contrast, detritus was comparatively abundant; detrital biomass averaged about twice that of algae in two of the three plots.

The biomass of epilithic algae was found to be significantly positively correlated with the amount of sediments they accumulated ($p = 0.002$). However, within this relationship, algal biomass was highly variable at any given value of sediment load (Fig. 4.3a); the correlation coefficient which reflects this variability was quite low ($r = 0.28$). This result is in stark contrast with the tight correlations between EAC canopy height and sediment load (Chapter 3; $r = 0.83$).

Detrital biomass was also significantly correlated with sediment loads on reef substrata ($p < 0.001$). In contrast to the case with algal biomass, this relationship was much stronger across the range of measured values (Fig. 4.3b; correlation coefficient, $r = 0.93$). The inference is that the conditions which affect sediment accumulation within EACs have a similar influence on detritus accumulation, with these two components co-varying in a linear way amongst zones.

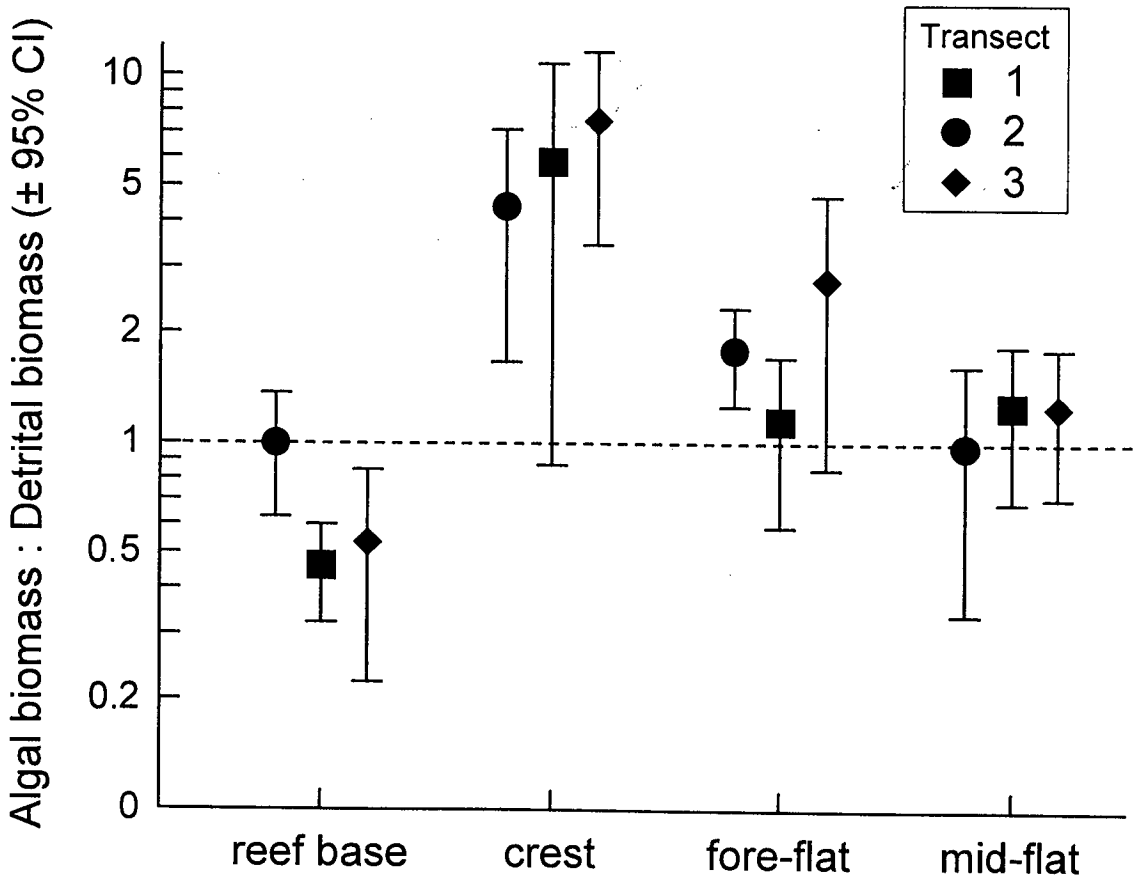


Fig. 4.2. Mean biomass ratios of algae:detritus from paired measurements (n = 5) within each plot, expressed on a $\log_{10}$ scale; i.e. a value of 2 means twice as much biomass of algae, whereas a value of 0.5 means twice as much detritus. Mean biomass of algae is not significantly different from that of detritus where confidence intervals include 1; $\alpha = 0.05$.

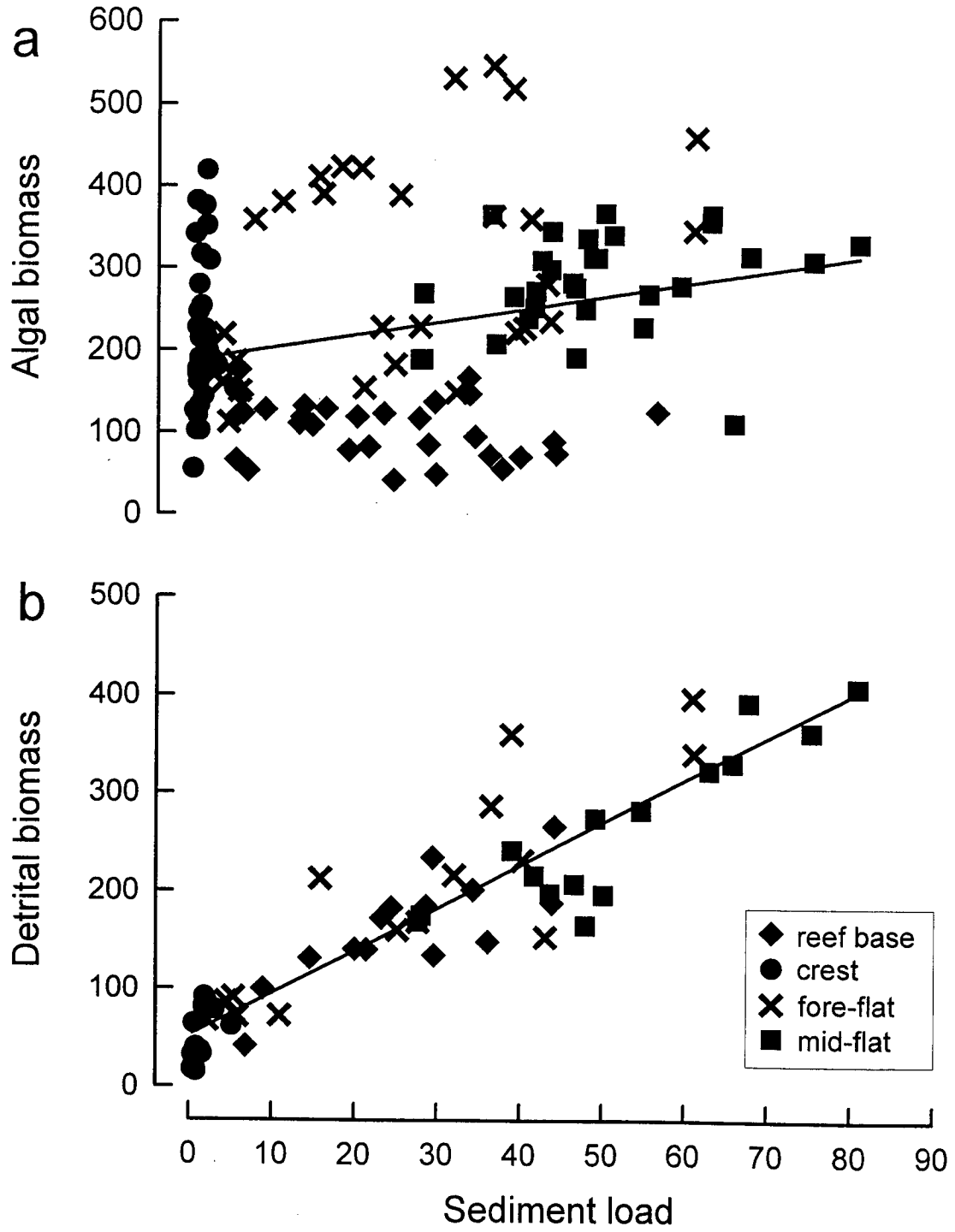


Fig. 4.3. Relationship of food resource biomass (mg organic carbon.dm^{-2}) vs. sediment load (g dry wt.dm^{-2}) for the combined data from fore-reef habitats for (a) algae (r = 0.28, p = 0.002; n = 120) and (b) detritus (r = 0.93, p < 0.001; n = 60). Lines are best linear fit for correlative trends (see text).

The finding that the relative contribution of organic detritus to the total weight of particulate material (i.e. sediment + detritus) within EACs can vary considerably amongst zones is of particular relevance to the ecology of bottom-feeding detritivores. There was a striking pattern that reef crest substrata accumulated particulates with a significantly higher proportion of detritus than any other zone (Fig. 4.4a). Relative differences in detrital contribution amongst zones were, however, different amongst the three transects (interaction $F_{6, 108} = 6.79$, $p < 0.001$). A Tukey's test showed that detritus constitutes a significantly higher percentage of the particulate material (by dry weight) on crests (approx. 14%) than other zones (less than 5%). These multiple comparisons were unable to detect differences in detrital contribution to the particulate mass amongst the reef base, fore-flat and mid-flat. Particulate material on the mid-flat was especially predominated by sediment, with detritus making up only 1% by weight.

Spatial patterns and results of statistical analyses of algal:sediment ratios mirrored those described above of particulate contribution of detritus (Fig. 4.4b). These illustrate that although the biomass of epilithic algae may also be moderately low on the crest, these communities bind on average at least four times less sediment per unit of plant biomass than in other zones. Interestingly, the algal biomass:sediment load ratio on the crest substratum on transect 3, which was noted to be defended by the surgeonfish *Acanthurus lineatus* (Linneaus), was significantly higher than on crest substrata of the other transects.

4.3.2. *Food resource quality*

The relative content of nitrogen and phosphorus (with respect to carbon) in algae differed amongst zones, and differences were found to be inconsistent amongst transects; significant zone x transect interactions for mean N:C and P:C atomic ratios were detected ($F_{6, 108} = 3.49$, $p < 0.01$, and $F_{6, 108} = 4.44$, $p < 0.001$ respectively). At the scale of the study site, there was a

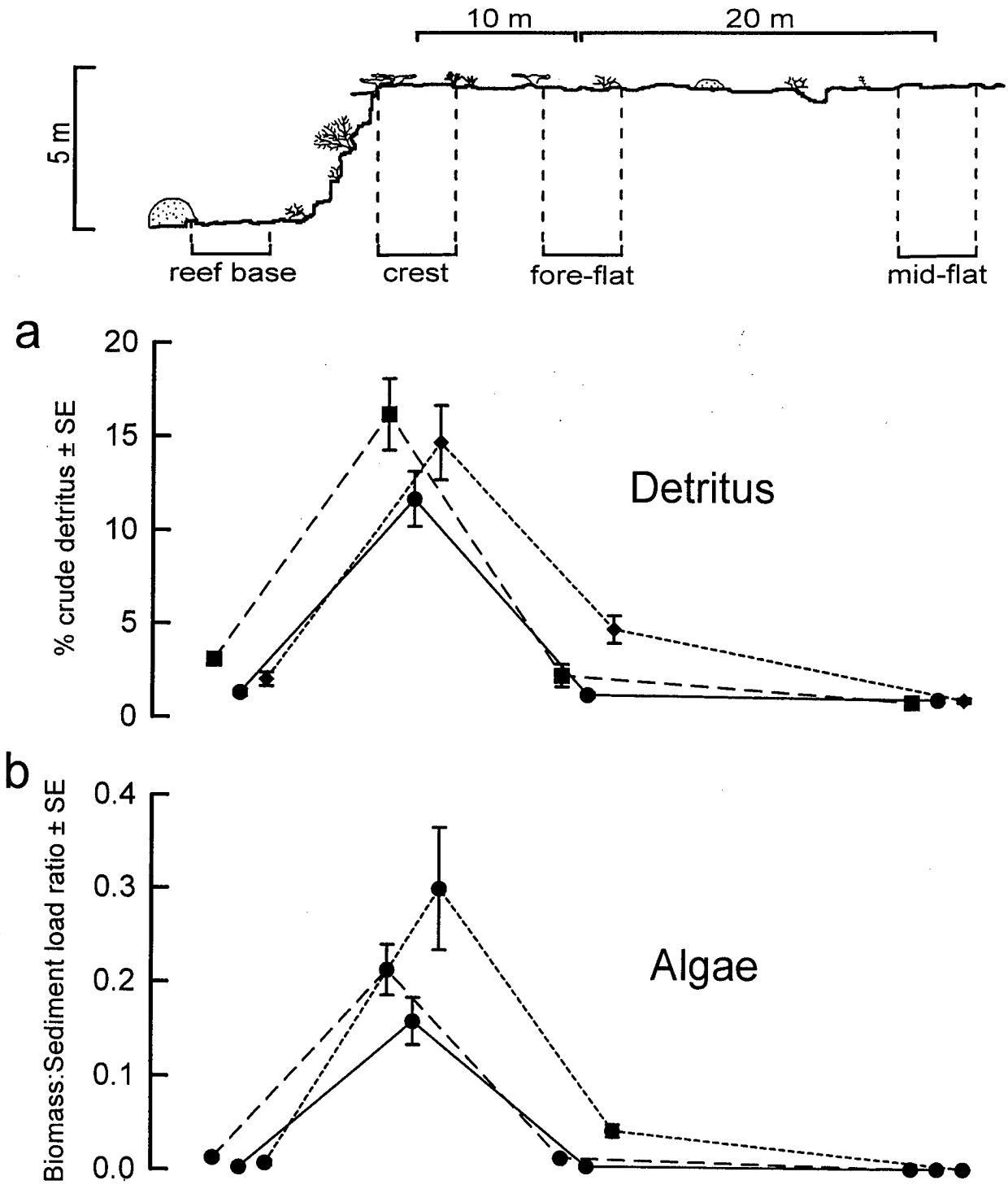


Figure 4.4. Patterns of relative contributions of food resources compared with sediment load for (a) detritus (% crude material of total particulates (by dry wt); n = 10) and (b) algae (wt organic carbon algae/dry wt sediment; n = 10) amongst successive zones for each of three transects. Schematic profile of reef platform above.

high degree of overlap in the relative proportions of N and P in algae amongst zones (Fig. 4.5). Differences amongst zones were non-significant in the two-way ANOVA of N:C ratios ($F_{3, 6} = 1.03$, $p = 0.44$), but were significant for P:C ratios ($F_{(3,6,)} = 7.50$, $p = 0.02$). The only significant differences detected in Tukey's tests was relative phosphorus content of mid-flat algae which was found to be significantly higher than that on the reef base or crest. The results therefore suggest that algal quality at a local scale (~ 10 m) can be variable amongst neighbouring areas, but at the broader scale of the whole reef (~ 500 m) it is fairly comparable among these four forereef zones. The average C:N:P molar ratios for epilithic algae and detritus over all zones were 121:13:1 and 92:11:1 respectively.

Nutrient ratios of detritus differed in spatial heterogeneity and magnitude from those depicted for epilithic algae. Notably, although nutritive quality (N/C ratio) of detritus varied within plots, average values were found to be similar among zones and transects (respectively: $F_{3, 6} = 0.91$, $p = 0.49$, and $F_{2, 6} = 1.59$, $p = 0.28$; Power = 0.15 and 0.22). Most variation in relative nutrient content of detritus appears to be attributed to phosphorus rather than nitrogen (Fig. 4.6). While differences in mean P:C ratios of detritus amongst zones were not the same for each transect (interaction $F_{6, 48} = 2.92$, $p = 0.02$), overall the crest was shown to be different from the other zones in having significantly lower relative phosphorus content (Tukey's test). The broad spatial pattern was that relative content of phosphorus in detritus increased with distance from the crest; P:C ratios were generally lowest on the crest, increased about 2-fold on the fore-flat and about 3-fold on the mid-flat (Fig. 4.6).

Ratios of algal N content:detrital N content and algal P content:detrital P content were calculated for each paired observation to facilitate direct comparisons of the two food resources amongst the zones. The analysis of these values reveals that the average relative N and P content in algae were generally lower than in detritus (Fig. 4.7a and b), although the relative

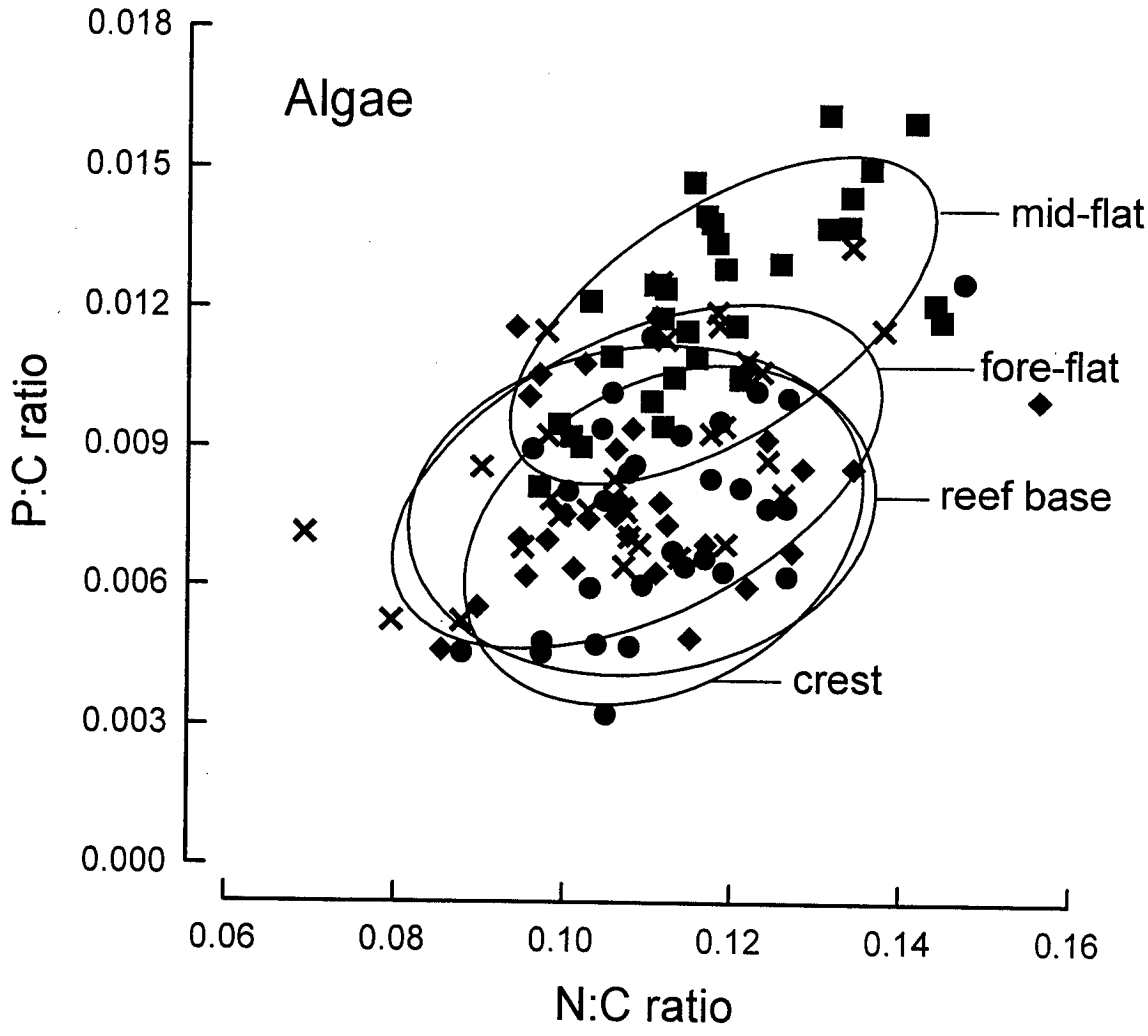


Fig. 4.5. Bivariate plot of relative nitrogen content (N:C ratio) vs. relative phosphorus content (P:C ratio) of algae for data combined amongst transects. Confidence ellipses (80%) of the individual points for the reef base (◆), crest (●), fore-flat (**X**), and mid-flat (■); n = 30 for each zone. Each ellipse delineates the 80% likelihood of any individual random sample having a nutrient content within the outlined range.

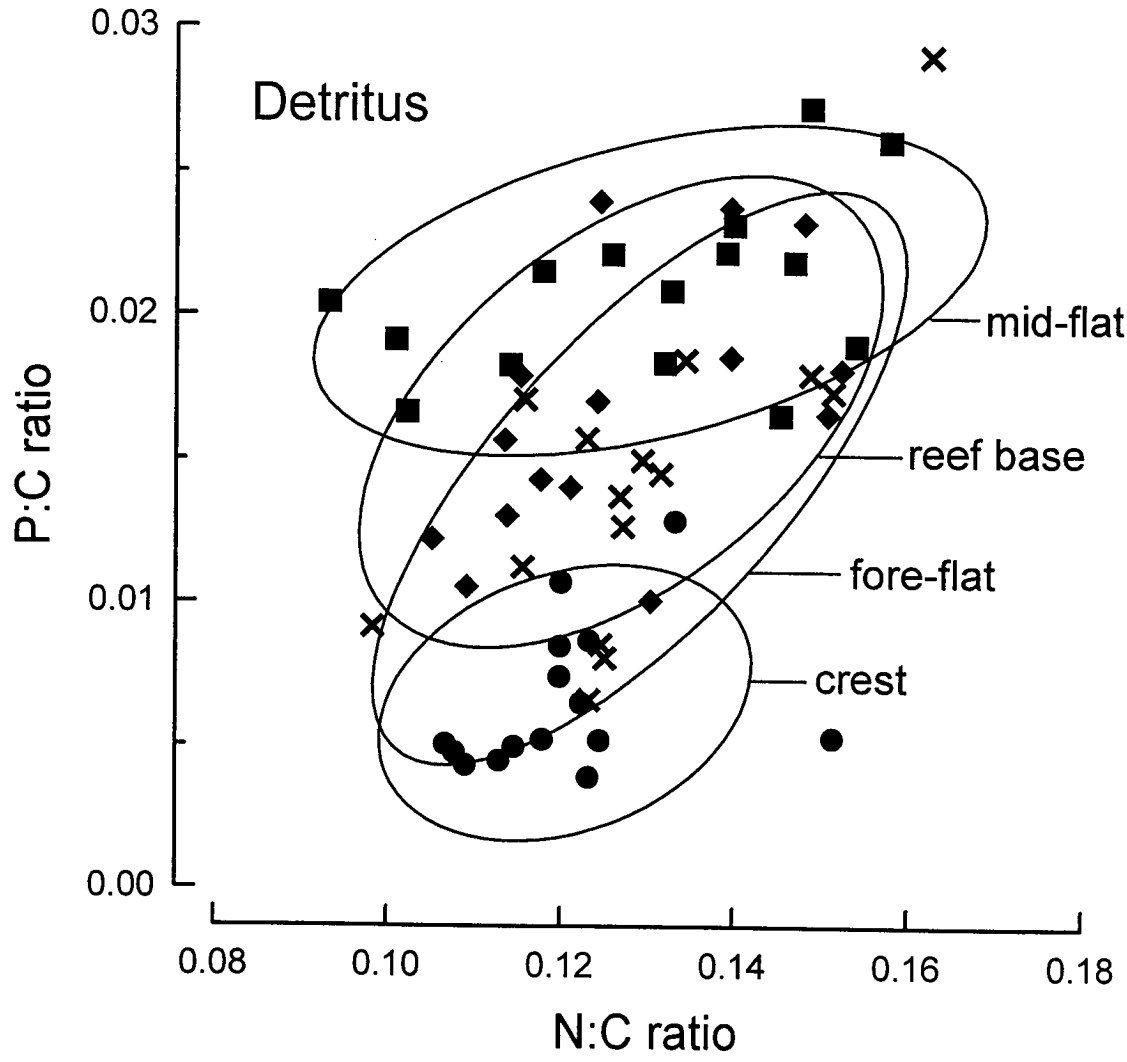


Fig. 4.6. Bivariate plot of relative nitrogen content (N:C ratio) vs. relative phosphorus content (P:C ratio) of detritus for data combined amongst transects. Confidence ellipses (80%) of the individual points for the reef base (◆), crest (●), fore-flat (**X**), and mid-flat (■); n = 15 for each zone. Note change in scale from that in Fig. 4.5. Each ellipse delineates the 80% likelihood of any individual random sample having a nutrient content within the outlined range.

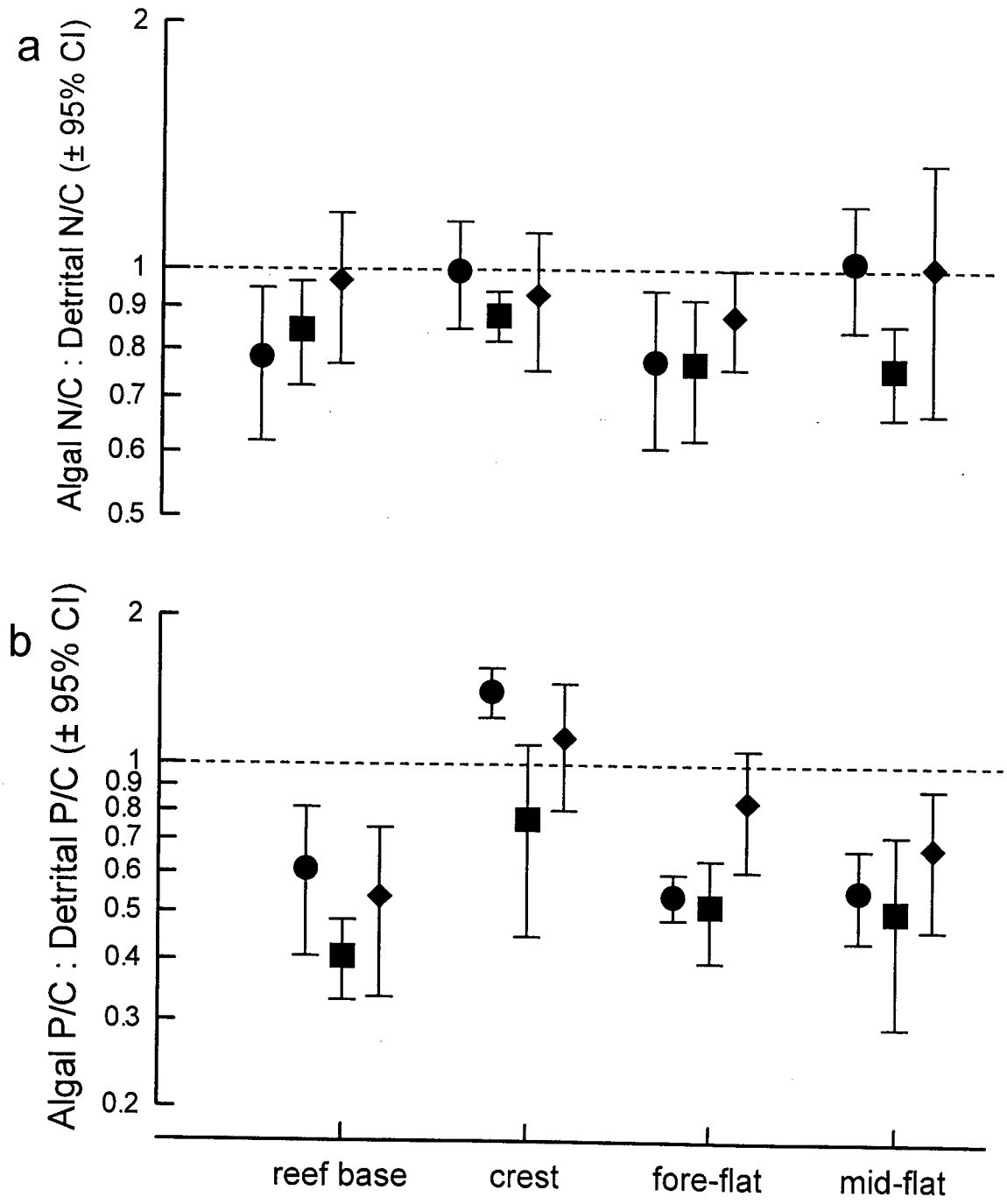


Fig. 4.7. Mean relative comparisons (ratios) of nutrient content : organic carbon content ratios between algae and detritus (n = 5) for each plot of substratum; (a) nitrogen and (b) phosphorus, expressed on a Log_{10} scale. Mean nutrient ratios of algae and detritus are not significantly different if confidence intervals include 1; α = 0.05.

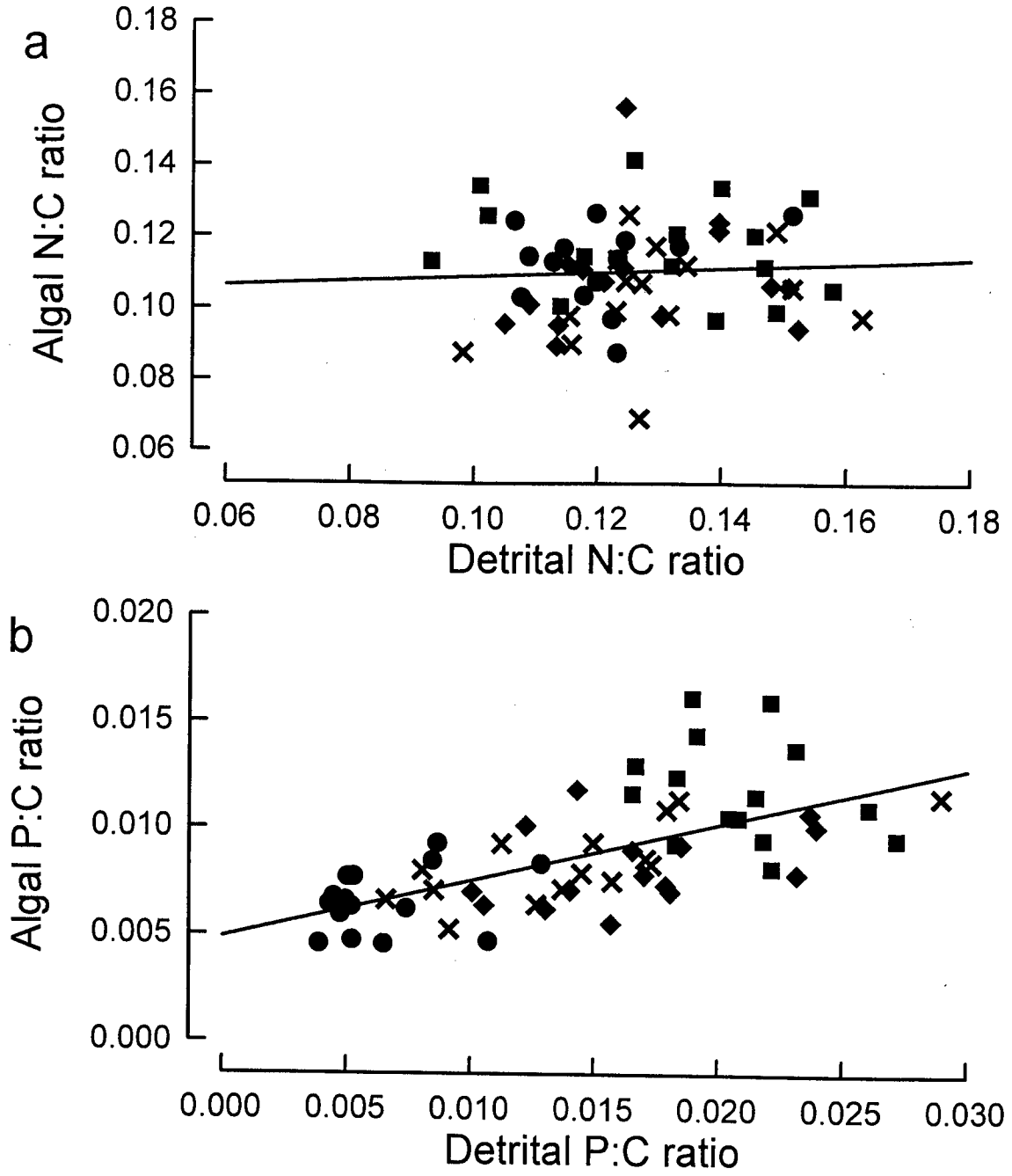


Figure 4.8. Relationship of relative nutrient content in algae vs. detritus for: (a) nitrogen (r = 0.07) and (b) phosphorus (r = 0.65) for the combined data from forereef habitats (n = 60). Lines of best linear fit are for correlation analyses (see text). Point symbols for habitats are: reef base (◆), crest (●), fore-flat (**X**), and mid-flat (■).

differences between these resources were quite variable at a within-plot scale. For all data combined, estimates of nutritive quality of algae (N:C ratio) were on average 11% lower than those of their accumulated detritus (Fig. 4.7a). At a fine scale, however, this relationship was not consistent, with some plots within reef base, crest and mid-flat zones displaying comparable N:C ratios. Infrequent similarities in relative phosphorus content between algae and detritus also occurred (Fig. 4.7b) but were mainly on crest substrata, where P:C ratios of algae were not significantly different from detritus within two plots, and were greater than detritus on the third plot. Excluding these crest data, P/C ratios of algae were, on average, 42% lower than paired detrital samples.

Finally, bivariate correlation analyses were conducted to investigate whether the relative N or P content of algae correspond to that of their detritus. While these analyses failed to detect any relationship between the relative nitrogen content of algae and that of detritus (Fig. 4.8a; $p = 0.59$, $r = 0.07$), they reveal that the relative phosphorus content of algae was significantly correlated with that of detritus (Fig. 4.8b; $p < 0.001$, $r = 0.65$). Given the best fit for this relationship, 2-fold increases in detrital P:C ratios correspond to increases in algal P:C ratios of about 35%.

4.4. Discussion

This study is the first to examine spatial patterns in the abundance and quality of both epilithic algae and detritus among zones on coral reefs and it provides information on how these co-occur and co-vary with accumulated sediments. Forereef zones are active areas for the production of sediments (Davies 1983, Bellwood 1995) and organic detritus (Hatcher 1983b, Polunin and Klumpp 1992). Much of the sediments are transported eventually to leeward zones, but can be held temporarily within forereef EACs. Broad patterns of sediment and detritus accumulation on forereef zones are likely to

be similar amongst midshelf platform reefs of the GBR because most have forereef margins facing the dominant SE trade winds.

This study shows that the magnitude of sediment/detrital accumulation can be correlated to the standing crop and relative phosphorus content of epilithic algae. Sediments and detritus occur as particulate 'aggregates' which both became increasingly accrued in successively distant areas from the windward reef margin. The strong correlation detected between sediment load and detrital biomass indicates that inorganic and organic particulates form a functional aggregate on forereef substrata, and/or that similar mechanisms affect the accumulation of each component within EACs. A comparison of the correlations between sediment load and algal canopy height (Chapter 3) and biomass would suggest that sediment accumulation is due more to boundary layer effects related to EAC canopy height (cf. Carpenter and Williams 1993) rather than the biomass *per se*, as these were more strongly linked to sediment loads. Corresponding increases in algal biomass perhaps suggest that sediments tend to accumulate where there is more algae or that sediments may physically protect algae against intense grazing. Further work is needed, however, on the relationship between EAC biomass and sediment loads, because algal abundance and distribution on reefs of the GBR can be temporally variable (Klumpp and McKinnon 1989, McCook *et al. in press*).

It has also been suggested that nutrient-enriched sediments and/or detritus may consequently increase resident nutrient supply to enhance algal growth (Patriquin 1972, Smith 1984, Johnstone *et al.* 1990, Stimson *et al.* 1996). Phosphorus for example, is a key nutrient for algal growth on coral reefs and is thought to be recycled efficiently within benthic communities (Lewis 1977, Atkinson 1983, Kinsey 1985). A leeward gradient of increasing P:C ratios of detrital/sediment aggregates may reflect increasing bacterial colonisation of detritus, as detrital bacteria tend to absorb and retain much phosphorus (Pomeroy 1980, Costantini and Rossi 1995). Work by Uthicke

(1994) at a neighbouring site at Lizard Island showed that detrital bacteria in sediments increased in abundance with leeward distance from the reef crest. Coral reef sediments can contain appreciable amounts of phosphorus which can be transferred to EACs (Entsch *et al.* 1983) and perhaps this phosphorus may also be utilised by benthic consumers. The present findings indicate that detrital/sediment aggregates of reef flats are repositories for phosphates to a greater extent than EACs. The strong positive correlation between the relative phosphorus content (P:C ratio) of detritus and that of algae is consistent with the potential for transfer of this nutrient between these aggregates and algal communities. If phosphorus supply from detritus or sediments is significant, then this may indeed enhance algal growth where these aggregates are more accumulated. However, although nitrogen supply is also considered to limit algal production on coral reefs (Smith *et al.* 1981, Hatcher and Larkum 1983, Smith 1984), the relative content in algae varied independent to that of detritus on the study reef. It is possible that potential differences in the scale of nutrient flux differ between nitrogen and phosphorus species. However, these correlative relationships provide only tentative information on the dynamics of nutrient transfer between sediment/detrital aggregates and do not resolve the process by which algal biomass is enhanced.

Sediments have been considered as structural constituents of EACs on temperate reefs (Stewart 1983). On the forereef in the present study, sediment loads altered the state in which algae and epilithic detritus are presented for consumption to bottom-feeders. Spatial variations in sediment loads within EACs were not of the same scale as variations in algal or detrital biomass, and as a result, these variations alter the proportions of inorganic and organic material on substrata. That is, although the biomass of algae and detritus tended to be greater where sediment loads were higher, the relative changes were asymmetric amongst the zones. Algal-bound sediments may be detrimental to herbivores by decreasing the nutritional return per feeding episode (Choat 1991). If this is an important factor in habitat selection, then one could argue that herbivores should favour reef crests which exhibited

consistently high algal-biomass:sediment ratios. Evidence supporting this argument comes from several studies on similar GBR reefs (i.e. windward-facing midshelf platforms) which show that forereef crests are regions of high grazing intensity (Hatcher 1981, Russ 1984, Polunin and Klumpp 1992, Bellwood 1995). The present study suggests that herbivores would need to be increasingly selective on exposed algae in successively leeward areas from the crest if they are to avoid consuming large quantities of sediment. An example of this selectivity can be seen in the browsing surgeonfish *Acanthurus nigrofuscus* (Forsskål), which peaks in abundance on reef flats of outer shelf GBR reefs (Russ 1984) and avoids sediment by cropping only the tips of algae which protrude from the sediment layer on this reef flat (*pers. observ.*).

Provided that carbon:nitrogen ratios approximate nutritional quality (as discussed), algal nutritive quality at the scale of this study reef (~ 200 m) was comparable amongst zones but was significantly patchy on a local scale (~ 10 m). While the composition of algae (based on broad functional groupings) was shown in Chapter 3 to be broadly comparable amongst zones, species composition may have been quite variable. It is possible that such differences could explain some of the patchiness in algal quality, as nutrient content in these algae is often species specific (Niell 1976, Atkinson and Smith 1983). To a similar extent, local (within-plot) heterogeneity occurred also in detrital nitrogen content (N:C ratio) amongst the forereef zones examined, which may be attributed to micro-climate conditions that modify nutrient content of microbial populations (Odum *et al.* 1979). Given these findings, foraging intensity of herbivores and detritivores on similar forereefs are expected to be spatially variable at local scales, given that their food preferences have been linked to nutritional quality of algae (Hughes 1980, Montgomery and Gerking 1980, Bruggemann *et al.* 1994a, c) and detritus (Moriarty 1982, Hammond 1983).

It was interesting that in half of the plots, abundance of detritus was statistically comparable to that of algae. On the shallow reef crest and fore-flat, mean biomass of algae was higher than that of detritus. Herbivory is thus likely to be more significant in terms of trophic energy transfer in these zones than detritivory, but it is worth noting that standing stock of algae or detritus is a static measure of the balance between production and biomass removal (Carpenter 1985, Steneck and Dethier 1994). Productivity of EACs has been shown to differ amongst various forereef zones, being generally highest on windward crests (Polunin and Klümpp 1992). Because of this high productivity, herbivores of reef crests may have a high supply of algae even though instantaneous standing crop may be low. Likewise, the potential supply of detritus to reef crest substrata appears, from work at One Tree Reef in the southern GBR, to be very high (Koop and Larkum 1987) even if this material is washed away or consumed rapidly. Therefore, while the present study indicated the instantaneous abundance of detritus and algae on this forereef, the trophic significance of food sources, in terms of energy transfer within different zones should be addressed by investigating their turnover rates.

In terms of resource quality, much of the dissimilarity in detritus amongst zones appears to be due to detritus:sediment ratios, which were by far the highest on reef crest substrata. Hughes (1980) outlined that rates of procurement and processing are predicted to be optimised in deposit-feeders. Under his "Energy Maximization Premise", the crest of the study reef would be expected to be a favoured foraging area for fast-feeding detritivores with small gut volumes. Provided that their summed bites contact a large surface area, to compensate for low detrital biomass per unit area, their ingesta will contain more detritus and less sediment than if they had fed in other zones. This observation may be a key factor in fidelity to reef crests as detrital foraging zones depicted in the abundant surgeonfish *Ctenochaetus striatus* (Quoy and Gaymard)(Choat and Bellwood 1985) and large blennies (Odum and Odum 1955). Novel morphological adaptations to jaw flexibility and

dentition in *C. striatus* (Purcell and Bellwood 1993) and certain coral reef blennies (Ebner 1993) enable these fishes to comb detritus from EACs, providing a successful mechanism for accessing a detrital diet in these zones. However, the dynamics of food webs on the crest, where detritus was found to be less abundant and is probably more ephemeral due to episodic hydrodynamic events, are predicted to be less stable than in other areas (see DeAngelis 1975).

The ratio of detritus to sediment may not be optimised for all detritivores, due to differing constraints on detrital procurement amongst taxa. A number of species of aspidochirote holothurians, for example, can consume large quantities of sediment and detritus (Birkeland 1988), but because they are slow moving, their feeding may be constrained by the rate at which they can cover substrata. Several abundant species forage on sediment-covered reef flats (Birkeland 1988, Uthicke 1994). Although assimilable detritus comprises a small fraction of the particulate material, holothurians may feed successfully in these zones due to selective feeding (Moriarty 1982, Hammond 1983) and the higher abundance of this material per unit area. Additionally, small infaunal crustaceans and blennoid fishes of sediment-covered reef flats feed at a scale where individual detritus-rich aggregates can be identified and consumed without ingesting excess sediment. Therefore, for some detritivores, the importance may be the biomass of detritus per unit of substratum rather than the relative proportions of detrital material compared to sediments.

Detritus has been widely researched in lentic freshwater and coastal marine systems, where it is believed that detrital feeding is a trade-off between high availability and low nutritive quality (e.g. Valiela 1984, Ahlgren 1990, D'Avanzo and Valiela 1990). However, studies by Johnstone *et al.* (1990) and Hansen *et al.* (1992) on the GBR showed that detritus in lagoon sediments can be a high quality food source, with molar C:N ratios of 5.7 and 3.7 (4.9 and 3.2 if wt/wt) respectively. The results of the present study

suggest that the nutritive quality of forereef detritus (mean [molar] C:N = 8.0) was relatively comparable to, and often better than, that of algae (mean [molar] C:N = 9.1). Additionally, many algae contain secondary metabolites which may deter herbivory (see Paul 1992) and can inhibit the digestibility of plant proteins (Boyd and Goodyear 1971), but these are likely to be less concentrated in detritus due to autolysis (cf. Rice and Tenore 1981). Detritivores on similar forereef areas are therefore presented with a reciprocal scenario of trade-offs from those of lentic freshwater systems; i.e. of low availability, but high nutritional quality.

Although the bulk of detritus on coral reefs is considered to be derived from triturated algal tissue with lowered nitrogen content, it is mixed with bacteria, fungi, and microscopic invertebrates (Alongi 1988). This 'composting' community presumably accounts for the fact that detrital C:N:P ratios were lower, on average, than that of Redfield's ratio for plant material, and indicates higher protein content (Odum *et al.* 1979) of detritus compared with epilithic algae. The spatial homogeneity of C:N ratios suggests that animal constituents of detritus may be evenly mixed, with micro-invertebrates colonising dead algal tissue to a similar extent among forereef zones. These findings suggest that detritus on similar forereef zones contributes potentially more nutrition to non-selective bottom feeders than algae, particularly in areas where these two food sources were equally abundant.

Chapter 5

Short-term effects of sediment loads on coral reef epilithic algae.

5.1. Introduction

Sediments on coral reefs are readily trapped by epilithic algal communities (EACs). The amount (load) of sediments held within EACs can vary both spatially and temporally due to different hydrodynamic conditions which redistribute these deposits (Suhayda and Roberts 1977, Davies 1983). Algal-sediment dynamics within this context are of interest because of the importance of EACs in primary production, and because changes in sediment loads represent natural 'stresses' (*sensu* Grime 1979) to the biota of reef habitats. Additionally, sedimentation on coral reefs induced by human activities can increase the loads and types of sediments (e.g. fine siliceous particles) affecting reef biota. This is of particular interest in view of the dramatic effects of sediments on reef building corals recorded worldwide (review by Rogers 1990, Brown *et al.* 1990, Stafford-Smith *et al.* 1994). Similarly, variations in sediment loads could have comparable deleterious effects on EACs which play a critical role in the trophodynamics of coral reefs.

Carbon fixation by EACs on reefs is crucial for generating energetic capital for these systems and their recipients. Epilithic algae are the main diet of the dominant herbivores on coral reefs (Hatcher 1983a, Russ and St. John 1988, reviewed by Steneck 1988), and as a reciprocal result of intense grazing, EACs are kept in a highly productive state (Hatcher 1981, Carpenter 1986). As a consequence, standing stock (biomass) of EACs on coral reefs are usually low, with rates of grazing of algal tissue by herbivores being largely affected by productivity rates of EACs (Hatcher and Larkum 1983). Epilithic algae are also key components in biochemical cycles (D'Elia and

Wiebe 1990) due to nutrient uptake from surrounding waters and autochthonous (= 'within the system') fixation of nitrogen by blue-green algae. These processes are often linked to rates of productivity of EACs (Wilkinson *et al.* 1985, Atkinson 1988), and allow algae to produce essential dietary components, such as protein, for growth of heterotrophs. EACs are thus substantive to reef-trophic processes, especially when these are intensely grazed by herbivores. As in corals, growth of epilithic algae is also predicated on abiotic variables, such as nutrient concentrations, water flow, temperature, light and perhaps sediment load. Coral reefs therefore persist as healthy, functioning ecosystems when the environmental and ecological conditions foster high rates of production and removal of algal tissue by herbivores. If management strategies concerning sedimentation on coral reefs are to be adopted, knowledge on the effects of sediment loads on EACs is an essential pre-requisite.

Chapters 3 and 4 have shown that patterns of sediment distribution on an upper reef platform correspond to patterns of EAC biomass and height, but that the loads of these sediments do not appear to correlate with the nutritional quality of the algae. These correlative observations however, do not allow causal inferences about effects of sediments on EACs. Herbivore grazing, in particular, has been demonstrated to strongly affect algal abundance on coral reefs (Wanders 1977, Sammarco 1982, Hatcher and Larkum 1983, Hughes *et al.* 1987, McCook 1996, McCook *et al. in press*), and could interact with parameters of EACs and confound simple correlative relationships.

What then, are the likely effects of sediment loads on the growth or nutritive quality of EACs on coral reefs? Choat (1982) argued that one of the best ways to show cause and effect relationships in these situations is by using appropriately designed field experiments. This study specifically addresses this question by means of a multi-factorial field experiment which subjects established coral reef EACs to different sediment loads within grazer

exclusion cages and in the open with grazers. Such field manipulations offer considerable scope in assessing the effects of natural and anthropogenic disturbances on coral reefs (Brown and Howard 1985). This chapter also details preliminary sampling programs and experiments for validation of experimental treatments, with the combined work investigating the responses of epilithic algae to sediment loads.

5.2. Materials and Methods:

5.2.1. *Study site and design*

The study was conducted on a coral reef platform located between Palfrey and South Island (14°42.0'S, 145°26.7'E), two mid-shelf continental islands adjacent to Lizard Island on the Great Barrier Reef (see Fig. 5.1). This reef is exposed to the predominant SE trade winds (at an angle of approx. 20°), and is influenced periodically by high wave energy. The reef is situated away from major plumes of terrigenous sediment, with water visibility ranging from 5 to 25 m. Two study sites (30 x 10 m areas; denoted as 'A' and 'B') were located within the reef flat habitat, approximately 10 metres behind the reef crest margin, with both sites approximately 20 to 40 cm below tide chart datum. Site B appeared to be slightly shallower and more exposed to wave action than site A. Substrata were covered predominantly by short EACs which were grazed by the site attached damselfishes *Pomacentrus chrysurus* (Whitley) and *P. wardi* (Cuvier), as well as roving acanthurids, scarids and siganids.

Square tiles 12x12x1.5 cm were cut from coral heads (*Porites sp.*) to provide replicate, natural substratum units for field experiments on EACs that could be sampled quickly and consistently. In early June 1993, 60 tiles (10 blocks of 6 tiles) were attached to the substratum at both sites, using

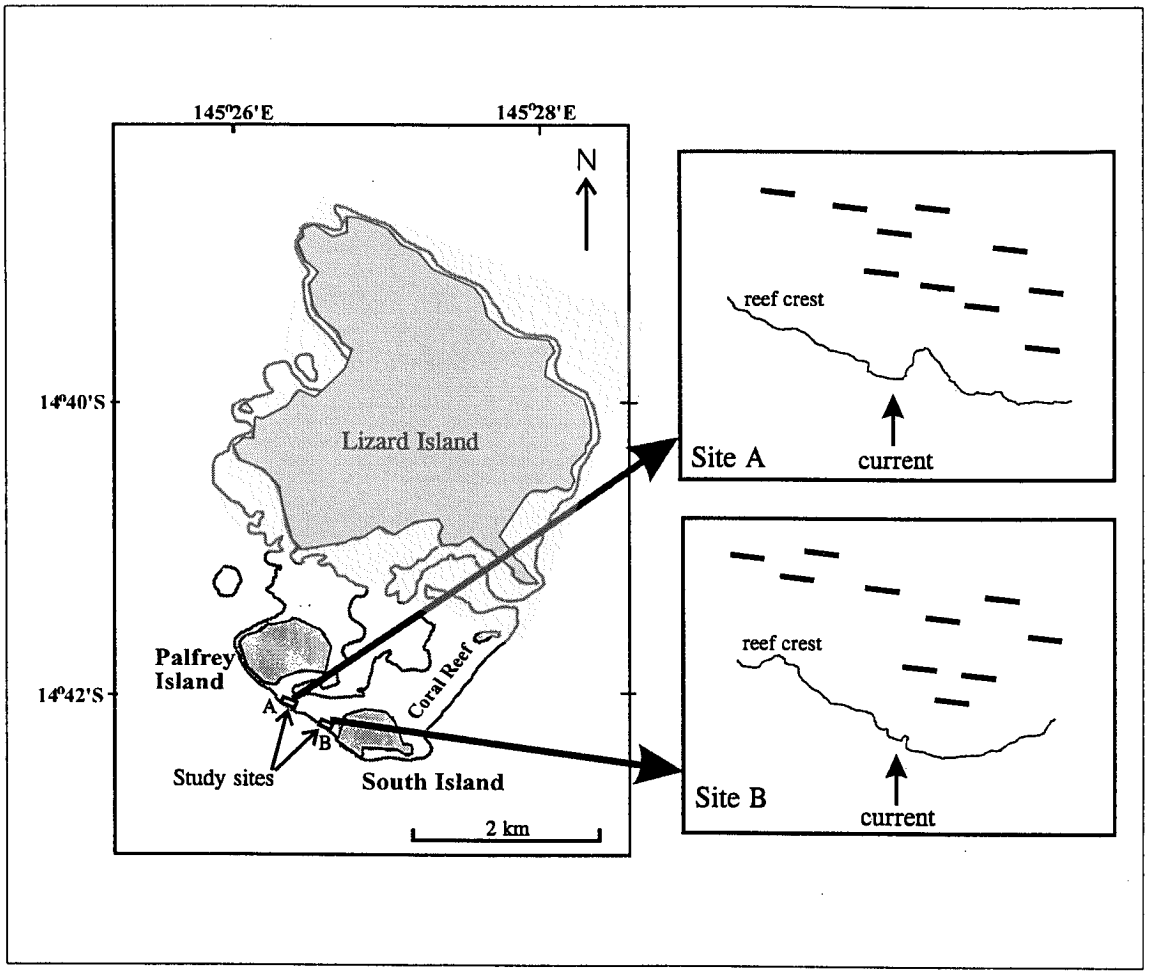


Fig. 5.1. Map showing the location of study sites A and B near Lizard Island, in the northern Great Barrier Reef. Orientation of tile blocks within each site (shaded rectangles; n = 10) is perpendicular to the dominant water current.

stainless steel screws inserted through a hole in the centre of the tiles (Fig. 5.1, 5.3). Tiles in each block were aligned in a row, perpendicular to the dominant SE current, with 10 cm space between each tile, except for the middle two tiles which were 15 cm apart, creating two 'subsets' of three tiles. Blocks were situated haphazardly at least 2 m apart on substrata that were a) approximately horizontal, b) free of corals, c) not adjacent to sand pits, d) dominated by epilithic algae and, e) not adjacent to territories of 'farming' pomacentrids (eg. *Stegastes sp.*, *Dischistodus sp.*). Both sites were partitioned with string along an East-West axis and the position and orientation of blocks recorded on underwater data board using SCUBA.

5.2.2. *Preliminary sediment samples*

Sediments within EACs of natural substrata were sampled on 13 October 1993 to provide a basis for nominating realistic sediment loads and formulating an appropriate grain size composition of sediments for experimental manipulations. Pilot sediment samples from 3 different sites around Lizard Is. indicated that 8 replicates should achieve a sampling precision (SE/mean) of <0.2. Samples of surface sediments ($n = 8$) were collected at site B, using the sediment sampler described in Chapter 1, from 1 dm^2 areas of substrata; areas were randomly chosen for sampling after meeting four *a priori* requirements. These were that they be (1) covered predominantly by turfing algae, (2) $< 15^{\circ}$ from horizontal, (3) free of pits for sediment retention, and (4) free of macroalgae taller than 20 mm. In the laboratory, each sample (sediment and water) was placed into a 50 cm high column, with a collection funnel at the bottom, for 3 hrs. Water was then drained out of a side tap and the settled sediments washed out of the funnel into vials. Sediments were cleared of organic material following the procedure outlined in Chapter 1, oven-dried at 70° C, and weighed to the nearest 0.1 mg; these values are the 'sediment load'. To permit analysis of the proportional grain size composition of sediments, each sample was also dry-

sieved through a series of six mesh screens (63 to 2000 μm) and each fraction weighed to the nearest 0.1 mg.

5.2.3. *Experiment 1 - Loss and accumulation of sediments within EACs*

A preliminary experiment was conducted from 17-23 October 1993 at site B (see Fig. 5.1) to estimate the rates of sediment accrual and loss on algal-covered tiles. It aimed to add or remove sediments from tiles at the beginning of the experiment, then sample the sediment load on tiles (without replacement) on successive days. The inferred temporal profiles of sediment loss and accumulation provide the rates for maintaining the treatment loads for Experiment 3 and information about temporal-physical dynamics of sediments in short algal communities on a coral reef.

Tiles had been attached to the reef for 4 months. Although this period would seem from some reports from the GBR as sufficient to acquire an established EAC (4.5 to 5 months, Russ 1987; 4 to 5 months, Scott and Russ 1987), it should be noted that other workers suggest longer periods (Hatcher and Larkum 1983, Larkum *et al.* 1988, Klumpp and McKinnon 1989). These tiles accumulated less sediment than surrounding substrata, probably because their upper surfaces were 1.5 cm above the reef surface. A sediment load of 30g (20.8 g per 100 cm^{-2}) was chosen as a realistic high treatment for the subsequent sediment load experiment (see Results - *Preliminary sediment samples*). These allocations were formulated to the grain size composition of the preliminary sediment samples using washed and dried coral reef sediments. Sediments <63 μm were not included, as these contributed little (by weight) to natural sediment samples from this and neighbouring reefs (see Chapter 3) and would probably be lost (via re-suspension) soon after applying these onto tiles.

Tiles were assigned, by randomisation among blocks, to one of three sediment treatments: high (n = 24), low (n = 24), or ambient (no treatment; n = 12). On the first day of the experiment, sediments on six ambient tiles were sampled on SCUBA, using the sediment sampler (Chapter 1), to estimate the initial sediment load on tiles. The 30 g sediment allocations were then applied to each of 24 high treatment tiles by firstly fitting a 10 cm high perspex column around the tile, then sprinkling the sediments evenly within the column and allowing these to settle on the tile for 1 min before removing the column. Sediments were then blown off the 24 low sediment treatment tiles using the exhalant water current of the sediment sampler (Chapter 1). The exhalant hose was placed approx. 5 mm above each tile at an angle while running the sampler pump (flow speed approx. 30 cm sec^{-1}) for 60 sec. The remaining six ambient treatment tiles were left untreated, and sampled at the end of the experiment to detect any significant changes in mean ambient load over the course of the experiment.

Sediments on low and high treatment tiles from each of 6 blocks were collected using the sediment sampler after 1 hr; this is the *effective* loads for low and high treatments at the start of the experiment. Sediments on six tiles within low and high treatments were also collected after 1, 3, and 5 days. Following each collection, sediments were settled in columns and processed as outlined for *Preliminary sediment samples.* They were then dried at 70° C and weighed to the nearest 0.1 mg. Data was analysed using Tablecurve® (Jandel Scientific) software to determine the most appropriate curves (by r^2 rank) explaining sediment loss and accumulation on tiles through time.

5.2.4. *Experiment 2 - Effects of caging*

Grazer exclusion cages were necessary in *Experiment 3* for partitioning the confounding effects of grazing (primarily by herbivorous fishes) from those of sediment manipulations on EACs. This experiment was conducted to

examine the possible confounding effects of grazer exclusion cages (e.g. reduction of water movement and light) on sediment load and growth of epilithic algae on natural substratum tiles.

Due to logistical constraints of incorporating caging treatments into Experiment 3, a caging experiment was carried out eleven weeks prior, from 22 Oct. to 23 Nov. 1993 at site A only, using the same tile arrangement. Each sub-set of 3 tiles was allocated one of the five treatments: no cage (open); within exclusion cages (caged); within cages with sides only (partial cages); open within a larger cage (double open); and caged within a larger cage (double caged). This experiment was designed to test separate comparisons of (1) partially caged tiles vs tiles in the open, and (2) between open and caged (grazer exclusion) tiles within a larger cage, with tiles in the double open treatment tested against those in single cages to check for artifacts of the large cage. Variables to be tested were summed sediment load and algal biomass on tile subsets after a 1 month period of exposure to caging treatments. Theoretical considerations of these controls are discussed later. The metal cage frames (larger ['double'] cage 145x37x15 cm, all other cages 71x27x10 cm) were covered with galvanised steel wire mesh (1.25x1.25 cm, 0.8 mm diameter wire). The frames were painted with a greenish-brown coloured non-toxic paint (Wattyl® 'Permachlor', bronze-olive) to help minimise inhibition of fishes feeding around the cages. A mesh strip (5 cm) on the bottom rim of the cages eliminate gaps for macro-herbivores. The cages were fastened onto steel mounts (also painted) which were permanently bolted flush with the reef. Four replicates of each caging treatment were randomised among the tile blocks, with each of these replicates covering 3 tiles (Fig. 5.2).

Cages were fastened over tiles on the first day of the experiment and were brushed clean midway through the experiment. At the end of the experiment (after one month), the cages were removed between 10:00 to 15:00 hrs and the sediments that had naturally accrued on tiles were

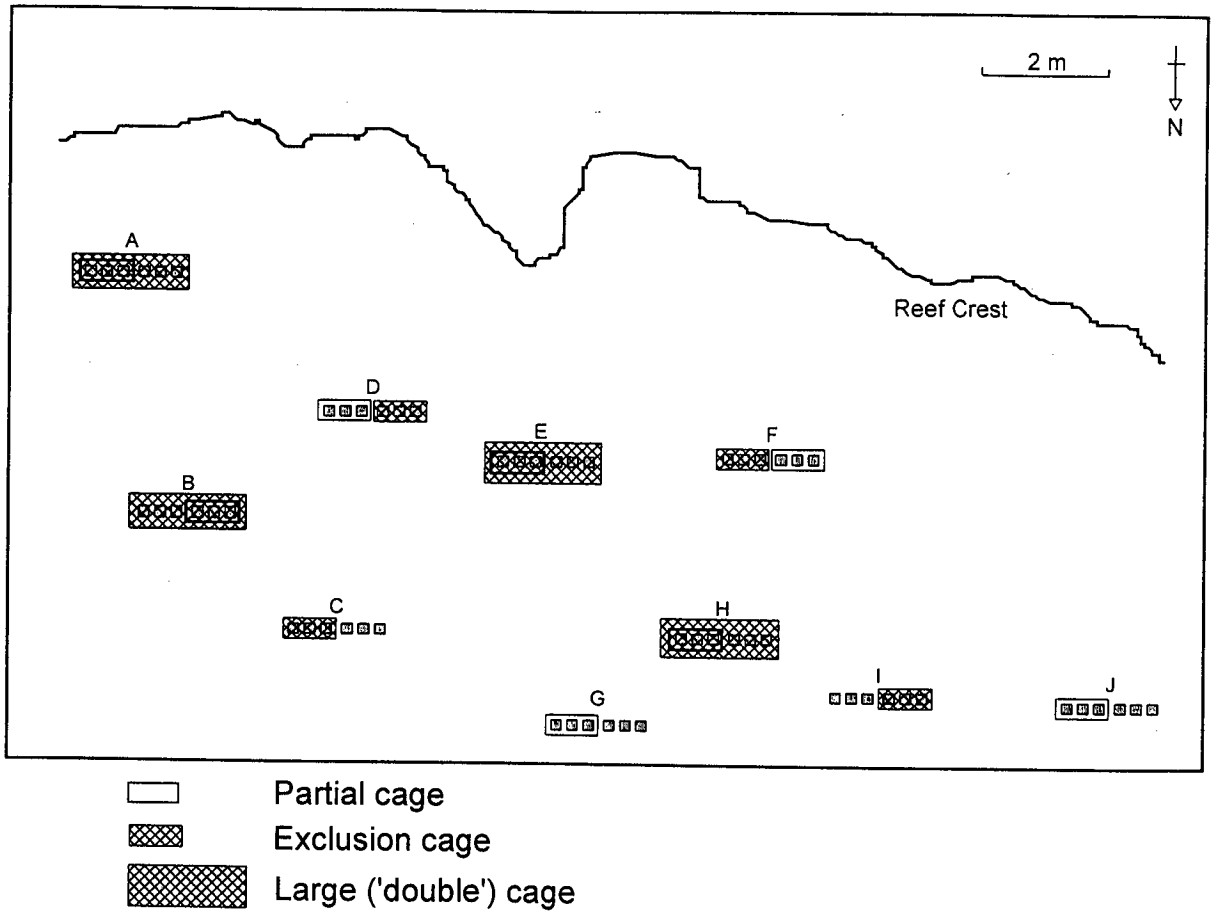


Fig. 5.2. Randomised arrangement of the caging and cage control treatments amongst the ten blocks (A - J) of tiles within study site A for Experiment 2. Overhead view with shaded squares representing tiles bolted on the reef platform.

sampled *in situ* using the sediment sampler. Tiles were then unbolted from the reef, sealed in plastic bags and kept on ice during transit to the laboratory. In the lab, each tile was rinsed briefly with fresh water, and an 11x11 cm template, covering all but the outer 5 mm edge, placed over the upper surface. Exposed algae on the border of tiles were removed by scraping the carbonate surface with a steel spatula down to a depth of 1 mm. This algae was discarded, and the first template was exchanged with one that covered the central 4 square centimetres (to exclude algae affected by the central bolt assembly). The remaining exposed algae, constituting a sample from 117 cm^2, was scraped from the tiles in the manner described above and dried at 60° for 24 hours. The dried algae were ground with mortar and pestle and the organic carbon content analysed in triplicate using a LECO auto-analyser and the acid pre-treatment outlined in Chapter 2; these determinations provide a measure of the final biomass of the EAC on tiles.

For each subset of tiles, data of EAC biomass and sediment load were summed to ensure independence of replicates; $n = 4$ (instead of 12) for each treatment. Sediment load data for caged, double-open and double-caged treatments were square-root transformed to improve homoscedasticity for parametric tests. Two-way ANOVAs were used for comparisons of 'partial' vs. 'open', and 'double-open' vs. 'double-caged' treatments, for both EAC biomass and sediment load. Caging and block factors are fixed and orthogonal. Due to the fact that two subsets of each of the partial and open treatments occurred with the caged treatment, these are considered within the same blocks for the purpose of the analyses. One-way ANOVAs were used to test differences between caged and double-open treatments for EAC biomass and sediment load, as replicates occurred within different blocks.

5.2.5. *Experiment 3 - Effects of sediment loading on EACs*

The sediment loading experiment was carried out from 11 Feb. - 9 Mar. 1994 at the two reef flat sites, and using the same spatial arrangement of tiles, as previously outlined. The field-conditioned tiles (n = 120) were attached to the reef on November 29, 1993 and left uncaged to acquire an established EAC. The experiment is a split-plot design in which caging and sediment load treatments were assigned to tile blocks within each site using a two-step randomisation (Fig. 5.3). Grazer exclusion cages, as described above (71x27x10 cm), were firstly randomised between the sub-sets of tiles within each block. Each of the 10 blocks of tiles within each site thus had 3 tiles (i.e. one sub-set) excluded from large herbivores and 3 tiles in the open. Three sediment treatment loads were then randomised amongst tiles within each subset (see Fig. 5.3) for the entirety of the experiment. The treatment loads were: low - sediment blown off daily (as in *Experiment 2*); medium - sediment load not altered (i.e. = ambient load); and high - 13 g of sediment added every two days (as in *Experiment 1*). Each tile was photographed on SCUBA with a Nikonos V camera prior to establishing the sediment load treatments.

On the first day, the ambient load on low treatment tiles was blown off for 60 sec. On subsequent mornings, a 30 sec interval was used, which appeared sufficient to remove sediment accumulated over the 24 hr period. This technique was intended to simulate wave action on the attached algae which can naturally remove sediment. Algae were never dislodged using this method. Washed and dried carbonate sediments for high treatment tiles were weighed to the nearest 0.01 g from a stock batch, with the same grain size composition as those collected from natural reef flat substrata (see *Natural substratum sediments*), excluding the <63 µm fraction. On the first day of the experiment, 30 g of these sediments were added to each high treatment tile, as described above, to initiate the treatment load, then 13 g allotments were applied every second morning to maintain the load. Cages were

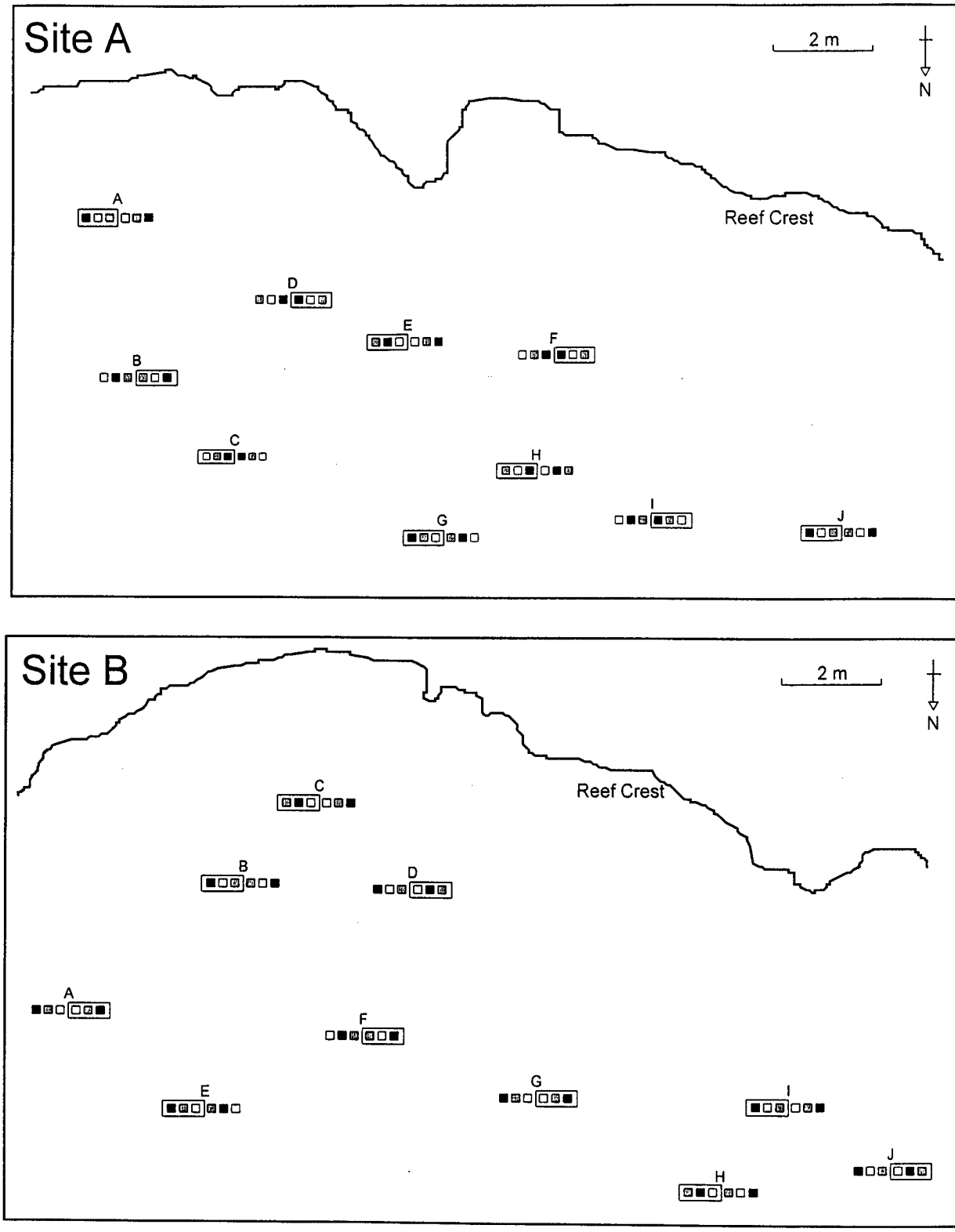


Fig. 5.3. Randomised arrangement of caging and sediment load treatments amongst the ten blocks (A -J) of tiles at study sites A and B for Experiment 3. Overhead view with hatched boxes representing grazer exclusion cages over tiles. The three sediment load treatments denoted as: unshaded squares = low, shaded squares = medium, and solid squares = high.

removed briefly from their mounts to permit maintenance of sediment treatments on enclosed tiles, and were periodically scrubbed during this period to remove adhering algae and detritus. Sediment additions and removals were carried out using SCUBA between 0800 and 1100 hrs.

Weather conditions were calm to moderate (0-15 knot wind speed) throughout the experiment, which is similar to conditions experienced during the prior experiments. After nearly 4 weeks of maintaining sediment loads, the tiles were removed from the reef to assess the biomass and nutritive quality (indicated by C:N ratios) of the adhering EACs. On the morning of the final day, tiles were unbolted from the reef, taking particular care not to disturb the accumulated sediments or algae. While on SCUBA, the sides and bottom of each tile were carefully brushed with a toothbrush to remove all sediments other than those which were on the upper surface. Sediments on the upper surface of the tiles remained bound within the EACs, and loss of sediments from the EACs appeared to be negligible. Each tile was then sealed in a plastic bag, and brought to the surface. Tiles were then placed on ice, and later refrigerated at 5° C until processed. Sediment loads were not manipulated on the morning of collection. The sediments on the tiles thus represent *effective* loads prior to maintenance, i.e. on high treatment tiles 2 days after last application, and on low tiles 1 day after last blown off.

Within 2 days of collection, each tile and bag was rinsed thoroughly with filtered tapwater into containers to collect loose sediment, and the tiles placed into large (80 litre) tubs filled with filtered seawater. The remaining bound sediment was then vacuumed off of the tiles underwater using the sediment sampler and associated technique described in Chapter 1. Sediments were sieved through a 63 μm mesh screen during collection, and were added to the (unbound) sediments collected previously. After 1 hr settling time, excess water was decanted from the containers and each sediment sample was rinsed into a vial. These were then cleared of organic

material using concentrated bleach (see Chapter 1), oven-dried at 70° C and weighed to the nearest 0.1 mg; these values are total sediment load on tiles.

Following removal of sediments, each tile was rinsed briefly with freshwater, and the EAC (including fleshy and coralline algae) scraped and collected using the procedure outlined above. Algal samples were immediately frozen in vials, freeze-dried, weighed to the nearest 1 mg and ground with a mortar and pestle. Total organic carbon in algal samples was determined in triplicate using a LECO auto-analyser and acid pre-treatment as outlined in Chapter 2. For nitrogen analyses, aliquots of ground algae were treated with a modified Kjedahl digestion (Chapter 2) which oxidises the samples in catalysed hydrogen peroxide and sulphuric acid. Nitrogen content was then determined colorimetrically using the salicylate-hypochlorite method of Baethgen and Alley (1989).

Tiles were colonised by 'filamentous and small branched' algae and crustose algae. The percentage surface area covered by these two functional groups on each tile was determined by projecting the slide photographs to actual size onto a Houston Instruments (Hi-Pad) digitising pad. Area coverage was then digitised using Sigmascan® (Jandel Scientific V3) software, with the outer 5 mm border and the inner 4 cm^2 of each plate omitted so that the area digitised was identical to that from which the algae had been collected.

During the experiment, sediments within EACs of natural substrata were collected (n = 10) from each site (1 dm^2 areas next to each block) using the sediment sampler, and were processed in the same manner as described in *Preliminary sediment samples*. These reef flat sediments are re-distributed amongst EACs during bed-load transport to leeward habitats (see Chapter 3). These samples provide, therefore, a check that sites were broadly comparable in terms of the load and grain size composition of sediments that would naturally be deposited (permanently and temporarily) on tiles.

The mesh of cages was not small enough to exclude small benthic invertebrates which could graze on EACs. A single census of these motile cryptofauna (*sensu* Hutchings 1983) on tiles was conducted on one night during the last week of the experiment when the effects of sediment loads on algal biomass were established. It is assumed that the numbers of invertebrates on tiles at night would reflect the level of their grazing on EACs, and would provide an indication of the relative impact of sediment or caging treatment effects on patterns of cryptofaunal grazing. Live animals greater than 3 mm in length (those smaller could not be distinguished) were counted with the aid of underwater torch-light and classified into broad taxonomic categories. Animals were not removed from tiles. All tiles at sites A & B were censused on SCUBA from 2000 to 2100 hrs and 2100 to 2200 hrs respectively.

Surgeonfishes (f. Acanthuridae), parrotfishes (f. Scaridae) and rabbitfishes (f. Siganidae) were thought to be the main algal grazers on uncaged experimental tiles. Censuses of these fishes at each site were therefore carried out during the experiment to examine the species composition and abundance of these fishes, and to determine the extent of variability between the two sites (see Appendix 1 for methodology).

Differences in final biomass (g organic carbon) and nitrogen yield (total mmol N) of EACs on tiles amongst sediment load and caging treatments were tested using a 4-way split-plot ANOVA with site replication (see Steel and Torrie 1980); $\alpha = 0.05$. For this model, caging and sediment load factors are fixed and orthogonal, with blocks (random factor) nested within sites (random factor). The split-plot model provides more statistical power for detecting effects of sediment loads (allocated to subplots) at the expense of detecting caging effects (allocated to whole plots). Terms involving blocks (whole plots) in the model are not tested, but provide the appropriate error terms to test for site effects and site x treatment interactions. For tests on data for C:N ratios of algae and total number of invertebrates on tiles, all terms involving site

were non-significant. Data for these two tests were, therefore, pooled between sites and tested with a simpler, tri-factorial split-plot model which provided more power for detecting treatment effects. For these split-plot tests, sediment x block and sediment x block x caging interactions are pooled into the residual error term (Steel and Torrie 1980). Homoscedasticity and normality of data distributions were confirmed using Cochran's test and box-plot analysis respectively. The difference in mean sediment load on natural substrata between sites was tested using a two sample t-test.

5.3. Results

5.3.1. *Preliminary sediment samples*

Sampling of sediments held within EACs of the surrounding (natural) substratum at site B revealed that sediment loads were variable (range: 8 to 41 g dm^{-2}), averaging 22.5 g dm^{-2} (± 11.3 g dm^{-2} SD). The grain size composition of these sediments is shown in Table 5.1. These proportional values were used to formulate sediment allocations for experimental manipulations.

Table 5.1. Average proportional grain-size composition of sediments naturally occurring within site B (n = 8).

Size Fraction (mm)	>2000	>1000	>500	>250	>125	>63	<63
Contribution (%)	1.3	14.7	39.3	26.6	13.3	4.3	0.3

5.3.2. *Experiment 1 - Loss and accretion of sediments on EAC-covered tiles*

This experiment showed that about one-third of the sediments were washed off high treatment tiles within the first hour after application, and that approx.

43% are lost from the effective load within 2 days (Fig. 5.4). However, despite a high initial loss of unbound sediments, a significant proportion of sediments from single additions are held within EACs over a long period. Based on these data, it was estimated that 13 g of sediment should be added to tiles every 2 days to 'top-up' the sediment load to the 30 g treatment level for the sediment load experiment. The temporal profile of sediment accumulate on the low treatment tiles (Fig. 5.4) indicates that sediments were accrued rapidly over the first 24 hrs when algae were cleanest, with sediment loads reaching ambient levels within several days. This finding and the fact that ambient sediment loads on tiles were relatively low compared to surrounding substrata indicated that sediments needed to be blown off low treatment tiles every day to maintain this treatment at a sufficiently low level.

5.3.3. *Experiment 2 - Effects of caging*

The results of this experiment (Fig. 5.5) provide the basis for using grazer exclusion cages in the sediment load experiment and interpreting the results therein. The experiment should be viewed as separate, yet simultaneous tests. In the first, algal biomass and sediment loads on tiles within partial cages are compared to those of tiles in the open. Assuming that grazing was the same for both treatments, a significant difference between treatments for either response variable could be attributed to the partial cages. The two-way ANOVA showed no significant differences in the summed algal biomass and sediment loads on tiles within partial cages compared to tiles in the open (Table 5.2). This test indicates that the exclusion cage structure does not exert a significant effect on sediment load or algal biomass.

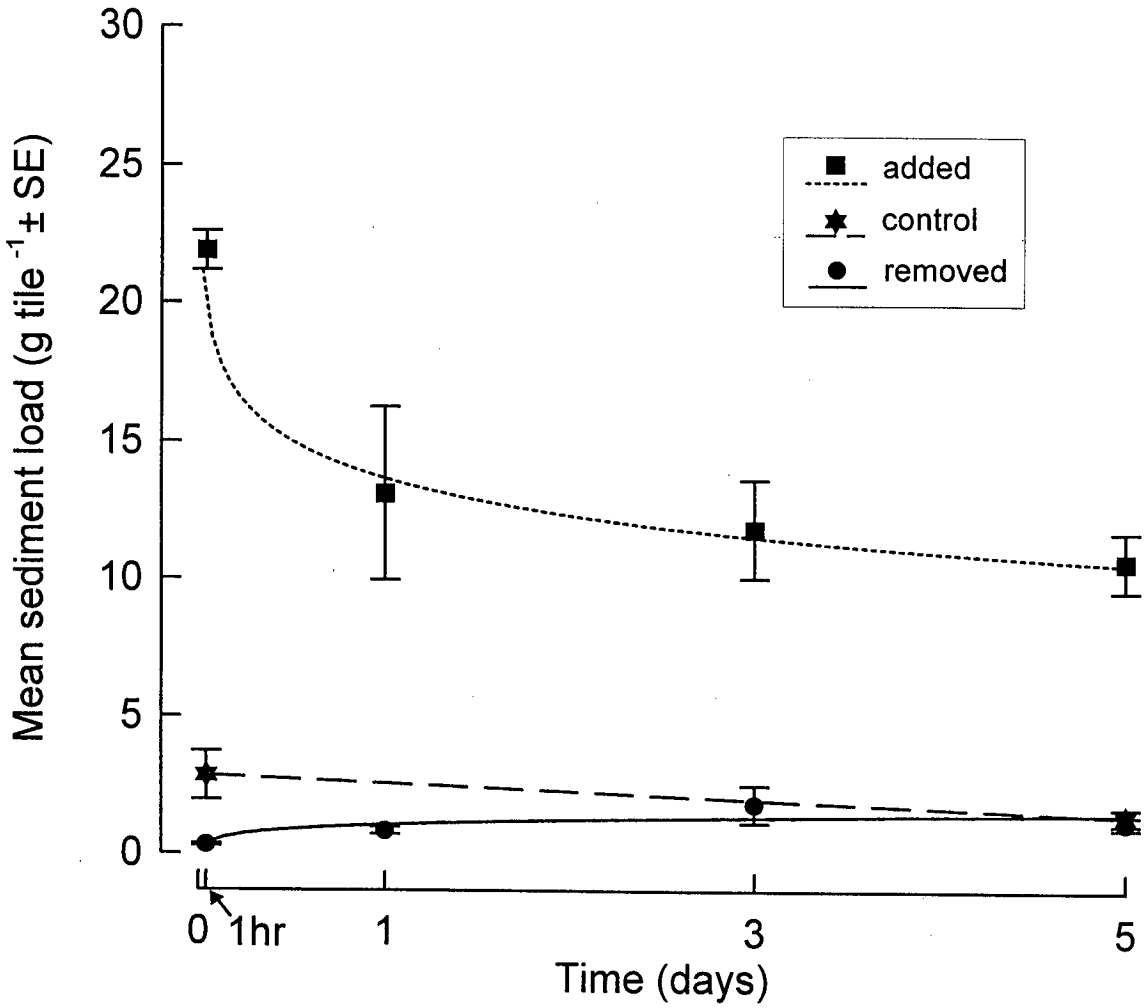


Fig. 5.4. Results of *Experiment 1* showing mean sediment loads on tiles at 1 hour, and 1,3, and 5 days after manipulations. Estimated temporal profiles are of the reduction of mean loads where sediment was added (dotted; $y = 356 - 343\ x^{.0057}$; $r^2 = 0.51$) and of the increase in mean loads where sediments were washed away (solid; $y = -5.95 + 7.02\ x^{.0357}$; $r^2 = 0.21$). Change in mean ambient sediment load over the 5 days (dashed) was minimal. For each mean, $n = 6$.

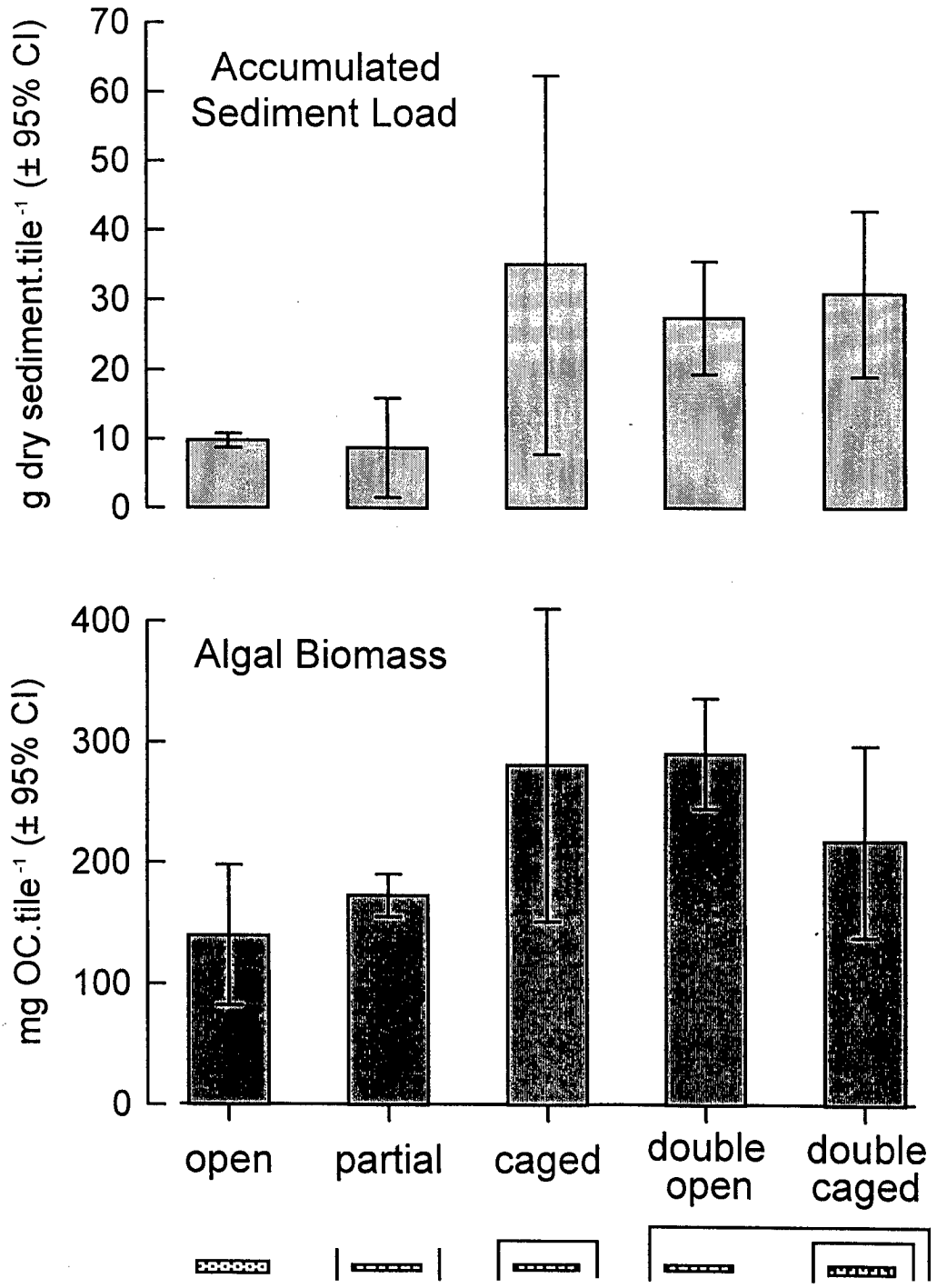


Fig. 5.5. Results of *Experiment 2* (caging experiment with naturally acquired sediment loads) at study site A. Graphs of mean ambient sediment load (above) and mean algal biomass (below; organic carbon (OC) content) on sub-sets of tiles for each of the cage and cage control treatments. For each mean (summed for tiles in sub-sets), $n = 4$.

Table 5.2. Two-way ANOVAs of differences in EAC biomass and accumulated sediment load between 'partial' vs. 'open' caging treatments and blocks.

	Source	SS	d.f.	MS	*F*	*p*
EAC biomass:	Treatment	2158.83	1	2158.83	5.11	0.11
	Block	3054.17	3	1018.06	2.41	0.24
	Treatment x block	1266.27	3	422.09		
Sediment load:	Treatment	2.18	1	2.18	0.23	0.66
	Block	34.46	3	11.49	1.22	0.44
	Treatment x block	28.22	3	9.41		

The second test examines caging artifacts using the double caging control. It assumes that effects of cages should be additive, i.e. a caging artifact will be more pronounced on tiles within the double-caged treatment (tiles covered by two cages) compared to tiles within the double-open treatment (tiles covered by one cage). The two-way ANOVA on mean summed sediment loads failed to detect a significant difference between treatments, but the test on EAC biomass detected a significant difference amongst the two treatments (Table 5.3); biomass of EACs on tiles within double-caged treatment were on average 25% lower than within the double-open treatment. This test suggests that the natural sediment regime is similar on tiles inside and outside exclusion cages, but there may be a direct effect of exclusion cages on EACs which decreases growth and hence the final biomass of algae on tiles.

Finally, testing differences between tiles within the caged and double-open treatments provides a check that potential effects from the large (double) cage are the same as those for the (normal) exclusion cage. One-way ANOVA tests on summed sediment loads and EAC biomass failed to detect

Table 5.3. Two-way ANOVAs of differences in EAC biomass and accumulated sediment load between 'double caged' vs. 'double open' treatments and blocks. Sediment data was square root transformed.

	Source	SS	d.f.	MS	*F*	*p*
EAC biomass:	Treatment	10495.03	1	10495.03	20.57	0.02
	Block	8407.01	3	2802.34	5.49	0.10
	Treatment x block	1530.56	3	510.19		
Sediment load:	Treatment	0.19	1	0.19	0.56	0.51
	Block	1.11	3	0.37	1.09	0.47
	Treatment x block	1.02	3	0.34		

significant differences between these treatments (Table 5.4), indicating that the exclusion effect and potential artifacts of large cage were similar to those of the exclusion cage.

Table 5.4. One-way ANOVAs of differences in EAC biomass and accumulated sediment load between 'double open' vs. 'caged' treatments and blocks. Sediment load data square-root transformed.

	Source	SS	d.f.	MS	*F*	*p*
EAC biomass:	Between treatments	78.08	1	178.08	0.05	0.83
	Within treatments	2316.28	6	3719.38		
Sediment load:	Between treatments	0.69	1	0.69	0.67	0.44
	Within treatments	6.10	6	1.02		

5.3.4. *Experiment 3 - Effects of sediment loading on EACs*

Although experimental sedimentation rates on tiles at the two sites were identical, *effective* sediment loads within EACs on tiles were significantly

lower at site B (Fig. 5.6). This corresponds with more crustose algae which has been shown to be linked to lower sediment accumulation compared with filamentous and small branched forms (Chapter 3). Regardless of the size of effective loads, however, the *profiles* of differences in loads amongst sediment load treatments were similar between sites; effective loads from high treatment were many times higher than ambient loads, which were relatively low, but still higher than low treatment loads.

The split-plot ANOVA of algal biomass on tiles revealed a significant sediment x caging x site interaction; algal biomass differed amongst sediment treatments depending on the caging treatment and the site examined (Table 5.5). Trends of the differences in EAC biomass and effective sediment loads on tiles between treatments are, however, of a similar nature, but differing in magnitude, between sites (Fig. 5.6). Within both sites, mean EAC biomass on tiles in the open (exposed to herbivores) was consistent amongst low, medium and high sediment load treatments. Therefore, herbivore grazing in the open apparently kept algal biomass on tiles of differing sediment treatments at equal levels. However, the lack of an effect of sediment load on algae in the open is confounded by herbivore grazing; the key finding is revealed through comparisons of caged tiles. At both sites, mean final EAC biomass on tiles within exclusion cages was markedly different amongst the three sediment load treatments; mean EAC biomass was highest on tiles where sediment had been repeatedly blown off and decreased in treatment levels with increasing sediment load. On average, sediment loading caused a difference in the final algal biomass on high sediment treatment tiles by 81% at site A and by 25% at site B compared to tiles with ambient sediment loads. Due to the fact that EAC biomass on caged tiles would reflect net growth rates of algae, the findings show that when subjected to increased sediment loads, these EACs were less productive. In view of these results, herbivore grazing in the open apparently kept algal biomass on tiles of differing sediment treatments at equal levels.

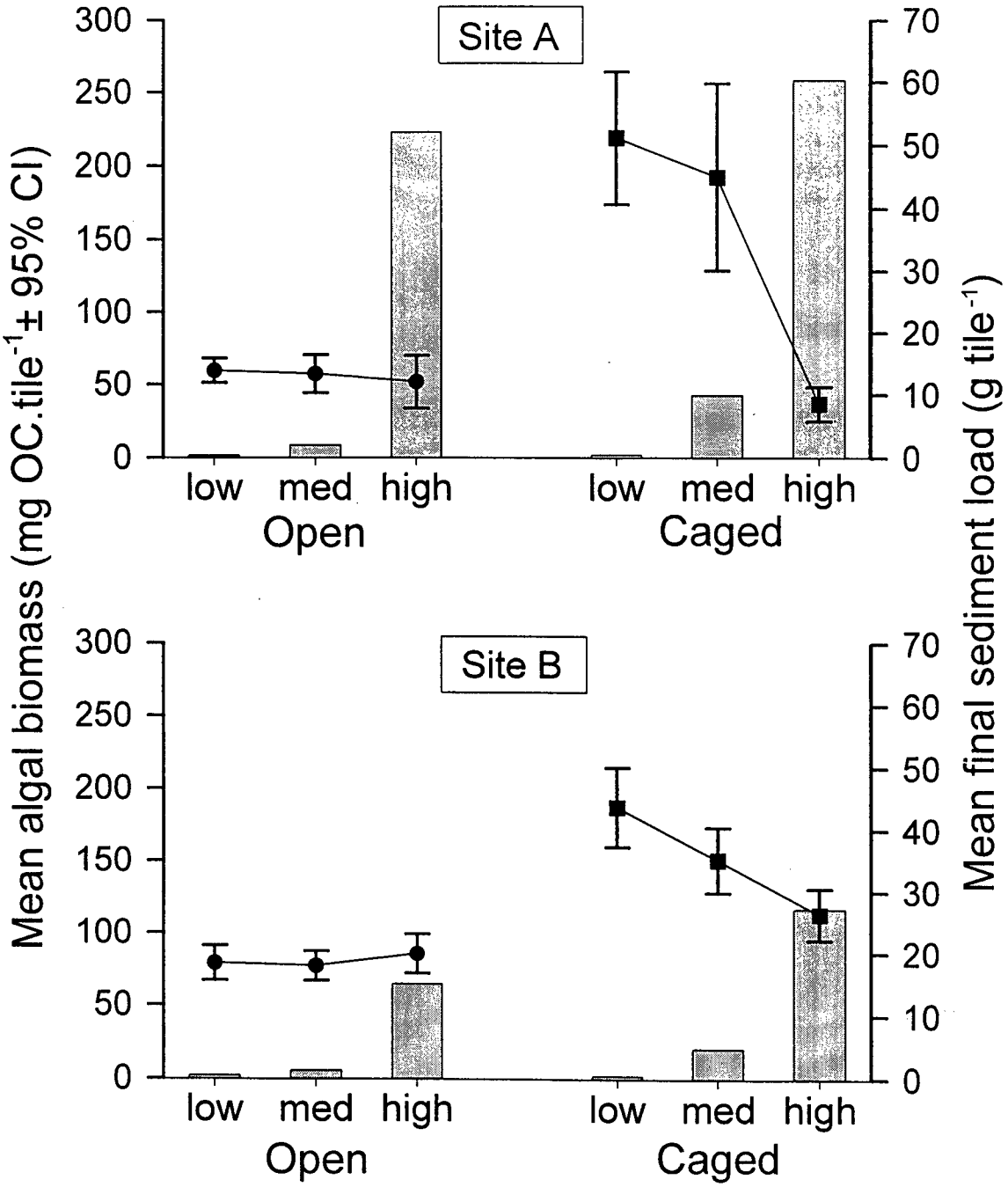


Fig. 5.6. Graphs of the final mean effective sediment loads (shaded bars) and algal biomass (± 95% CI; organic carbon (OC) content) on tiles within sediment load treatments (*low*, *med* (=medium) and *high*) and both caging treatments (*Open* and *Caged*) at sites A (above) and B (below) at the end of *Experiment 3*. For each mean, n = 10.

Table 5.5. Results of 4-way split-plot ANOVA of differences in EAC biomass on tiles amongst treatments replicated between sites. The sediment load factor is denoted as 'sediment'.

Source of Variation	SS	d.f.	MS	*F*	*p*
site	4637.08	1	4637.08	1.79	.198
caging	199461.60	1	199461.60	49.07	.090
caging x site	4065.00	1	4065.00	2.85	.108
sediment	89867.78	2	44933.89	3.30	.233
sediment x caging	89832.94	2	44916.47	5.44	.155
sediment x site	27241.67	2	13620.83	10.23	<0.001
sediment x caging x site	16510.63	2	8255.32	8.49	.001
block(site)	46724.85	18	2595.82		
caging x block(site)	25651.98	18	1425.11		
sediment x block(site)	47921.34	36	1331.15		
sediment x caging x block(site)	34996.62	36	972.13		

Sediment load and grazing pressure appear to affect also the total amount of nitrogen within EACs per unit area. Patterns of total nitrogen per tile amongst the three sediment treatments (Fig. 5.7) varied significantly between caging treatments and between sites (interaction $F_{2,36} = 10.19$, $p < 0.001$), and were strikingly similar to those shown for final biomass of EACs (Fig. 5.7; cf. Fig. 5.6). At both sites, the mean quantity of nitrogen per tile across sediment treatments was relatively even in the open, but was variable within cages. The total amount of algal-nitrogen on caged tiles was lowest, at both sites, in the high sediment treatment.

Differences in relative content within algal tissue, i.e. C:N ratios, within and amongst caging and sediment treatments were found to be non-significantly different between sites A and B. The tri-factorial split-plot ANOVA (Table 5.6) showed, however, that patterns of C:N ratios amongst sediment treatments differed between open and caged treatments (Fig. 5.8). As a trend for open and caged tiles, algal-C:N ratios were low for EACs in the

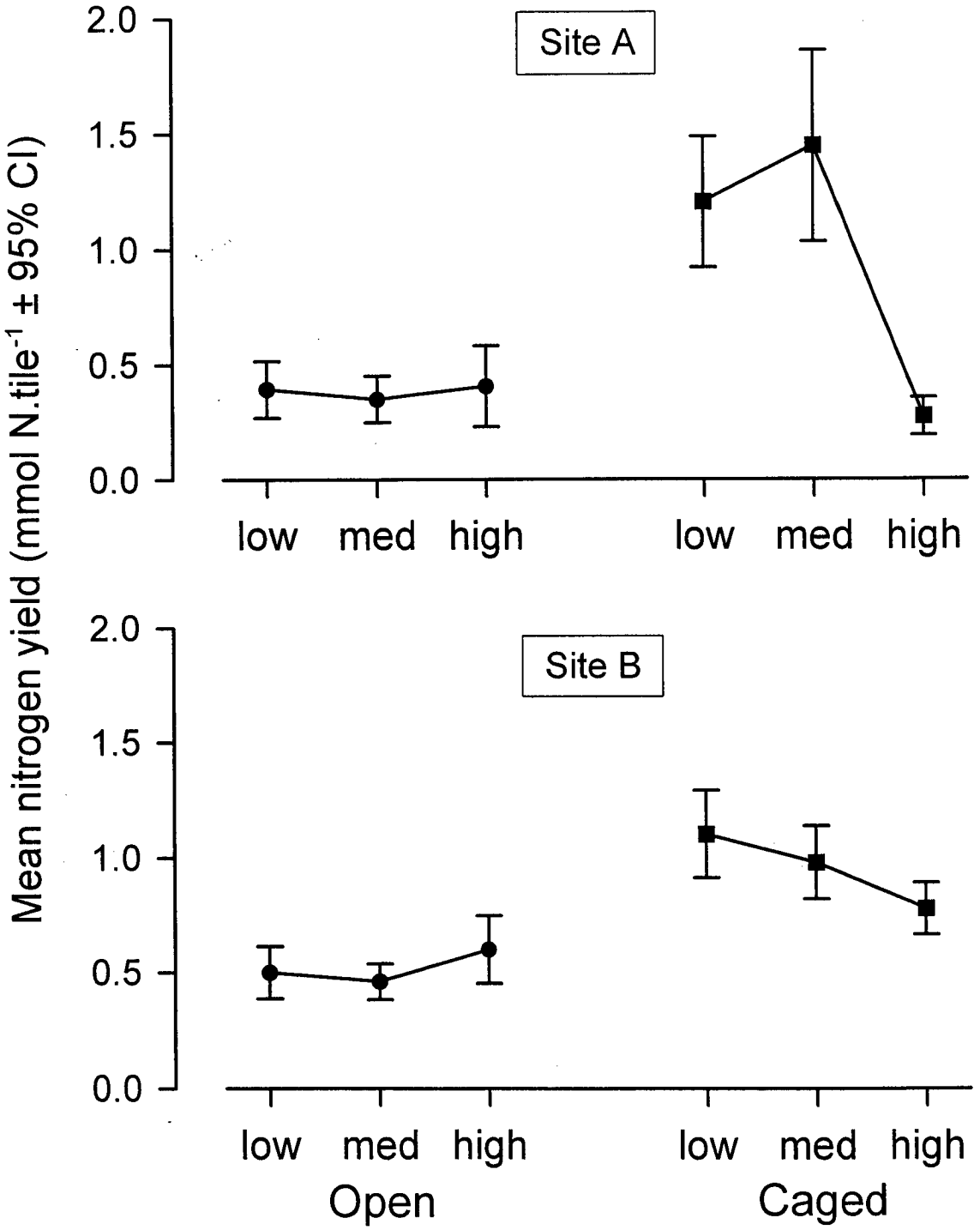


Fig. 5.7. Mean total nitrogen yield from algae per tile for each sediment load treatment and both caging treatments at sites A and B at the end of *Experiment 3*. Note similarity of trends with those of algal biomass (Fig. 5.6). For each mean, n = 10.

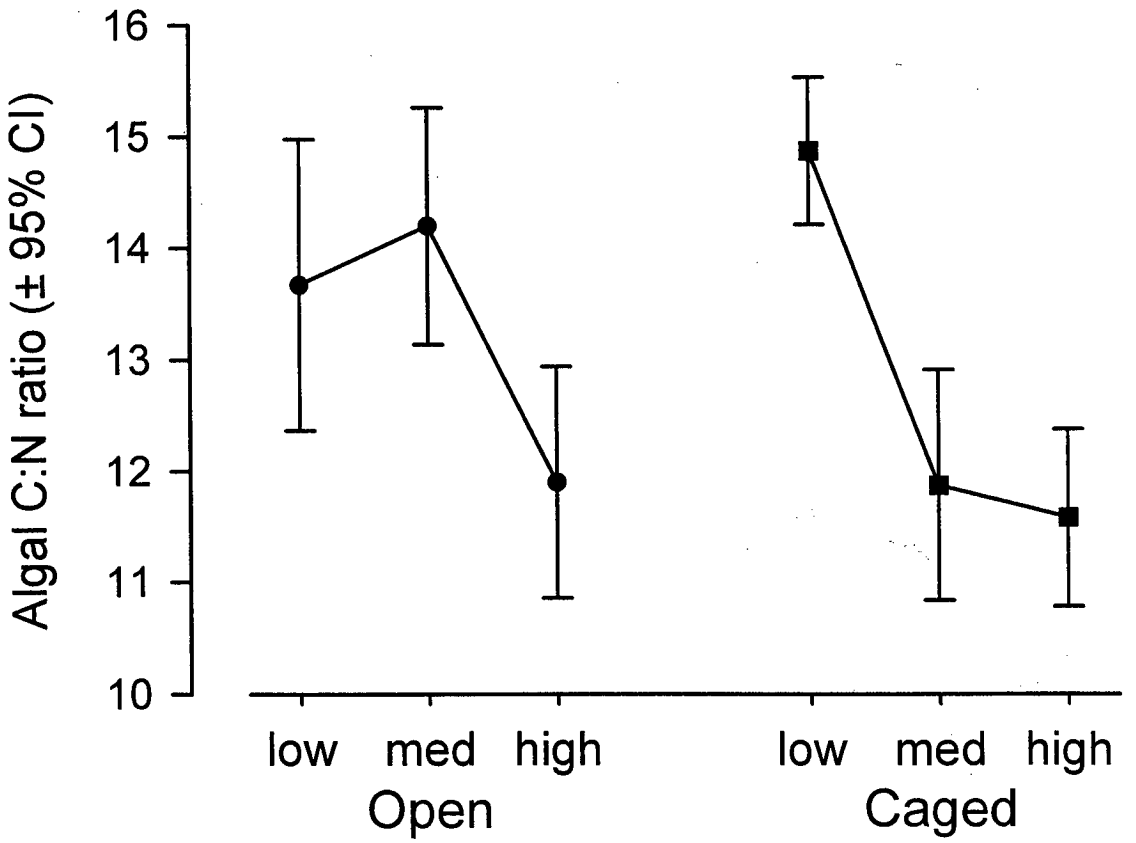


Fig. 5.8. Molar carbon:nitrogen (C:N) ratios from algal tissue for each sediment load treatment and both caging treatments at the end of *Experiment 3*. Sites were pooled following non-significance of site terms in the 4-way split-plot ANOVA. For each mean, $n = 20$.

high sediment load treatment and high in the low sediment treatment. Mean C:N ratios of algae in the medium sediment load treatment, however, differed between caging treatments, being relatively high in the open and low within cages. Nutritive quality of EACs, as indicated by C:N ratios, therefore appears to be better under higher sediment loads; mean C:N ratios of algae on high treatment tiles were relatively low.

Table 5.6. Results of tri-factorial split-plot ANOVA of differences in C:N ratios of algae on tiles amongst treatments pooled across sites. The sediment load factor is denoted as 'sediment'.

Source	SS	d.f.	MS	*F*	*p*
block	102.62	19	5.40	1.22	.266
caging	7.19	1	7.19	1.58	.225
sediment	128.27	2	64.13	14.48	<.001
sediment x caging	62.40	2	31.20	7.04	.002
block x caging	86.66	19	4.56		
residual	336.70	76	4.43		

The night-censuses of motile cryptofauna on tiles showed that overall, gastropods were the most common group recorded (91%) with hermit crabs (7%) and isopods (2%) contributing less to total abundance. A tri-factorial split-plot ANOVA revealed that mean invertebrate abundances were significantly patchy amongst blocks ($F_{19,76}$ = 1.97, p = 0.020), and were significantly affected by sediment loads ($F_{2,76}$ = 3.71, p = 0.029). For all groups combined, invertebrates were more abundant amongst EACs with less sediment (Fig. 5.9); at both sites there was an increase in the average number of invertebrates on tiles with decreasing sediment loads. The vast majority of animals recorded were small enough to pass through the mesh of cages. Although the power to detect differences in invertebrate numbers between caged and open tiles was fairly low (power = 0.37), the test indicates that these animals were not attracted to algae on caged tiles significantly more than on open tiles ($F_{1,19}$ = 2.90, p = 0.105).

Visual censuses of roving herbivorous fishes showed that adult acanthurids, scarids and siganids were equally abundant at both sites during this experiment (see Appendix 1). The numerically dominant species was the brown surgeonfish, *Acanthurus nigrofuscus* (Forsskål), followed in abundance by the surf parrotfish, *Scarus rivulatus* (Valenciennes).

Digitisation of photographs, taken just prior to the beginning of the experiment, showed that on average, the coverage of crustose corallines on tiles from site B (25.56% ±1.83% SE) was markedly higher than on tiles from site A (0.26% ±0.08% SE). However, 'filamentous and small branched' algae was the dominant functional group on tiles at both sites. Mean sediment loads on natural substrata, adjacent to the tiles, at sites A and B (20.2 ± 5.0 g dm^{-2} SE, and 24.9 ± 4.8 g dm^{-2} SE respectively) were not significantly different (t_{18} = 0.69, p = 0.50). Furthermore, the grain size composition of these sediments was similar to that of the preliminary sediment samples from site B, and was comparable between sites (Fig. 5.10).

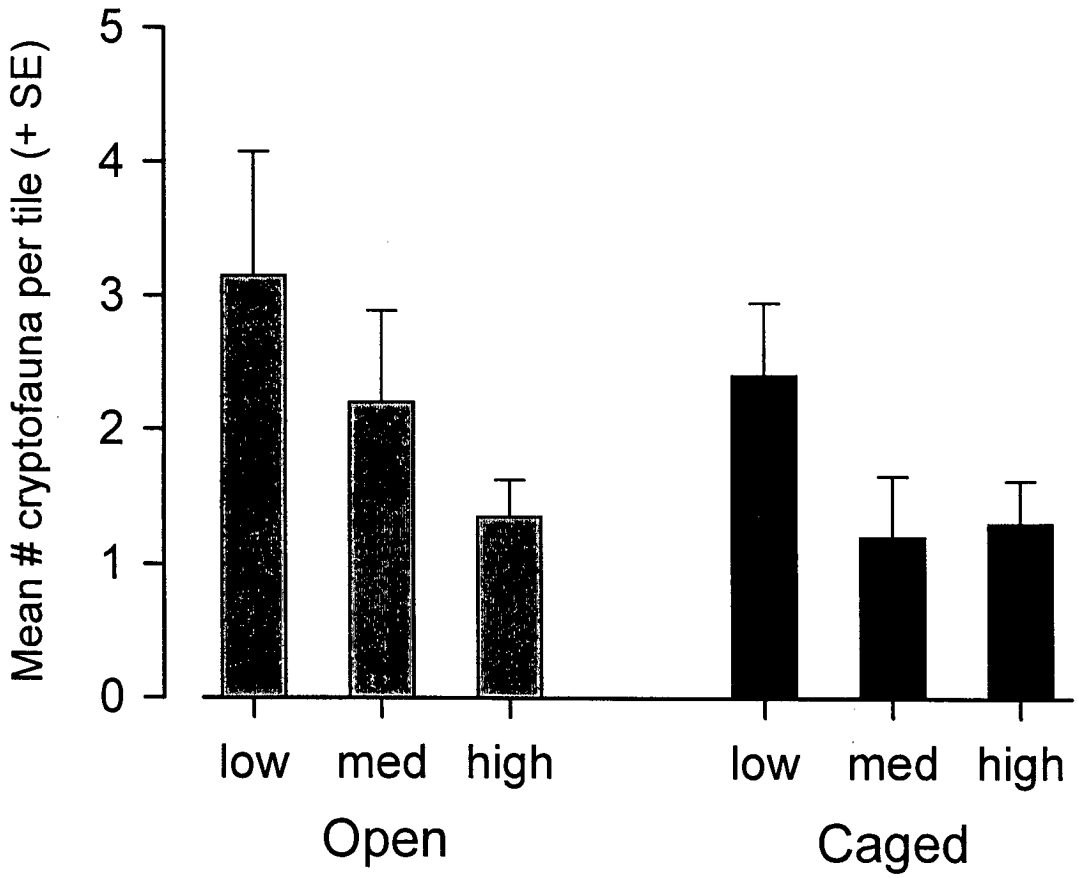


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Fig. 5.9. Results of night censuses of motile cryptofauna on tiles during *Experiment 3*. Mean abundances on tiles for each sediment load treatment and both caging treatments. Data for sites are pooled, following non-significance of terms involving site in the 4-way split-plot ANOVA. For each mean, n = 20.

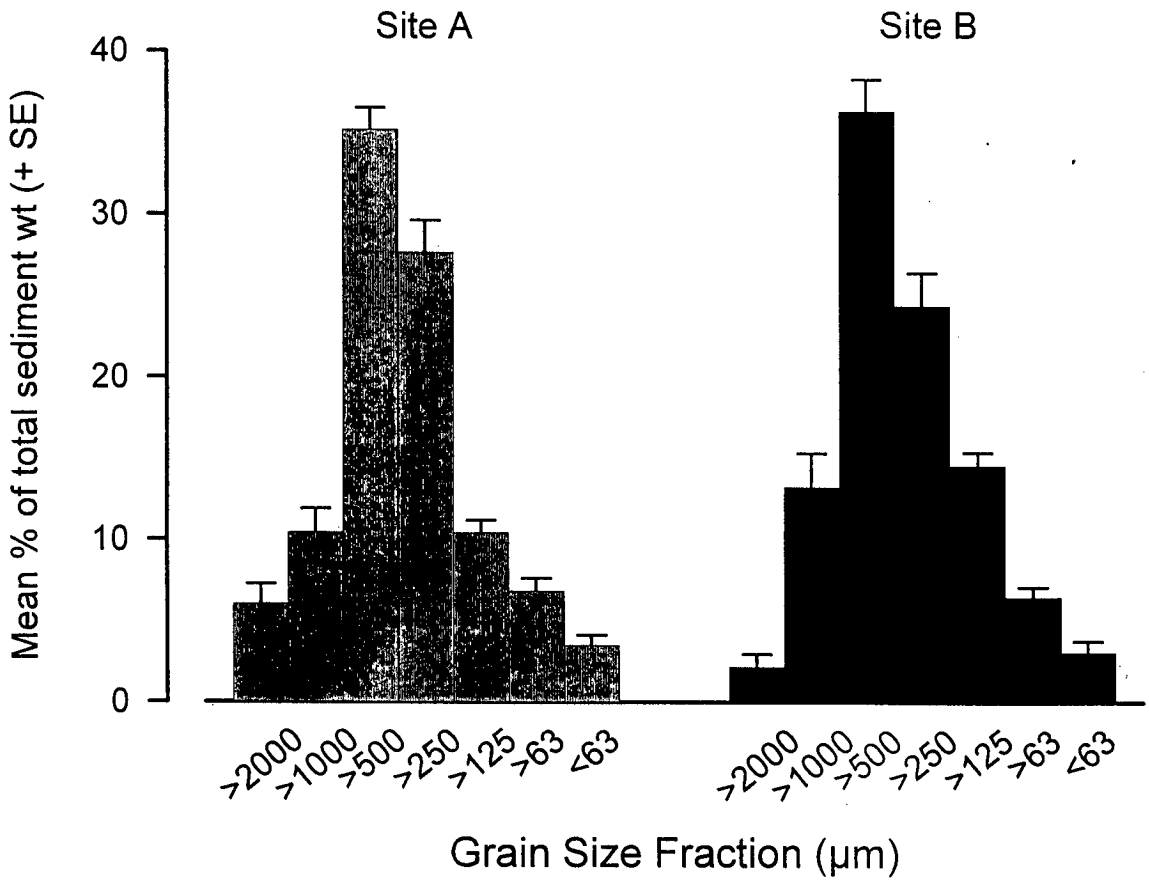


Fig. 5.10. Graphs of grain size composition of sediments collected from neighbouring (natural) substrata at both sites during *Experiment 3*. Particle size distributions of sediments are clearly very similar between sites. For each site, n = 10.

5.4. Discussion

5.4.1. *Methodological considerations*

Loss and accumulation of sediments within EACs

Wave action on coral reefs can remove and re-distribute sediments amongst EACs, particularly on exposed reef crests. The experimental manipulations here showed that sediments can accumulate on and be lost from EACs rapidly. Sediment loads within EACs were shown in Chapter 3 to reflect their heights above the substratum and it is likely that EACs have particular 'threshold' sediment loads, whereby the spaces amongst algae are filled and any added sediments are not trapped, but will lie unbound above the EAC canopy where they are removed easily by water movement.

The profile of sediment loss from EACs loaded with sediments raises a few interesting points. Firstly, EACs do not necessarily have accumulated sediment loads at their 'threshold' level. This is indicated by the initial low ambient sediment loads on tiles combined with the fact that an appreciable amount of the sediments added to EACs remained after 5 days. Secondly, the temporal profile of sediment retention suggests that sedimentation events may have long-lasting effects on EACs. Some studies on sedimentation on coral reefs have shown that sediments can remain in these systems for several seasons (Chansang *et al.* 1992, Lawn and Prekker 1993).

Knowledge of sediment retention and transport is important to understanding organism and ecosystem responses to sediment stress (Rogers 1990). The present data show that, following sediment loading, EACs can act as repositories for sediments and prolong their activity (i.e. inducing stress) in reef habitats. Finally, the loss of nearly half of the sediments added to tiles in the first hour suggests that unbound sediments in habitats with high energy are removed rapidly.

Caging controls

The most commonly used method for excluding the effects of herbivory on benthic algae is enclosure of substrata with cages. Exclusion cages are designed to partition the effects of large mobile herbivores and generally should:

a) have large enough mesh such that light reduction is negligible,

b) exclude grazers from the substrata,

c) have a minimal effect on local current flow,

d) have a minimal impact on the biota on the surrounding substrata.

Problems can arise if one or more of the above requirements are not met, with the result being a caging artifact, i.e. effects not exclusively due to the exclusion of herbivores. These problems necessitate the use of appropriate controls to test for such artifacts.

Partial-cages are one such control which attempt to retain the same structure of the exclusion cage, and its corresponding effect, while at the same time allowing herbivores access to experimental substrata. Although this premise is questionable, as a significant portion of the original cage needs to be removed to permit similar grazing pressures as on uncaged substrata, use of partial cages has been widespread . There have been two approaches in the usage of 'partial' cage controls. To test for overall effects of the cage structure, small patches of mesh are removed to allow access by herbivores, while attempting to retain as much of the original cage structure (e.g. Wanders 1977, Hay 1981, McCook 1996). Alternatively, to test for caging artifacts caused by altering a particular environmental variable (eg. reduction in incident light or current velocity), the cage consists only of the section likely to be creating the artifact, as in cages with roofs or sides only (e.g. Underwood 1980, Sammarco 1982, 1983, Hay 1981, Carpenter 1986, Sammarco *et al.* 1986, Hixon and Brostoff 1994). When using a partial cage, one assumes that: a) a majority of the original cage structure has been

retained in the control, and b) herbivores have equal access to algae under open and cage control treatments, with equivalent rates of herbivory.

Sammarco *et al.* (1986) used cages to exclude herbivores from natural substratum plates, with partial cages (to control for decreased light) consisting of cage tops with open sides. However, these workers showed that levels of bioerosion of substrata within partial cages were consistent with those under complete cages and differed significantly between most of the non-caged substrata. The potential for partial cages to deter or encourage some animals from substrata (e.g. Underwood 1980, Hay 1981, Sammarco 1983a, Steele 1996) is a problem which can confound these controls. Additionally, Jones *et al.* (1988) questioned the effectiveness of partial cages, as their results using partial fences are an example where these controls may not have influenced water movement in the same way as the complete fences.

The main purpose of no-roof cages used here was to test for potential effects of reduced water flow which could increase natural sedimentation on caged substrata. This validation was particularly relevant to interpretations of the effects of sediment manipulations in Experiment 3. In the present study, mean EAC biomass and sediment loads on tiles were high within complete cages, but were not found to be significantly different on tiles in partial or open treatments, indicating that sedimentation on tiles was not significantly modified by the cage structure. However, given the limitations outlined above, these interpretations are not equivocal and would benefit from comparisons with other caging controls.

Ideally, as Kennelly (1983) noted, a rigorous test of caging artifacts would involve selecting similar areas devoid of herbivores and comparing open and caged treatment substrata in this area. This situation rarely exists, apart from regions with mass faunal depletion. Herbivores can be also excluded from treatments by suspending experimental substrata at the same

depth away from the reef (Morrison 1988), but for the purpose of the present study, this strategy would be flawed if these areas have different regimes of water flow, nutrient supply or sediment supply. Alternatively, if caged and uncaged treatments can be isolated from herbivores by a larger cage (cf. Kennelly 1983, Russ 1987, Scott & Russ 1987, Kennelly 1991, Steele 1996) then the confounding effects of herbivory can be partitioned out from those of the cages themselves. Double caging of this sort has received less usage in field studies on benthic algal production compared with partial caging. This technique does, however, deserve special note as it alleviates some of the problems encountered with partial cages.

In using double cages, it is assumed that if caging *per se* is causing an effect on the response variable(s), then increased caging will generate a compounding effect; i.e. effects are additive. The double caging controls in this study showed that, in this case, effects were probably additive, with the detectable effect of double cages suggesting that exclusion cages decrease the net biomass of EACs. Hixon and Brostoff (1996) concluded that cage mesh, as used in the present study, had a minimal effect only in reducing water motion (0-10% reduction), but did reduced light levels somewhat (about 20%). While they refer to findings of Littler and Littler (1992) to argue that these reduced levels remained well above the photosynthetic saturation rates for a range of reef algae, other reports indicate that such reductions to light intensity may indeed limit maximum photosynthetic rates (e.g. Carpenter 1985, Williams and Carpenter 1990). Unfortunately, it was not possible to clean cages regularly for the caging experiment. The resultant algal fouling on mesh may therefore have decreased light intensities below the saturation threshold of these EACs, and reduced algal growth (cf. Underwood 1980). Given the potential of light reduction by cages, which was not measured, this may produce a caging artifact in Experiment 3. However, this would only effect the type I error of statistical tests by lessening the beneficial effects of caging on algal biomass.

In cage control experiments on a temperate rocky shore, Kennelly (1991) found a significant caging artifact of increased sediments, although this was attributed to fouling of uncleaned cages. Sediment loads in EACs in the present study increased in complete cages, but tests using partial and double caging techniques did not identify this as a significant cage-related artifact. Rather, increased sediment load inside complete cages appeared to be due to indirect effects of increased biomass of algae which promotes sediment accumulation (Chapter 4; cf. Wanders 1977, Kennelly 1983).

5.4.2. *Effects of sediment loading on EACs*

This field study illustrates that the amount of sediment within coral reef EACs can have a profound effect on the growth of the constituent algae. While the magnitude of effect of a sediment loading event may vary between sites, the nature of the effect is likely to be similar. With confounding effects of grazing excluded, growth of algae was retarded under high sediment loads and stimulated under low sediment loads. Within cages, a high sediment treatment resulted in a reduction in the average final biomass of 81% at site A and 25% at site B when compared with tiles with ambient loads. Effects of sediments on EAC productivity may be underestimated here within cages due to decreased photosynthesis from self-shading of algae at high biomass (Larkum 1983, Carpenter 1985, Williams and Carpenter 1990) and decreased light intensity. Similar detrimental effects of sediment loading (seen within cages) on EAC growth under natural conditions are likely, given that sediments were manipulated on established EACs on coral-carbonate surfaces, and that this trend was found at both sites. The absence of a detectable effect of sediment loading on epilithic algal biomass in the open does not mean it had no impact, but rather that any effects may have been masked by herbivore grazing.

The value of field experiments using factorial combinations of treatments is highlighted in this study. Exclusion cages were a prerequisite to revealing the effects of sediments on algae due to intense herbivory on EACs in the open. Moreover, the similarity in algal biomass on tiles in the open, despite differing sediment loads, indicates that an interaction exists between sediment loads and either EACs or herbivores. That is, that grazing was even amongst EACs with different sediment loads and this kept algae below a critical size at which responses to sediment loads could occur, or that the growth response of EACs in the open was comparable to that in cages (higher under lower sediment loads) but grazing intensity on EACs was inversely related to sediment load. Although these two alternatives cannot be separated in this study, recent field experiments using underwater video (Purcell *unpublished data*) support the latter idea of sediments deterring herbivores. These experiments show that the surgeonfish *Acanthurus nigrofuscus*, the most abundant roving herbivore at both sites in the present study (see Appendix 1), feed preferentially on EACs with sediments removed.

The experimental sedimentation rate on high treatment tiles (equivalent to 46 mg cm^{-2} day^{-1}) is realistic of a high sedimentation event, as it is less than some reported for broad-scale sedimentation impacts on coral reefs in the Caribbean, Hawaii and Thailand (see Cortés and Risk 1985, Maragos 1972 [cited in Rogers 1990], and Chansang *et al.* 1992 respectively). In this study, causal mechanisms of the negative effect of sediments on algae are likely to have been physical as the high treatment consisted of cleared (washed) sediments. Sediments can reflect and absorb the sunlight required by epilithic algae (Rogers 1990), potentially lowering the incident light below photosynthetic saturation rates of species within EACs (see Luning 1981, Littler and Littler 1992). In the case of epilithic turfing algae, it is conceivable that vertical growth could also be reduced if filaments are weighed down by sediments. It is also possible that the high sediment treatment reduced nutrient uptake and/or also produced anoxic or low CO_2 conditions within the sediments which affected algal gas exchange.

At both sites, average biomass of EACs within cages was highest where sediments were blown off (low treatment), even though the ambient loads were also quite low and would be expected to have little influence on the EACs. It is unlikely that this effect was due to a manipulation artifact, as sediments on low treatment tiles were blown off for 30 seconds only per day. Rogers (1990) concluded in her review on sedimentation on coral reefs that "we need data on the threshold levels for reef organisms...above which normal functioning of the reef ceases." The implication of the present experiment is that the growth of epilithic algae appears to be sensitive to modest changes in sediment load, and that sediment impacts may be incremental, without a particular threshold load for an effect. EACs of coral reefs may function 'normally' over a range of productivity rates depending on instantaneous sediment loads (and other physical and biological variables) with sedimentation impacts lowering this range and hence the overall productivity of the system. The magnitude of effects on EACs may be different for other types of sediments, such as fine siliceous particles, as these are denser and may smother underlying filaments more than reef-derived sediments.

Motile cryptofauna foraged amongst EACs on caged and open tiles at night. Although there are few dietary studies on such cryptofauna from coral reefs, they appear to be chiefly herbivorous (see Klumpp *et al.* 1988), thus the censuses of their abundance on tiles provides a test of the deterrence effect of sediments on an additional component of herbivory. The results did not correspond with previous findings that exclusion of herbivores and carnivores increases invertebrate abundance (Brawley and Adey 1981, Kennelly 1983). However, cryptofauna were most abundant on low sediment tiles and least abundant on high sediment tiles, suggesting that high sediment loads had a deterrent effect on these foraging invertebrates. This interpretation is supported firstly by the fact that the sediment treatment produced the only significant effect. This is particularly surprising, given the fact that the EAC biomass, which is reported to correlate strongly with

cryptofaunal abundance (Klumpp *et al.* 1988), was so different between caged and open treatments. Secondly, algae with high sediment loads (most avoided) had on average, the highest nitrogen, hence protein content (cf. Odum *et al.* 1979). Algae with a high protein content are reported to be preferred by coral reef herbivores (Choat 1991, Bruggemann *et al.* 1994a).

Perhaps sediments within EACs influence substratum or feeding preferences of invertebrates. Previous experimental work has shown that calcium carbonate incorporated in coral reef algae deters feeding in sea urchins, amphipods (Hay *et al.* 1994), and the sea hare *Dolabella* (Pennings and Paul 1992) possibly via mineral buffering of acid-mediated digestion, or as a result of abrasive (toughness) effects on feeding. In view of these studies, perhaps carbonate sediments adhering to epilithic algae also deter grazing by invertebrates. Regardless of the mechanism, the present study indicates that the deterrent effect of sediments within EACs is stronger than the benefits of higher nitrogen content or higher biomass of algae.

The effects of sediment loads on the nutritive quality of algae, as indicated by C:N ratios (cf. Russ 1987), are more difficult to interpret than the growth data. This is partly because the C:N ratios are a function of both carbon and nitrogen metabolism (Hanisak 1979). It was clear from the experiment that the total amount of nitrogen within EACs per unit area of substratum was related the amount of algal tissue present, with trends in the total nitrogen yield from algae per tile within and amongst treatments mirroring those of final biomass of EACs. This effect was also found by Russ (1987). However, this relationship between biomass and nitrogen content was not consistent at all sediment loads.

It has been suggested that nitrogen uptake by EACs is inversely related to grazing pressure (Wilkinson and Sammarco 1983, Sammarco *et al.* 1986, Wilkinson *et al.* 1985). In the present study, EACs in the open were heavily grazed and were therefore likely to have high rates of carbon fixation (see

Hatcher 1981, Carpenter 1986, Klumpp and McKinnon 1992). Sediment loading appears, therefore, to cause epilithic algal tissue to become enriched with nitrogen, but this seems to be attributed to nitrogen storage during slower rates of carbon fixation (cf. Hanisak 1979, Atkinson 1988, Stimson *et al.* 1996) rather than increased rates of nitrogen uptake *per se*.

This experiment shows that while sedimentation rates can be identical at different sites, these do not necessarily produce similar sediment loads. The difference between sites in sediment loads within EACs in the open was more than three-fold despite identical sediment manipulations; sediment load was lower at site B which may be attributed to higher cover of crustose corallines. The use of sedimentation data from sediment traps as a proxy for sediment loads on EAC-covered substrata may be therefore misleading.

To determine long-term effects of sediments on EAC productivity in future studies, rates of carbon fixation should be the measured response variable, as these can be repeatedly estimated non-destructively. Moreover, studies have shown that the productivity of EACs on midshelf reefs of the GBR is inversely correlated with their biomass, with heavily grazed EACs being most productive (Hatcher 1981, Klumpp and McKinnon 1989, 1992). Sediment loads may foster regimes in grazing pressure which act additively on the productivity of EACs, with reductions of carbon fixation rates being the sum of direct (light reduction and smothering) and indirect effects (herbivore deterrence).

Overview

Sediments can be deposited on the benthos of all coral reef habitats. Here they can characterise substrata and affect benthic biota. The distribution of sediment loads on reef substrata will be governed by hydrodynamic forces at most spatial scales (Suhayda and Roberts 1977, Davies 1983), and may also be affected by the topography of reef surfaces, which includes at smaller scales the living veneer of algae. The sampling device described in Chapter 1 enables sediments to be vacuumed from this living veneer where sediment layers are labile and can be held within epilithic algal communities (EACs) that form extensive mats of erect algal filaments on the carbonate reef framework. The efficiency of this device in collecting sediments from these communities (>90%) permitted the assessment of accumulated instantaneous loads on hard forereef substrata with a high resolution for relating these loads to fine-scale measurements on these EACs.

The physical characteristics of EACs affect their ability to trap sediments, thus mediating sediment distribution and the relative influence of sediments on biota. Measurements of forereef EACs and sediment loads (Chapter 3) showed that sediment distribution at the scale of among habitat zones (tens of metres) was related to the canopy heights of EACs and, to a lesser extent, EAC standing stock. The findings showed that EAC canopy heights were related also to sediment loads at the scale of within habitat zones (of a few metres wide), parallel to the front margin. At this resolution, the basic morphology of patches of algae within EACs appears to also play a role in sediment accumulation. Only canopy-forming algae are able to trap sediment. Field sampling showed that substrata with higher surface area cover of filamentous and small branched algae tended to trap more sediment than areas with high coverage of crustose forms in which sediment could be easily washed away. Results from the sediment loading experiment (Chapter 5) supports this idea also, as more sediment was held on tiles at the site with

higher cover of filamentous and small branched forms compared to crustose forms, despite equivalent artificial sediment loading rates.

While EACs with higher standing stock tend to accumulate more sediment, this relationship varies whereby EACs can exist with sediment loads well below 'threshold capacity'. A field experiment (Chapter 5) showed that when sediments are removed from EACs, these can re-accumulate rapidly. Conversely, pulse additions of sediments to EACs in this experiment showed that these communities can retain some of these sediments for long periods (i.e. many weeks). Both processes will of course be governed chiefly by sediment supply and hydrodynamic forces. Studies that attempt to forecast or monitor sediment impacts on coral reefs need to therefore consider that EACs may influence the time frame and magnitude of these events. Basic measurements of the heights of EACs and the relative contribution of 'filamentous and branched algae' and crustose alge may provide a higher resolution of potential effects on benthic biota in such studies.

Procedures developed for the analysis of carbon, nitrogen and phosphorus content of biological material from coral reefs (Chapter 2) permitted the examination of correlative relationships and experimental effects of sediments on EACs. These were also used to compare algal and detrital food sources on forereef habitat zones. These procedures are reliable and cost-effective and were shown to eliminate problems associated with the decarbonation of carbonate sediments during analyses. Laboratory tests showed clearly that studies should avoid ash-free dry weight (AFDW) determinations for assessing biomass of material containing coral reef carbonates, as this method will overestimate the role of organic material in these systems.

Sediments within EACs are commonly mixed with organic detritus (including a suite of composting organisms), thus presenting a heterogeneous

food source for reef grazers. The biomass of epilithic detritus was strongly correlated with sediment load across forereef habitat zones (Chapter 4), suggesting that these are aggregated together tightly, or that similar mechanisms affect the accumulation of each component within EACs. These particulate aggregates modify the state in which epilithic algae is available for consumption by herbivores in a physical sense, and perhaps also biochemically. While the standing stock of algae and detritus may be higher in zones further from the crest, these two epilithic food sources are associated with proportionally higher sediment loads. Conversely, although the biomass of algae and detritus on reef crests may be low, these food sources are present with proportionally much less inorganic sediment. Sediments can decrease the relative gain per feeding episode (Choat 1991), hence these patterns in the proportional contribution of sediments to algae and detritus may further explain habitat selection in herbivores and detritivores.

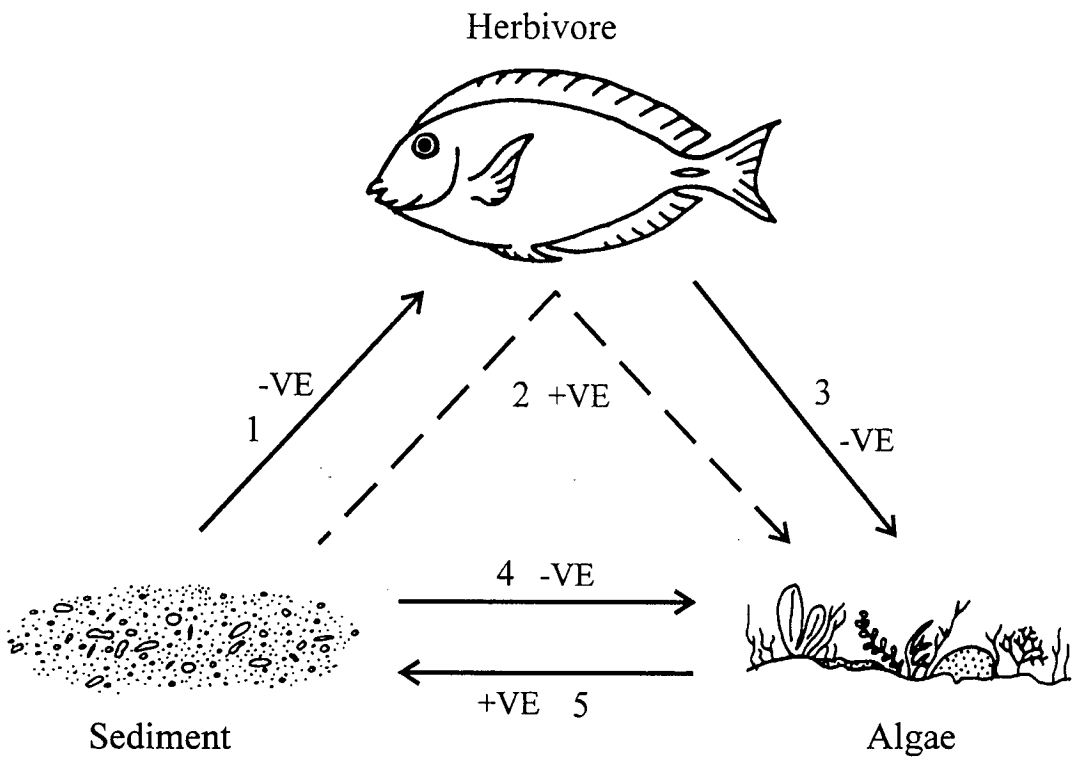
Algal and detrital food resources were shown to be comparably abundant, in terms of biomass per unit substratum, in many forereef areas (Chapter 4). Towards the reef crest, algae were shown to be the dominant epilithic food source, with about 5 times the biomass of detritus. In deeper areas at the front reef base, detrital biomass can be twice as abundant as algae. The results showed that in most cases, the nutritional quality of detritus, in terms of nitrogen and phosphorus content, was better than that of epilithic algae. The nutritional quality of algae and detritus, in terms of protein content inferred through carbon:nitrogen analysis, varied independently within, but not among, habitat zones. The load of reef sediments did not appear, from correlative data, to influence nitrogen content of algae or detritus, but did relate to phosphorus content. It is possible, at low sediment loads, that the benefits to growth of EACs from detrital- or sediment-associated phosphorus are greater than the negative, physical effects of smothering and light reduction from sediments (Chapter 5). The physical effects of sediments on nutrient dynamics in EACs, however, are not

entirely clear. The sediment loading experiment showed that the physical effects of sediments can decrease the nitrogen uptake by EACs per unit area. However, under sediment stress, rates of carbon fixation may be depressed to a greater extent than rates of nitrogen uptake, with the result being increased relative concentration of nitrogen per unit algal-biomass. While these findings provide some information on potential effects of sediments on nutrient uptake of EACs, further work is required under a variety of conditions to ground our understanding of these processes. This is especially important, as the concentration and state of nutrients in sediments arising from human activities may be different from those in the sediments investigated in this project.

The cause of ecological patterns in nature can be confounded by interacting factors. This caution is germane to coral reefs, where the effects of physical and biotic processes on individuals and communities can be complex and may not be complementary. For instance, Hay (1981) and McCook (1996) used grazer exclusion cages in transplant experiments on coral reef algae to show that algal distribution can be influenced by herbivory to a greater extent than by the physical characteristics of reef habitats. In the present project, field measurements of sediments and algae supported the suggestion that sediments may benefit from algal growth, as higher sediment loads corresponded to taller EACs with higher standing stock. The field experiment in Chapter 5 partitioned the effects of macro-herbivores and habitat variations from those of sediment load to examine the causes of this trend. This experiment, however, revealed an opposite effect from that expected from the observational data; algal growth suffers markedly from sediment loading.

In a review of herbivory on coral reefs, Steneck (1988) concluded that there was ample scope for broadening our understanding of the mechanisms mediating algal-herbivore interactions on coral reefs. A paradox of the response by EACs to sediment loading may exist if herbivores are influencing

the interaction between sediment and epilithic algae on reefs. Previous work has shown that calcification in calcareous algae presents a mineral deterrent to a number of reef herbivores (Pennings and Paul 1992, Hay *et al.* 1994, Schupp and Paul 1994, Pennings et al. 1996). In the present project, there is circumstantial evidence that, due to a similar effect, reef sediments may deter grazing by herbivores not able to avoid ingesting sediment particles attached to epilithic algae. Firstly, reductions in sediment loads within EACs following rough weather were concomitant with reductions in the canopy heights of algae (Chapter 3), which could be attributed to a response by browsing fishes that nip the distal tips of algae. Secondly, during the sediment loading experiment (Chapter 5), cryptofauna that forage at night were found to be attracted to EACs with less sediment. Finally, in this experiment also, macro-herbivores apparently grazed algae on open tiles with varying sediment loads to similar levels. If the effects of sediments on algae were comparable in the open, at low standing stock, then this removal of algae by macro-herbivores was greater under lower sediment load, and this may have been due to sediment deterrence. These interpretations appear valid, in view of video footage of recent field experiments showing that many acanthurid and siganid species markedly prefer EACs with less sediments (Purcell *unpublished data*). A possible model that integrates herbivore effects to explain the paradox , ie. that algal growth is reduced by sediments (Chapter 5) even though algal standing stock is higher where sediment loads are high (Chapter 3) is provided below:



Model of interactions among sediments, epilithic algae and herbivores (depicted as a browsing surgeonfish). The influences in the model, indicated as positive (+ve) or negative (-ve), are:

1. Sediments deter grazing/browsing in some herbivores
2. By deterring herbivores, sediments indirectly benefit EAC standing stock and/or canopy height
3. Herbivory reduces canopy heights and standing stocks of EACs
4. Accumulated sediments decrease algal growth
5. Increased canopy heights and biomass of EACs enhances sediment retention

Sediments appear to decrease the growth rate of EACs, and hence are likely to have profound effects on algal-based food chains on coral reefs. Observable responses of EACs to sediment loading impacts may, however, be difficult to predict in view of potential interactions with herbivores. For instance, following a sediment loading disturbance, EACs may achieve a high standing stock due to sediments providing an associational refuge from herbivory, but are likely to have decreased rates of carbon fixation. This could

generate a feedback loop, whereby the higher standing stocks of algae trap more sediments. Such a situation could be particularly detrimental to coral reef communities, given that high algal biomass may reduce the recruitment and survivorship of corals (Banner 1974, Walker and Ormond 1982, Hughes *et al.* 1987). Simple measurements of standing stock of EACs, therefore, may not provide the information required to determine the nature of direct effects of sediments on these communities or of the health of algal-based food chains. If the proposed model of sediment-algae-herbivore interactions is appropriate, then maintaining herbivore populations on sediment-affected coral reefs, especially for species able to feed on sediment-filled EACs, should be a management priority.

The physical structure of tropical coral reefs can be viewed in two parts, the first being the matrix of carbonate rock, and the second being eroded sediments in a labile mosaic on top of the matrix. Arioldi et al. (1996) studied sediment dynamics on a rocky shore, and stated that sediment load may be a potential critical source of stress and disturbance for communities of hard substrata. The significant, incremental effects of sediment loads on epilithic algal growth and the variable nature by which sediment loads on hard, coral reef substrata are likely to persist through time indicates that sediments may also be a critical source of stress and disturbance for benthic coral reef communities. Sediment loads amongst hard substrata of reef platforms probably vary periodically via storms and changes in hydrodynamic conditions which redistribute these deposits. Given the findings of this project, such temporal fluctuations in the spatial mosaic of sediments on reefs may propagate reciprocal spatial mosaics (i.e. opposite spatial patterns of differences) in the productivity of EACs, and potentially also in herbivory. Epilithic algae in areas where sediments are temporarily deposited may then receive less grazing pressure, but would also be less productive, whereas the opposite would occur where sediments were washed off substrata. In this context, sediment inputs mediated by human activities will increase the

average reference level about which sediment loads affect benthic reef communities, and may alter the scale at which these mosaics fluctuate.

For a broader model, further work would benefit from examining effects on a wider range of algal communities, and monitor these over a time frame over which sediment perturbations would persist on coral reef substrata. It is quite possible that under chronic sediment stress, EAC composition shifts towards species or growth forms that are able to better tolerate sediment stress; the implications of these shifts for the productivity of algal-based food chains should also be a management concern. There is currently ample scope for expanding our understanding of the interactions between sediments and biota of hard substrata of coral reefs, particularly within the context of broader temporal and spatial trends.

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Appendix 1.

Census of grazing fishes during the sediment loading experiment.

Species composition and abundance of roving herbivorous fishes at the two study sites (A and B) were estimated from visual surveys within belt transects. Three, adjacent, 5x50 m transects were established (1 day before the first census) and marked out with cord along an East-West line at each study site. For both sites, the transects were situated so that the area made up by all three included all of the experimental blocks, as well as 10 metres at each end of the study sites. Each group of three transects was censused once on March 8, 1994, between 16:00 and 17:30 hrs, and twice on March 12, 1994, between 10:30-12:40 hrs and 14:55-16:10 hrs. Transects were covered by a single diver on SCUBA, close to the substratum at approx. 3 m min^{-1}. All fishes within the families Acanthuridae (surgeonfishes), Scaridae (parrotfishes) and Siganidae (rabbitfishes) within the transect were recorded on underwater data board. Two omnivorous butterflyfishes, *Chaetodon auriga* and *C. ephippium* (Chaetodontidae), were also seen feeding amongst the EACs at the study sites and were included in censuses. Individuals smaller than 100 mm estimated length were recorded as juvenile. Data from consecutive swims of the three transects at both sites were pooled to provide 3 replicate censuses of the abundance of these fishes at each study site (Table A.1).

Table A.1. Average abundances of large herbivorous and detritivorous fishes within the families Acanthuridae, Scaridae, Siganidae, and Chaetodontidae at sites A and B during the sediment loading experiment; n = 3 censuses from 750 m^2 areas (summed abundance from three 5x50 m transects).

Species	Mean Abundance per site (± SE)	
	Site A	Site B
Acanthurus nigrofuscus	23.67 (± 4.26)	37.33 (± 4.67)
Scarus rivulatus	22.67 (± 4.91)	25.67 (± 8.67)
Scarus psittacus	16.00 (± 3.21)	13.33 (± 1.33)
Juvenile scarids	12.67 (± 6.94)	37.00 (± 11.02)
Ctenochaetus striatus	8.67 (± 2.73)	12.67 (± 0.88)
Chlorurus sordidus	7.00 (± 3.51)	3.67 (± 1.33)
Siganus doliatus	4.67 (± 0.67)	4.67 (± 1.20)
Scarus globiceps	4.00 (± 2.65)	1.00 (± 0.58)
Scarus schlegeli	3.67 (± 3.18)	7.00 (± 3.61)
Chaetodon auriga	2.67 (± 0.67)	1.00 (± 1.00)
Zebrasoma veliferum	2.33 (± 1.45)	3.00 (± 1.53)
Zebrasoma scopas	1.00 (± 0.58)	0
Siganus argenteus	1.00 (± 0.58)	21.00 (± 10.60)
Scarus chameleon	1.00 (± 1.00)	0
Juvenile acanthurids	1.00 (± 1.00)	8.67 (± 1.20)
Siganus punctatus	0.67 (± 0.67)	0
Chaetodon ephippium	0.33 (± 0.33)	0
Calotomus carolinus	0.33 (± 0.33)	0
Scarus frenatus	0	3.67 (± 0.88)
Scarus ghobban	0	1.00 (± 0.58)
Naso brevirostris	0	1.00 (± 0.58)
Siganus vulpinus	0	0.67 (± 0.67)
Siganus corallinus	0	0.67 (± 0.67)
Chlorurus gibbus	0	0.67 (± 0.33)
Acanthurus olivaceous	0	0.67 (± 0.33)
Cetoscarus bicolor	0	0.33 (± 0.33)
Acanthurus nigricauda	0	0.33 (± 0.33)
Acanthurus blochi	0	0.33 (± 0.33)