




**GREAT BARRIER REEF**  
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**Water quality, sediment and  
biological parameters at four  
nearshore reef flats in the  
Herbert River Region, Central GBR.**

Britta Schaffelke  
Sven Uthicke  
David Klumpp



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## EXECUTIVE SUMMARY

This report summarises the results of a study from 1995 to 1997 estimating the nutrient status of four inshore fringing reef flats in the vicinity of the Herbert River mouth in the central section of the Great Barrier Reef World Heritage Area. The study sites were at Great Palm Island, Fantome Island, and North Island of the Brook Islands group. Variables measured were nutrient parameters and biological parameters that may serve as proxy measures for nutrient availability.

Inorganic water column nutrient concentrations on the reef flats were low [0.06-1.75  $\mu\text{M}$  dissolved inorganic nitrogen (DIN); 0-0.25  $\mu\text{M}$  phosphate], whereas concentrations of organic nutrients were higher [3-10  $\mu\text{M}$  dissolved organic nitrogen (DON), 0.02 to 0.21  $\mu\text{M}$  dissolved organic phosphorus (DOP)]. Nutrient concentrations in the sediment pore water were substantially higher (up to 4.65  $\mu\text{M}$  DIN, 0.85  $\mu\text{M}$  phosphate, 9.66  $\mu\text{M}$  DON, 0.50  $\mu\text{M}$  DOP). Most water column nutrient parameters were lower at Great Palm Island than at Fantome Island and Brook Islands.

The study reef flats were dominated by macroalgae, especially by large brown algae such as *Sargassum* spp. Interspersed were microalgal-rich sediment patches and individual hard corals. Further seaward was a fringing reef with abundant and diverse soft and hard corals.

Particle deposition rates were higher in the seaweed zone [15.6 mg dry weight (DW)  $\text{cm}^{-2} \text{d}^{-1}$ ] than in the hard coral zone (2.7 mg DW  $\text{cm}^{-2} \text{d}^{-1}$ ). Mean relative nutrient contents in the particulate material ranged from 0.26 to 0.31% DW nitrogen (N) and from 0.04 to 0.05% DW phosphorus (P). Correlations of deposition rates with water flow measurements showed a positive relationship, indicating the importance of resuspension processes on the reef flats.

Sediment quality parameters were in a range previously reported for coral reefs (0.017 to 0.025% DW N; 0.17 to 0.23% DW organic carbon). The proportion of calcium carbonate in the sediments ranged from 56 to 82%. The chlorophyll *a* content of the sediments ranged from 1.36 to 1.85  $\mu\text{g g DW}^{-1}$ . The sediments also contained a high proportion of phaeophytin, an indicator for dead plant biomass. The parameters that are potentially related to nutrient availability (N, organic carbon, chlorophyll *a*) showed distinct difference between reefs, with Brook Island having the highest values and Great Palm Island having the lowest.

Nutrients in macroalgal tissue showed a similar trend with high values at Brook Island (1.0% DW N; 0.1% DW P) and low at Great Palm Island (0.88% DW N; 0.08% DW P).

The biological sediment parameters, diatom and bacteria counts, also showed significantly higher values at Brook Island ( $2.21 \times 10^6 \text{ ml}^{-1}$  and  $2.93 \times 10^8 \text{ ml}^{-1}$ ) than at Great Palm Island ( $1.71 \times 10^6 \text{ ml}^{-1}$  and  $2.45 \times 10^8 \text{ ml}^{-1}$ ).

Microbenthos community production and production of the dominant seaweed *Sargassum baccularia* were only measured at the reef flat at Great Palm Island, because of resource constraints. These measures showed a significant seasonal difference with higher net production values during the summer months (microbenthos: 0.25 to 0.79  $\text{g C m}^{-2} \text{d}^{-1}$ , *S. baccularia*: 0.43 to 3.0  $\text{g C m}^{-2} \text{d}^{-1}$ ). Extrapolated values for the annual net production of the microbenthos community were 168  $\text{g C m}^{-2}$ , and of the *Sargassum* zone 548  $\text{g C m}^{-2}$ .



Most measured variables indicated a higher nutrient availability at Brook Island compared to the sea-ward site at Great Palm Island, with the two Fantome Island sites being intermediate. We suggest that this is the result of:

- the greater distance of the Great Palm Island site to the mainland and, hence, to the more nutrient-rich coastal mixing zone; and
- the more frequent inundation of the Brook Islands with Herbert River water, due to the predominantly north-ward transport of flood plumes.

Of the variables measured, the sediment parameters, i.e. organic carbon, nitrogen, chlorophyll *a*, and bacteria, were considered as most suitable and cost-effective to detect changes in nutrient availability. These parameters allowed the detection of differences between sites and/or seasons and were robust to patchiness and methodological variability, as indicated by small standard errors of the means. In contrast, water column nutrient data showed a high variability, and although differences between reefs and seasons were detected, this was only possible due to the relatively high number of samples and a rigorous sampling design.

For future monitoring programs we recommend a stronger emphasis on parameters that integrate nutrient availability over longer time periods. However, because of the apparent variations between sampling months, a high level of temporal replication is desirable, i.e. several sampling occasions per year.

## INTRODUCTION

Over the past decade there has been considerable concern that nearshore fringing reefs of the GBR are becoming degraded due to human influences. Terrigenous run-off of nutrients and sediments from rapidly expanding land use is considered to be one of the most severe impacts on coastal areas of the Great Barrier Reef World Heritage Area (GBRWHA) as well as of other Australian regions (GESAMP 1990, Zann 1995). However, the fate of this imported material and its effects on marine ecosystems are still poorly understood. Riverine input has been identified as the largest external source of nutrients to the GBR lagoon (Mitchell & Furnas 1997). The bulk of sediments and nutrients is discharged during flood events, with flood plumes predominantly impinging on the coast and areas of the inner shelf, but occasionally extending into the mid-shelf of the GBR (Steven et al. 1996, Devlin et al. 2001).

The nutrient and sediment load of rivers is directly influenced by land use activities. The watersheds of rivers in Queensland have been extensively modified since European settlement by clearing, followed by forestry, mining, urbanisation and agriculture. Clearing of forest and woodland has continued throughout the last 130 years with extensive loss of rainforest areas, coastal wetland forest, and open woodland (Johnson et al. 1998, Gardiner et al. 1988). In the Herbert catchment, Melaleuca wetlands have been reduced in area from 30 000 ha in pre-European times to less than 5000 ha in 1996. The National Greenhouse Gas Inventory Committee Report (1999) estimated that in the period between 1988 and 1998 an estimated 3 million hectares of land has been cleared in Queensland. The loss and disturbance of riparian vegetation in agricultural areas leads to increased erosion and enhanced turbidity in stream waters (Moller 1996). Land use statistics and trends for the GBR Catchment have been collated by Gilbert (in press). Grazing of cattle for beef production is the largest single land use (66%) on the Herbert River catchment with cropping, mainly of sugarcane (8%) and urban/residential development (3%) less important. The sugarcane cultivation area has increased steadily over the last 100 years, and associated with this, total fertiliser application has increased rapidly since 1950 (Pulsford 1996). Estimates of sediment land run-off vary widely but agree upon a minimum figure of a four-fold increase since European settlement (Neil & Yu 1996). Because nutrients are associated with sediments, e.g. bound to soil particles, it is very likely that nutrient run-off increased as well, but actual estimates are scarce (Neil & Yu 1996).

In the coastal zone of the GBRWHA the nearshore fringing reefs are of particular importance to the multiple users due to their easy accessibility. The proximity to the coast, however, subjects fringing reefs to pressure by activities such as fishing, tourism and recreation, by facilities such as resorts and marinas, and by land run-off, sewage and stormwater inputs. The GBRWHA contains more than 500 fringing reefs along the mainland coast and around high continental islands, with a total area of ~350 km<sup>2</sup> (Hopley & Partain 1989). The continental islands of the GBR integrate many different habitats on a small spatial scale such as coastal rainforest, freshwater streams, mangroves, beaches, seagrass beds, lagoon and coral reef areas. The fringing reefs of the inner shelf of the GBR have evolved under very different geological, hydrographical, and chemical conditions than the platform reefs of the outer shelf (Hopley et al. 1983).

Since the early 1980s fringing reefs have been recognised as habitats that are particularly susceptible to human impacts. The well-known studies of Kaneohe Bay, Hawaii (Smith et al. 1981), Reunion Island in the Indian Ocean (Cuet et al. 1988), and the Florida reef tract (Lapointe 1989) described 'worst-case scenarios' of human impacts

that adversely impacted, changed or even destroyed coral reef communities. These cases were mostly attributed to increased inputs of nutrients and sediments to the coral reef waters. The likely causes for the serious degradation of Jamaican fringing reefs have been identified as a combination of over-fishing, natural disasters and increased nutrient inputs (Hughes 1994, Lapointe et al. 1997, Lapointe. 1999).

In recognition of such serious threats to fringing reefs, a workshop was conducted in 1989 (Baldwin 1989) to summarise and to identify gaps in then current knowledge on the biology, ecology, and management of the GBR fringing reefs. Since then, a considerable body of scientific information has been gathered on the state of GBR nearshore fringing reefs.

Over the past decade, a number of studies have obtained information on the abundance and biodiversity of ecologically important organism groups on the nearshore fringing reefs of the GBRWHA (e.g. Williams 1982, Ayling 1997, Lee Long & Coles 1997, McCook et al. 1997, Sweatman et al. 1998, De'ath & Fabricius 2000). The reef slopes of nearshore fringing reefs of the Herbert River region have abundant and particularly species-rich hard coral communities (DeVantier 1997, Sweatman et al. 1998, Klumpp et al. in press). However, reef-flats of these reefs have high abundances of non-reefbuilding organisms such as soft corals and macroalgae (Klumpp et al in press, Schaffelke & Klumpp 1997, Fabricius & De'ath 1997), which has been suggested as one of the first indicators for reef degradation (Done 1992, Hughes 1994). To date, we can not identify whether GBR nearshore reefs are already degraded or if they are still in a 'natural' state due to the scarcity of historical survey data. Wachenfeld (1997) compared historical photographs of reef-flats with their present day status and reported that some reefs show signs of degradation. On most nearshore fringing reefs, distinct zones with high algal cover are found very close to the shores and on reef flats (pers. obs., Morrissey 1980, McCook 1997). In general, macroalgae are more common on nearshore reefs than on midshelf and offshore reefs (Done 1982, McCook et al. 1997).

Macroalgae, such as the ubiquitous algal turf (epilithic algal community, EAC) have been recognised as important primary producers on coral reefs (Hatcher & Larkum 1983, Williams & Carpenter 1988, Klumpp & McKinnon 1989, 1992). The microalgal and microheterotrophic production on soft sediments is equally important with a proportion of 20 to 37% of the total primary productivity of coral reefs (Masini 1990, Sorokin 1993). These high figures result from a high primary production of the microbenthos communities (Sournia 1976, Sorokin 1978) and from the large area covered by sediments in the lagoons and on reef flats. On the GBR as a whole, 51% of the areas classified as reefs are in fact shallow sandy lagoons or reef flats with sand patches (Furnas et al. 1995). No data are available on the production of seagrasses in the GBR region, which are abundant in coastal areas and also as components of the enigmatic deep water soft bottom communities of the GBR lagoon (Lee Long & Coles 1997). A comprehensive energy budget has not yet been assembled for nearshore reefs of the GBR region. However, the distinct composition of benthic communities on nearshore reefs, with a prevalence of macroalgae, filter feeders, and certain hard and soft coral species suggests a higher availability of nutrients and suspended sediments in these coastal areas.

Sediment and nutrients load have been estimated for a number of North Queensland rivers, however, data for major flood events are limited (Mitchell & Furnas 1997). This information gap will be closed by a program currently underway using automated river-loggers (M. Furnas, AIMS, pers. comm). A large proportion of the riverine

sediment is assumed to be deposited in low salinity (< 10 ppt) areas in the river mouths and estuaries (Wolanski & Jones 1981, Wasson 1997). The remaining sediment load is transported not far away from river mouth and is deposited in a nearshore sediment wedge (~10 km from the coast). Very little material accumulates over time because most sediment is held in suspension or transported northward by the prevailing south-easterly winds (Woolfe & Larcombe 1998, Larcombe & Woolfe 1999). However, traces of terrigenous carbon have been found in corals up to 110 km from the coast (Risk et al. 1994).

Average nutrient levels in water of the GBR lagoon are often close to the detection limit (Furnas et al. 1995). However, peak levels at nearshore locations are often much higher (Walker and O'Donnell 1981, Brodie et al. 1989) and may reach concentrations as high as 4.10  $\mu\text{M}$  ammonium, 2.95  $\mu\text{M}$  nitrate and 0.90  $\mu\text{M}$  phosphate (Revelante and Gilmartin 1982). The paradigm that coral reefs only flourish in low nutrient conditions (Odum & Odum 1955) may be still valid for the majority of offshore reefs, but probably does not apply for the nearshore reefs of GBR and for coral reefs in higher latitudes (Hatcher & Hatcher 1981, Crossland et al. 1984). The bulk of the existing nutrient data for the GBR were measured in the open water of the lagoon (eg. Furnas et al. 1995, 1997), and very few data exist from waters directly from the reefs or in coral reef lagoons (LIMER Expedition Team 1976, Hatcher & Hatcher 1981, Wilkinson et al. 1984, Ayukai 1993, data compilation in Blake 1994).

Concentrations of organic nutrients in waters of the GBR are much higher than inorganic nutrients (Furnas et al. 1995, 1997). Organic nutrient species may be utilised by microbial periphyton on coral reefs (Sorokin 1990) or by phytoplankton (Flynn & Butler 1986, Antia et al. 1991); which essentially transforms dissolved nutrients into particulate form. Particulate nutrient species and concentration of suspended sediments are significantly higher in waters of the inner shelf (to the 20 m depth band) than further offshore (Furnas et al. 1995, 1997). The suspended organic matter is consumed by zooplankton and filter feeders or deposited in the sediment, both leading to remineralisation of nutrients (Alongi 1989, Capone et al. 1992, DiSalvo 1974, Entsch et al. 1983, Risk & Müller 1983). Sediment nutrients are released into the water column by wind-driven re-suspension, bioturbation, or diffusion (Alongi 1989, LIMER Expedition Team 1976, Walker & O'Donnell 1981), or may be directly used by benthic microalgae (Uthicke 1998), some macroalgae and seagrasses (Williams 1984, Larned & Stimson 1996).

The production of biomass by primary producers such as phytoplankton, benthic micro- and macroalgae, and seagrasses requires dissolved inorganic nutrients. Chlorophyll *a* concentrations in the water column have been used as an integrative parameter to monitor nutrient concentrations in the GBRWHA (Brodie et al. 1997, Steven et al. 1998). Comparing chl *a* data from the present with historic data, Bell (1991, 1992), and Bell & Elemetri (1995) concluded that the inner GBR lagoon is becoming eutrophic. This argument has been abated by Brodie et al.'s (1997) long-term data, which show very high temporal variability that renders conclusions based on snap-shot measurements equivocal. However, the fact that chl *a* concentrations in coastal waters are higher than further offshore (Brodie et al. 1997) indicates that more nutrients are available in this area.

Taking the collective evidence available it is reasonable to assume that human activity in the coastal region has caused or will cause long-term changes of the nutrient stocks and the benthic community composition on nearshore reefs. However, it is very difficult

to detect or to predict future changes without a detailed knowledge of the present status of these reefs. This report will supply relevant information to close gaps in our knowledge on the variability of the water quality at near-shore fringing reefs, and other aspects of the trophic status of inshore benthic communities. Original data on the nutrient status of four reef flats of nearshore fringing reefs will be summarised and analysed in conjunction with other available information on the Herbert River area. The report may be used as a data source and a baseline for future assessments of the status of nearshore reefs.

## MATERIAL AND METHODS

### Description of sampling locations and adjacent catchments

The four locations of the present study were on reef flats of fringing reefs of three nearshore continental islands (Fig. 1). These were Great Palm Island (Little Cannon Bay) and Fantome Island (station 1, Juno Bay; station 2, northern-most bay) of the Palm Island group, and the North Island of the Brook Island group (south-east bay; in the following called Brook Island). These island groups were selected as sampling sites because they are affected by two major river systems in the central GBR area, the Herbert River and the Burdekin River (Fig. 1).

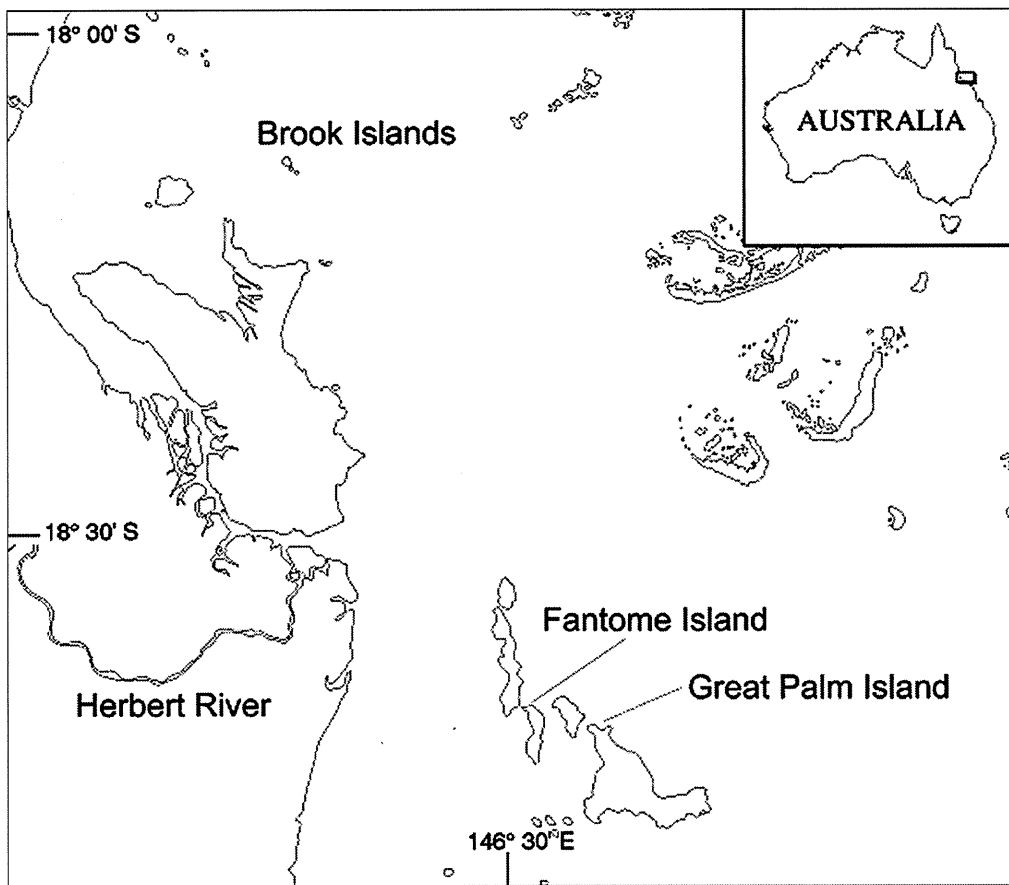


Figure 1. Study locations at nearshore islands in the Herbert River region

The oceanographic processes offshore the mouth of the Herbert river are strongly influenced by the large landmass of Hinchinbrook Island (Fig. 1). The Herbert River drains just south of Hinchinbrook Island, and the wind-driven currents close to the coast (Wolanski 1994) predominantly transport the water northward and push it into the narrow Hinchinbrook Channel. This effectively shifts the outflow of the river further north into Rockingham Bay. Less than 5% of the Herbert River catchment area is used for crop farming (mainly sugarcane), which involves extensive use of agricultural fertilisers (Pulsford 1996). However, the fertiliser use per hectare total catchment area is one of the highest of the Queensland coast, with a total amount of 9800 t nitrogen (N) and 1330 t phosphorus (P) applied in 1990 (Pulsford 1996). About 18% of the catchment is considered as being pristine (National Parks designated as World Heritage Area) and more than 70% is grazing land (Pulsford 1996). The Herbert River has both wet and dry catchment areas, which results in a year-to-year variability in rainfall and associated river discharge of ~70% (Mitchell & Furnas 1997). The chemical composition of the discharge water, especially dissolved and particulate nutrients, varied also during successive stages of a cyclone-mediated flood event (Mitchell et al. 1997).

The Burdekin River is the major river draining into the central GBR region in terms of catchment area and mean annual flow, and discharges about 150 km south of the Palm Island group (Fig. 1). It is the largest source of freshwater, and of associated nutrients and sediments to the central section of the GBRWHA (Neil & Yu 1996). Cyclonic flood plumes from this river are reported to extend as far as Innisfail, north of the Brook Island groups (Wolanski & Jones 1981, Devlin et al. 2001). The Burdekin River drains a dry catchment with a very high inter-year variability in rainfall and subsequent river discharge. Major flood events occur in variable cycles thought to be linked to the El Niño Southern Oscillation and to tropical cyclones (Lough 1994). The catchment area of the Burdekin River is about one order of magnitude larger than the Herbert River catchment area. Most of the catchment area is dry savanna woodland used for extensive rangeland grazing. Consequently, the use of fertiliser is much lower than in the Herbert catchment, with a total amount of 3180 t N and 256 t P applied in 1990 (Pulsford 1996). Because of the large area of the catchment, however, the sea-ward transport of particles and associated nutrients and other contaminants by the Burdekin River run-off may have a major impact downstream.

### **General sampling design**

At each of the four study reef flats, three sampling locations were chosen with similar distance to the shoreline and separated by ~50 m. On all reef flats the benthos in this sampling zone was composed of a mixture of very abundant large brown algae, sediment patches and individual coral colonies (= 'seaweed zone'). The sampling locations were revisited at each field trip with an accuracy of about 5 m with the help of terrestrial and underwater landmarks. The sampling dates of the various parameters are summarised in Table 1.

## **Dissolved inorganic and organic nutrients in the water column and interstitial water**

All nutrient samples were taken at high tide ( $\pm 1$  h) to minimise variation in concentrations due to the tidal cycle (Szmant & Forrester 1996). Samples were taken in triplicate by one snorkeller prior to any other activities at the sampling location to avoid contamination due to the presence of several divers. Water column samples were taken with a 25 ml syringe 50 cm above the sediment.

For pore water samples, a 10 ml syringe was carefully inserted 1 cm into the sediment and only 4 ml of pore water was extracted from the sediment to minimise contamination from the overlying water column. Two such samples were pooled to obtain a volume large enough for inorganic and organic nutrient analyses.

Sediment pore water samples and water column samples were immediately filtered (GF/F filter, 0.45  $\mu\text{m}$ ) and frozen ( $-20^{\circ}\text{C}$ ) until analysis. The samples were analysed for dissolved inorganic nitrogen (ammonium, nitrate, nitrite) and soluble reactive phosphorus using standard automated techniques (Ryle et al. 1981). Samples for total dissolved nitrogen and phosphorus were photo-oxidised in ultra violet light for 8 h to convert organic to inorganic nutrient species, and subsequent analyses were performed as described for the inorganic samples.

Concentrations of dissolved organic nutrients were calculated by subtracting the concentrations of the inorganic nutrients from the respective total values.

## **Water flow rates**

Weight loss of erosive blocks is proportional to the water flow rate (Jokiel & Morrissey 1993) and may thus be used to estimate an average flow rate. Erosive blocks were prepared from dental cement (Fabricius & De'ath 1997). Before deployment in the field, dental cement blocks were dried, pre-weighed and fixed with silicon paste to iron tiles. To obtain information on the range of flow occurring at the sampling station at Great Palm Island, three dental cement blocks were left at each of the three locations in the seaweed zone on the reef flat for about 24 hours. To prevent increased erosion by sweeping of seaweed thalli, the blocks were placed in patches clear of seaweed. Three other blocks were deployed at each of three corresponding stations approximately 50 m further seaward in the zone on the reef flat that is dominated by hard corals (front reef flat = 'coral zone'). These flow measurements were performed at six consecutive days in April 1997 and three days each in July and December 1997. The average flow rate over 24 hour periods ( $\text{cm s}^{-1}$ ) was calculated from the weight loss (DW) of each block after 24 h in the field using the calibration equation from Fabricius and De'ath (1997) with slight modifications to cover the observed range of weight loss (Fabricius pers. comm.). The flow rate measured for each block was calculated as

$$f = 0.51 * w - 1.023$$

with  $f$  = flow rate ( $\text{cm s}^{-1}$ ) and  $w$  = weight loss (g).

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**Table 1.** Sampling dates for the various sampled parameters. Dissolved nutrient: NO<sub>3</sub>, NO<sub>2</sub>, NH<sub>4</sub>, DON, PO<sub>4</sub>, DOP in the water column; sediment pigments: chlorophyll *a*, phaeophytin; sediment nutrients: dissolved nutrients (as before) in the porewater, nitrogen, inorganic and organic carbon.

Trip No.	Date	Dissolved nutrients	Sediment pigments	Sediment nutrients, bacteria	Sediment diatoms	<i>Sargassum</i> tissue N, P	Production microbenthos	Production <i>Sargassum</i>	Water flow rates	Sediment traps
	1995									
1	26-29 Jan					•				
2	02-08 Mar	•	•	•		•		•		
3	01-04 Apr	•	•			•				
4	01-05 May	•	•	•		•		•		
5	04-09 Jun	•	•			•				
6	16-23 Jul	•	•	•		•		•		
7	26-30 Aug	•	•			•		•		
8	03-07 Oct	•	•	•	•	•		•		
9	08-12 Nov		•			•		•		
10	18-23 Dec	•	•	•	•	•				
	1996									
11	01-07 Feb	•	•			•	•			•
12	21-27 Mar	•	•	•	•	•	•			•
13	02-08 May	•	•			•	•			•
14	05-08 Jun	•	•	•	•	•				
15	17-23 Jul	•	•	•	•	•	•			
16	26-30 Aug	•	•	•	•		•			
17	19-24 Dec						•			
	1997									
18	01-06 Feb						•			•
19	17-23 Apr								•	
20	01-05 Jul								•	•
21	17-23 Dec								•	•

### **Particle deposition rates**

Sediment traps were polycarbonate cylinders (diameter: 6.5 cm, height: 15 cm) fitted in triplicate into concrete blocks, which acted as both a holder and an anchor for the traps. The cylinders per block were considered as subsamples, i.e. blocks were replicates. Five blocks were placed in the seaweed zone and five blocks in the coral zone of the reef flat at Great Palm Island. After 24 h, cylinders were closed underwater with screw-top lids, retrieved, and new cylinders fitted. Two 24 h periods were sampled in each February, March, and May 1996 and February 1997. In both July and December 1997, particulate matter (PM) deposition was measured over three 24 h periods in the seaweed zone only. During each deployment period, three trap blocks were placed in the seaweed zone at the same stations as for the water flow measurements (see section 2.3). The samples were pre-filtered (500 µm mesh) and four aliquots per sediment trap jar were immediately filtered onto GF/F filters and stored at -20°C. The filters were dried (48 h, 60°C) to determine dry-weights of the deposited particles and stored at -20°C until further analyses for dry-weights and composition.

### **Sediment sampling**

Sediment samples for analyses of chemical and biological constituents were sampled from the upper 3 to 5 mm of sediment at each location. The samples were carefully scraped from the sediment surface layer with a spoon. For most sediment parameters a sediment volume of > 2 ml was measured in a 10 ml syringe with the tip cut off. The samples were transferred into scintillation vials and these samples were stored at -20°C until analysed. The sediment samples were later dried (48 h, 60°C) and for the chemical analyses ground to a fine powder in an electric grinder. For determination of bacterial- and diatom numbers, a one ml subsample of sediment was placed in 9 ml of 2% formaldehyde and stored at 4°C.

### **Chlorophyll a and phaeophytin in sediments**

For pigment analyses, 1.5 g sediment was extracted in 3 ml ethanol (70%), following the method of Sartory & Grobbelaar (1984). Absorbance of the extracts was measured in a spectrophotometer at 750 and 665 nm, before and after acidification. Chlorophyll *a* and phaeophytin concentrations were calculated applying the formula of Nusch (1980).

### **Bacteria and diatom numbers**

Bacterial numbers in the sediments were determined by direct counting with an epifluorescence microscope (Hobbie et al. 1977). The samples (1 ml sediment in 9 ml 2% formalin) were further diluted in formalin and, in a third step, in a citric acid buffer to a final dilution of 1:5000. Before every dilution step, samples were sonicated in a sonication bath for two minutes to achieve better dispersion of the bacterial cells (Velji and Albright 1986). Samples were stained with a 4'-diamidino-2-phenylindol (DAPI). One to 10 ml of the diluted samples (depending on the concentration of the bacteria) were then filtered onto a 0.2 µm pre-stained Nucleopore filter. For counting, the filter was embedded on a microscopic slide in immersion oil. For each sample, bacteria numbers were counted at 1000 times magnification in at least 20 fields.

Diatom numbers were counted at 400 times magnification on the same filters that were used for the bacteria counts. Each counting field was inspected using two different wavelength filters and diatom cells which contained apparently intact chloroplasts

(autofluorescence visible under excitation at 673 nm) and nuclei (stained with DAPI, excited at 365 nm) were counted and regarded as alive at the time of the sample. The poor state of taxonomy for tropical benthic diatoms did not allow any further taxonomic resolution of the samples within the time scale appropriate for the scope of this study. However, most diatom cells appeared to belong to common pennate genera like *Amphiora* or *Navicula*.

To obtain conversion factors from the volume based bacteria and diatom counts to weight based numbers, 20 sediment samples were cored with a 50 ml syringe (diameter: 1.44 cm) which was open at one end. The samples were frozen and the wet weight and the dry weight (48 h at 60°C) of the upper 5 mm of sediment of the cores was determined. These measurements showed an average water content of the sediment of 30.5% (SD: 2.5) and a density of 1.22 g ml<sup>-1</sup> (SD: 0.22) was calculated. Thus, bacteria and diatom numbers given in the results section may be divided by 1.22 to obtain numbers per g DW of sediment.

### **Sampling of macroalgal tissue**

Samples for the analyses of tissue nutrients were cut from entire *Sargassum baccularia* thalli. The samples were cleaned in seawater, briefly rinsed in freshwater, and immediately frozen. The tissue was then dried for 24 h at 60°C and subsequently ground with mortar and pestle to a fine powder and stored at -20°C until analyses.

### **Composition of deposited particles, sediments, and macroalgal tissue**

Total nitrogen and total carbon were analysed with an ANTEK C/N analyser. Organic carbon (deposited PM and sediments only) was analysed with a Beckman Tocmaster 915B after samples were dissolved in phosphoric acid to remove carbonate (Sandstrom et al. 1986) or with a Shimadzu total organic carbon analyser. Inorganic carbon content of the samples was calculated by subtracting the organic carbon concentration from the total carbon content. For analysis of total P, the samples were combusted for 1 h at 450°C, extracted with purified water for 12 h at 4°C, the extract filtered and determined for total phosphorus according to Koroleff (1983).

### **Microalgal community production**

We measured benthic microalgal community production (according to definition of Larkum 1983) in a four-chamber data logging respirometer described in detail by Klumpp et al. (1987). Four perspex dome chambers were deployed over the benthic community several hours before onset of the measurements to allow for recovery after potential disturbances. These dome chambers enclosed a water volume of 15 L, and covered a sediment area of 0.13 m<sup>2</sup>. The dome chambers were equipped with an oxygen probe, a stirrer, inflow, outflow and water sampling ports. The chamber rims were inserted 3 cm into the sediment and were fixed to the sediment with four 25 cm steel stakes. The Dome chambers were placed on sediment patches without apparent mounds of *Calianassa* spp. The respirometer was programmed to flush the chamber water for 4 minutes every 26 minutes. The flushing interval effectively pumped 15 L of ambient sea-water into each dome chamber. Oxygen concentration within the dome chambers, in situ irradiance and water temperature were recorded simultaneously at one minute intervals. Irradiance (as photosynthetically active irradiance, PAR) was recorded with a Li-Cor 192 SB underwater quantum sensor. All deployments lasted for at least 24 h. Trials with a control dome which was closed at the bottom and thus

contained only ambient sea water yielded no measurable production or respiration (see also Johnstone et al. 1990) of the plankton in the water column. Thus, this control was later omitted to achieve higher replication. On some days, equipment failure or physical disturbance of a dome chamber by swell or burrowing shrimps resulted in the reduction of the replicate number. Additionally, we could not measure over the same number of days on each field trip due to weather and time constraints.

Oxygen production or respiration rates of the benthic community were calculated from linear regressions of oxygen values recorded every minute during each 26 minute incubation period. Irradiance and temperature values were averaged over the same period. Carbon fixation was calculated from the oxygen production data assuming  $PQ = RQ = 1$ ; thus, 1 mg oxygen produced or respired is equivalent to 0.375 mg organic carbon. Areal net-production of the benthic community in each chamber was calculated by subtracting the total dark respiration from the total production over 24 hour periods; gross-production was obtained by adding dark respiration data to the daily production. Daily production data are thus directly measured over a 24 h period and not extrapolated from short term observations. Photosynthetic capacity ( $P_{max}$ ) was calculated from hyperbolic tangent functions (Chalker 1981).

### Macroalgal production

Productivity measurements were carried out at Great Palm Island in October 1995, February 1996, May 1996, July 1996 and August 1996. Young shoots with a length of 4 to 8 cm were cut from entire *Sargassum baccularia* thalli. These shoots were kept in flowing seawater in shipboard tanks for 24 h to recover from the cutting trauma which may enhance respiration rates (Drew 1983a). The shoots were then fixed to concrete blocks and placed for at least 24 h in the *Sargassum* zone. After this recovery time, single shoots were placed in the data logging respirometer (see above, here equipped with four 2.4 l-box chambers) deployed at the site of collection. Photosynthesis and respiration rates were measured continuously (every minute) for 24 h periods. The respirometer used allowed replicate measurements of four plants. On all sampling occasions, two 24 h runs were conducted, each with different shoots, giving a total number of eight replicate measurements. In some months, faulty oxygen probes resulted in reduced numbers of replicates. On these occasions, a third respirometry run was conducted and replicates were randomly selected to replace those where equipment failure had occurred in the original runs. Water in incubation chambers was automatically exchanged after each 15 minutes incubation period. Calculations were as for microbenthic production (see above). To improve similarity of light conditions, we chose only days with clear skies for productivity measurements. Areal productivity rates for Great Palm Island *Sargassum baccularia* stands were calculated using the averages of daily biomass-specific net production and the respective *S. baccularia* biomass data (Schaffelke & Klumpp 1997) for each sampling occasion.

### Statistical analyses

Water column and interstitial water nutrient concentration, and the sediment quality parameters were averaged for each of the locations at each field trip and data for each variable were analysed with a four-factor ANOVA. Factors in this model were *Reef*, with the factor *Location* nested within *Reef* as the error term. Variation between sampling months was investigated with the factor *Trip*. Since inspection of the raw data hinted to some seasonal variation for several parameters, it was decided *a posteriori* to partition variation between field trips into two *seasons* (factor season) and the remaining

variation between sampling dates (*Trip* nested in *Season*), the latter being the error term for the former. Although it is more common to include May into the winter season, and November into summer at the southern hemisphere, it was decided to group the months as follows since water temperatures during the sampling period were higher in May than in November. Thus, seasons were defined as the 'summer' lasting from December to May, and the 'winter' from June to November. The interaction term between *Reef* and *Trip* nested in *Season* was used as the error term for *Location* nested in *Reef*, *Trip* nested in *Season*, and the interaction of *Reef* \* *Season*.

Since samples for the count of diatom numbers were only collected on a subset of sampling trips, differences between the means were tested with a similar model, but without the additional factor *Season*.

The differences in water flow rates were investigated by a three-factor ANOVA, with Zone (reef flat or Sargassum zone) and Days as fixed factors. The three sampling Locations were nested in Zone. Thus, Locations within Zone was used as error term for Zone, and the interaction of Days \* Location nested in Zone as error term for the remaining factors.

The spatial differences in particle deposition rates at Great Palm Island were analysed with a three-factor mixed model ANOVA. Factors in this model were *Zone* and *Month*. Variation between sampling days was investigated with the factor *Day* nested in *Zone* and *Month*. The mean square of this factor were used as the error term for the main factors and for their interaction. The residual was used as the error term for the factor *Day* nested in *Zone* and *Month*. The relationships between water flow rates and particle deposition in the *Sargassum* zone at two sampling occasions were described by Pearson product-moment correlations.

The variation between sampling months in the nutrients in *Sargassum baccularia* tissue were analysed with a three-factor mixed model ANOVA. Factors in this model were *Reef* and *Season*. Variation between sampling months was investigated with the factor *Trip* nested in *Reef* and *Season*. The mean square of this factor were used as the error term for the main factors and for their interaction. The residual was used as the error term for the factor *Trip* nested in *Reef* and *Season*.

One factor ANOVAs for each calculated production parameter were used to compare means between the experimental months.

Water temperature data obtained during the production measurements are presented as averages for each day. Underwater light was integrated to total daily light sums and presented in Einstein m<sup>-2</sup> d<sup>-1</sup> (1E = 1 mol photons).

The Tukey HSD test was used for all parameters as a post hoc comparison of means.

All data were tested for homogeneity of variance using Cochran's Q test and appropriately transformed as indicated in the results section.

## RESULTS

### Water column nutrients

#### *Dissolved inorganic nutrients*

The ammonium ( $\text{NH}_4$ ) concentrations in ~ 40% of all samples were below the detection limit ( $0.1 \mu\text{M}$ ). Although levels were fluctuating (Fig. 2a) and a large amount of the variation can be attributed to variation between the sampling dates (factor *Trip*), the ANOVA indicated that the mean values of the ammonium concentrations were different between the reefs (Table 2). The post hoc comparison showed that the mean value at Fantome Island 1 ( $0.30 \mu\text{M}$ , SE= 0.06) was higher than the means at Brook and Great Palm Islands ( $0.22 \mu\text{M}$ , SE= 0.03 and  $0.19 \mu\text{M}$ , SE= 0.03). However, this difference was only marginally significant (Tukey HSD,  $p < 0.1$ ). No significant differences in  $\text{NH}_4$  concentrations were detected between the two seasons; however, winter means were consistently higher than summer mean  $\text{NH}_4$  concentrations (Table 4).

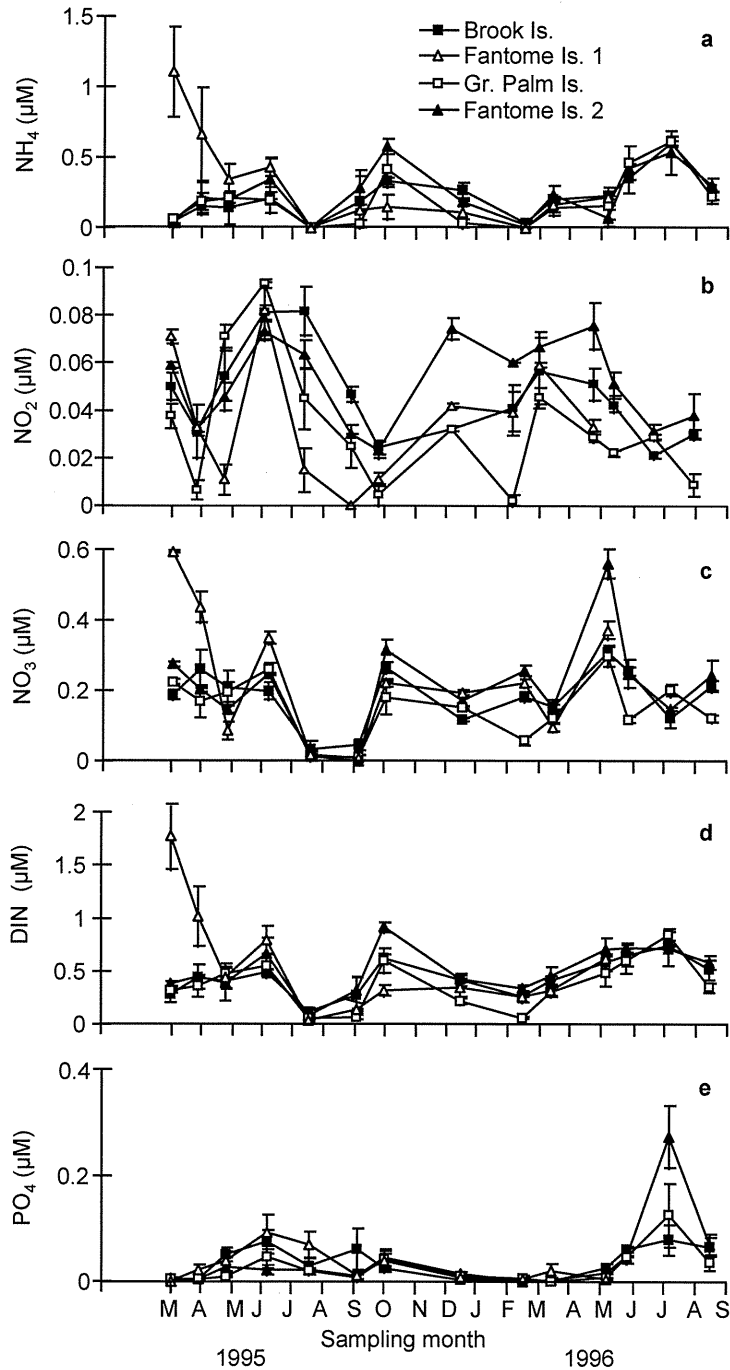
The nitrite ( $\text{NO}_2$ ) concentrations in most samples were above the detection limit (~ 85% of all samples  $> 0.02 \mu\text{M}$ ). Although concentrations peaked in the first winter (Fig. 2b), seasonal differences were not statistically significant (Table 2). The mean values of  $\text{NO}_2$  concentrations were significantly different between the reefs. The post hoc comparison of means showed that the mean values at Brook Island ( $0.046 \mu\text{M}$ , SE= 0.003) and Fantome Island 2 ( $0.052 \mu\text{M}$ , SE= 0.003) were significantly ( $p < 0.05$ ) higher than at Great Palm Island ( $0.032 \mu\text{M}$ , SE= 0.004) and at Fantome Island 1 ( $0.036 \mu\text{M}$ , SE= 0.004).

More than 90% of the samples had nitrate ( $\text{NO}_3$ ) concentrations that were well above the detection limit ( $0.05 \mu\text{M}$ ). Concentrations below the detection limit were found particularly in samples from July and August 1995. Apart from high values in March and April 1995 at Fantome Island 1, the  $\text{NO}_3$  concentrations were relatively constant over the sampling period (Fig. 2c). The ANOVA revealed highly significant differences between sample dates, but not between seasons (Table 2). Differences between the reefs were also highly significant (Table 2) and a post hoc comparison of the means revealed that the mean values at Fantome Island 1 and 2 ( $0.24 \mu\text{M}$ , SE= 0.03 and  $0.21 \mu\text{M}$ , SE= 0.02) and at Brook Island ( $0.18 \mu\text{M}$ , SE= 0.01) were significantly higher ( $p < 0.05$ ) than at Great Palm Island ( $0.15 \mu\text{M}$ , SE= 0.01).

In addition to the analyses of the three single inorganic nitrogen species, their sum was also analysed to investigate trends in total dissolved inorganic nitrogen (DIN). The variation observed in DIN (Fig. 2d) was closely related to the fluctuations detected in the  $\text{NH}_4$  concentrations, which was the major inorganic nitrogen species during most months. The ANOVA indicated significant differences between the reefs (Table 2). A post hoc comparison of the means showed, that mean DIN values at Fantome Island 1 and 2 ( $0.57 \mu\text{M}$ , SE= 0.08 and  $0.51 \mu\text{M}$ , SE= 0.04) were significantly higher ( $p < 0.05$ ) than at Great Palm Island ( $0.38 \mu\text{M}$ , SE= 0.04).

The concentrations of inorganic phosphate in the water were generally low and ~ 50% of all samples were below the detection limit ( $0.02 \mu\text{M}$ ). Phosphate concentrations appeared to peak in the winter (Fig. 2e). Statistical analyses (Table 2, factor *Season*) confirmed, that winter mean values ( $0.058 \mu\text{M}$ , SE= 0.007) were significantly higher than summer mean concentrations ( $0.01 \mu\text{M}$ , SE= 0.002). Also, there were significant differences in phosphate concentrations between the reefs (Table 2). The post hoc

comparison of means showed that mean phosphate values were higher at Fantome Island 2 (0.04  $\mu\text{M}$ , SE= 0.01) than at Great Palm Island (0.026  $\mu\text{M}$ , SE= 0.006).



**Figure 2.** Concentrations (mean values  $\pm$  SE) of ammonium (a), nitrite (b), nitrate (c), dissolved inorganic nitrogen, DIN (d), and phosphate (e) in the water column at four nearshore reefs in the central section of the GBR.

**Table 2.** ANOVA for phosphate (PO<sub>4</sub>), ammonium (NH<sub>4</sub>), nitrite (NO<sub>2</sub>), nitrate (NO<sub>3</sub>) and total dissolved inorganic nitrogen (DIN) in the water column at four nearshore reefs in the central section of the GBR. Data were log transformed, df: degrees of freedom, MS: mean squares, F: value of F statistics, p: significance levels: ns: not significant, \*: p < 0.1, \*\*: p < 0.05, \*\*\*: p < 0.01.

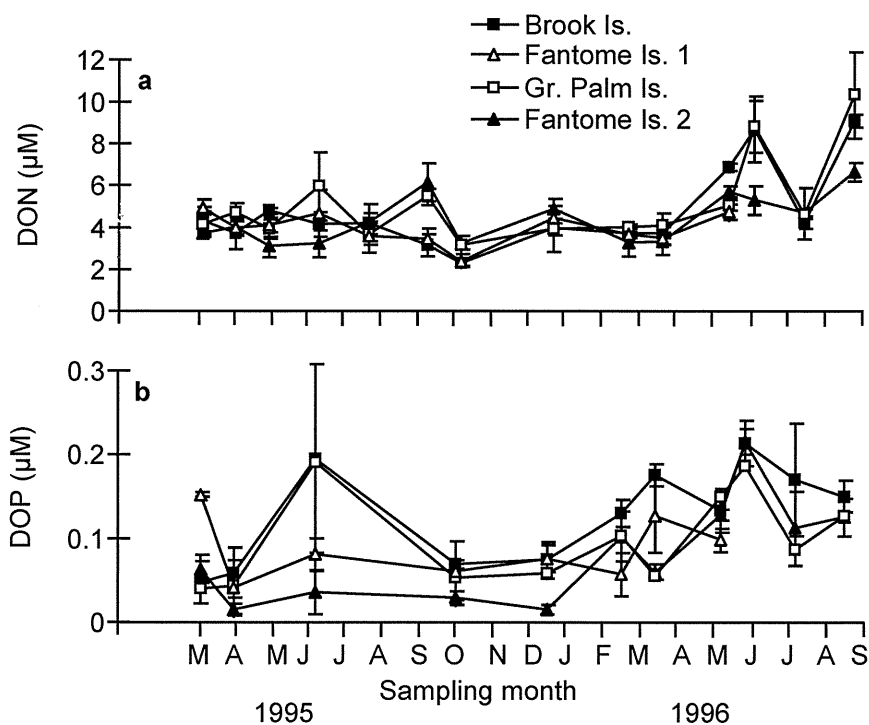
Source of variation	Df	NH <sub>4</sub>			NO <sub>2</sub>			NO <sub>3</sub>			DIN			PO <sub>4</sub>		
		MS (x 10 <sup>-4</sup> )	F	p	MS (x 10 <sup>-5</sup> )	F	p	MS (x 10 <sup>-4</sup> )	F	p	MS (x 10 <sup>-4</sup> )	F	p	MS (x 10 <sup>-5</sup> )	F	p
Reef	3	80	3.42	*	100	23.83	***	50	18.8	***	170	8.45	***	47.0	5.03	**
Location(R)	8	20	0.30	ns	2.9	0.24	ns	2.6	0.12	ns	20	0.23	ns	9.3	0.25	ns
Season	1	470	1.78	ns	44.4	0.66	ns	240	1.58	ns	10	0.02	ns	1800	10.40	***
Trip(S)	12	270	3.65	***	100	5.72	***	150	7.21	***	470	5.41	***	200	4.59	***
R x S	3	130	1.80	ns	20.7	1.76	ns	10	0.43	ns	140	1.59	ns	32.3	0.88	ns
R x T(S)	33	70	2.88	***	11.7	6.66	***	20	12.11	***	90	4.52	***	36.8	2.9	***
Residual	98	30	-	-	1.8	-	-	1.8	-	-	20	-	-	12.9	-	-



### Dissolved organic nutrients

No differences in dissolved organic nitrogen (DON) concentrations were detected between the seasons, but the variation between the field trips was significant (factor *Trip*, Table 3). The concentrations of DON were relatively constant over the sampling period. The occasional high values during several winter months (Fig. 3a) are a likely cause for the significant factor *Trip* (Table 3). Inter-reef differences in DON concentrations were also significant (factor *Reef*, Table 3). The post hoc comparison of the means revealed that the DON concentrations were significantly higher ( $p < 0.05$ ) on Great Palm and Brook Islands ( $5.16 \mu\text{M}$ ,  $\text{SE} = 0.36$  and  $4.79 \mu\text{M}$ ,  $\text{SE} = 0.34$ ) than at Fantome Island 1 ( $4.06 \mu\text{M}$ ,  $\text{SE} = 0.21$ ).

Similar to inorganic phosphate, dissolved organic phosphorus (DOP) was higher at some sampling occasions during winter (Fig. 3b); this was probably the reason for the significant differences between trips (factor *Trip*, Table 3). However, seasonal differences were not statistically significant (Table 3). The ANOVA detected significant differences in DOP concentrations between reefs. The mean concentration of DOP at Brook Island ( $0.13 \mu\text{M}$ ,  $\text{SE} = 0.02$ ) was significantly higher (Tukey HSD,  $p < 0.05$ ) than at Fantome Island 1 and 2 ( $0.085 \mu\text{M}$ ,  $\text{SE} = 0.011$  and  $0.082 \mu\text{M}$ ,  $\text{SE} = 0.011$ ).



**Figure 3.** Concentrations (mean values  $\pm$  SE) of dissolved organic nitrogen (a: DON) and dissolved organic phosphorus (b: DOP) in the water column at four nearshore reefs in the central section of the GBR.

**Table 3.** ANOVA for concentrations of dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) in the water column at four nearshore reefs. Data were log-transformed. Field Trips four, six and seven were omitted from analyses for DOP concentrations due to technical problems with the phosphate analyses. For significance levels and abbreviations: see Table 2.

Source of variation	DON				DOP			
	df	MS ( $\times 10^{-2}$ )	F	p	df	MS ( $\times 10^{-3}$ )	F	p
Reef	3	2.1	10.05	***	3	2.0	5.06	**
Location(R)	8	0.02	0.18	ns	8	0.38	0.56	Ns
Season	1	7.8	0.78	ns	1	6.0	2.00	Ns
Trip(S)	12	9.6	8.65	***	9	3.0	4.18	***
R $\times$ S	3	1.0	0.83	ns	3	0.3	0.49	Ns
R $\times$ T(S)	33	1.2	1.45	*	24	1.0	1.52	*
Residual	98	0.8	-	-	74	0.4	-	-

Table 4 summarises the overall means of the water column nutrient concentrations for the different reefs and for the two seasons, summer and winter. It is interesting to note that all dissolved inorganic nutrient species were lowest at Great Palm Island, whereas especially the two Fantome Island sites but also Brook Island showed higher values. This situation is reversed in case of the organic nutrient species, where Great Palm Island and Brook Island have the highest concentrations.

**Table 4.** Summary of phosphate ( $\text{PO}_4$ ), ammonium ( $\text{NH}_4$ ), nitrite ( $\text{NO}_2$ ), nitrate ( $\text{NO}_3$ ) and total dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) concentrations in the water column at four nearshore reefs. Data are mean values (in  $\mu\text{M}$ ) pooled over seasons for the factor *Island* and over reefs for factor *Season*, with standard errors given in parentheses.

	Island				Season	
	Brook Is.	Fantome Is.1	Gr. Palm Is.	Fantome Is.2	Summer	Winter
$\text{NH}_4$	0.215 (0.028)	0.301 (0.067)	0.194 (0.031)	0.245 (0.031)	0.193 (0.029)	0.282 (0.026)
$\text{NO}_2$	0.046 (0.003)	0.036 (0.005)	0.032 (0.004)	0.052 (0.003)	0.044 (0.002)	0.039 (0.003)
$\text{NO}_3$	0.182 (0.013)	0.236 (0.032)	0.151 (0.013)	0.213 (0.020)	0.229 (0.014)	0.154 (0.013)
DIN	0.444 (0.031)	0.573 (0.094)	0.378 (0.037)	0.510 (0.037)	0.467 (0.038)	0.475 (0.035)
DON	4.792 (0.326)	4.055 (0.214)	5.156 (0.346)	4.411 (0.216)	4.243 (0.111)	5.073 (0.291)
$\text{PO}_4$	0.034 (0.005)	0.032 (0.007)	0.026 (0.006)	0.040 (0.011)	0.010 (0.002)	0.058 (0.007)
DOP	0.129 (0.015)	0.085 (0.011)	0.099 (0.012)	0.082 (0.011)	0.084 (0.006)	0.123 (0.012)

## The water column-sediment interface

### *Nutrients in the interstitial water*

The concentrations of most macro-nutrient species in the interstitial water of sediments at the three nearshore reefs were at least an order of magnitude higher than the respective concentrations in the water column (Table 5). The exceptions were DON concentrations, which are only approximately twice as high as in the water column; and DOP concentrations, which are four to six times higher in the interstitial water.

**Table 5.** Summary of nutrient concentrations (for abbreviations see Table 2) in the sediment pore water at three nearshore reefs. Data are mean values (in  $\mu\text{M}$ ) pooled over seasons for the factor *Island* and over reefs for factor *Season*, with standard errors in parentheses.

	Island			Season	
	Brook Is.	Fantome Is.	Gr. Palm Is.	Summer	Winter
PO <sub>4</sub>	0.77 (0.10)	0.56 (0.06)	0.85 (0.07)	0.71 (0.06)	0.75 (0.07)
NH <sub>4</sub>	2.02 (0.29)	2.52 (0.33)	3.98 (0.43)	2.90 (0.25)	2.79 (0.35)
NO <sub>2</sub>	0.11 (0.01)	0.11 (0.06)	0.08 (0.01)	0.12 (0.08)	0.08 (0.01)
NO <sub>3</sub>	0.85 (0.12)	0.69 (0.08)	0.59 (0.10)	0.70 (0.08)	0.72 (0.08)
total DIN	2.98 (0.33)	3.32 (0.33)	4.65 (2.24)	3.72 (0.26)	3.60 (0.35)
DON	8.87 (0.49)	9.66 (0.71)	8.72 (0.52)	9.17 (0.54)	9.01 (2.88)
PO <sub>4</sub>	0.77 (0.10)	0.56 (0.06)	0.85 (0.07)	0.71 (0.06)	0.75 (0.07)
DOP	0.45 (0.04)	0.45 (0.05)	0.45 (0.04)	0.50 (0.04)	0.41 (0.03)

Only very few nutrient concentrations in the interstitial water were found to be significantly different between the seasons or the three reefs (Table 6). The highest NH<sub>4</sub> concentrations were observed in the pore water of Great Palm Island. However, due to a marginally significant interaction term between *Reef* and *Season* these results should be interpreted with care.

The NO<sub>2</sub>, NO<sub>3</sub>, and PO<sub>4</sub> concentrations measured in the pore water showed no differences between *Reef*, *Location* or *Season*, only some variation between the sampling trips (Table 6).

**Table 6.** ANOVA for phosphate (PO<sub>4</sub>), ammonium (NH<sub>4</sub>), nitrite (NO<sub>2</sub>), nitrate (NO<sub>3</sub>) and total dissolved inorganic nitrogen (DIN) in the sediment pore water at three nearshore reefs. Data were log transformed. Significance levels and abbreviations: see Table 2.

Source of variation	df	NH <sub>4</sub>			NO <sub>2</sub>			NO <sub>3</sub>			DIN			PO <sub>4</sub>		
		MS (x 10 <sup>-4</sup> )	F	p	MS (x 10 <sup>-5</sup> )	F	p	MS (x 10 <sup>-4</sup> )	F	p	MS (x 10 <sup>-4</sup> )	F	p	MS (x 10 <sup>-4</sup> )	F	p
Reef	2	3142.1	5.44	**	67.1	1.81	ns	266.5	2.54	ns	1615.7	6.37	**	342.0	2.91	ns
Location(R)	6	578.1	1.72	ns	24.9	0.46	ns	104.8	0.63	ns	253.8	1.12	ns	117.7	1.94	ns
Season	1	606.2	0.34	ns	438.3	2.91	ns	0.2	<0.00	ns	318.1	0.20	ns	6.0	0.02	ns
Trip(S)	7	1779.1	5.23	***	150.5	2.77	**	572.1	3.46	**	1618.7	7.16	***	249.0	4.11	**
R x S	2	1075.6	3.20	*	18.6	0.34	ns	232.4	1.41	ns	508.8	2.25	ns	125.2	2.07	ns
R x T(S)	14	335.7	1.27	ns	54.4	1.14	ns	165.3	2.02	**	226.0	1.31	ns	60.5	1.01	ns
Residual	48	263.4	-	-	47.9	-	-	82.0	-	-	171.6	-	-	59.8	-	-

The total dissolved inorganic nutrient (DIN) concentrations in the interstitial water were different between the reefs sampled (Table 6). The mean value at Great Palm Island was significantly higher than on Brook Island (Tukey HSD,  $p < 0.05$ ) but the difference to the mean concentration at Fantome Island was not significant (Tukey HSD,  $p > 0.1$ ).

Organic nutrient concentrations (DON and DOP) in the pore water were not different between the reefs and the seasons, and only DON concentrations showed variation between the sampling dates (Table 7).

**Table 7.** ANOVA for dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) concentrations in the sediment pore water at three nearshore reefs. Data were log-transformed. Field trips no. four, six and seven were omitted from the analyses of DOP concentrations due to technical problems with the phosphate analyses. For significance levels and abbreviations: see Table 2.

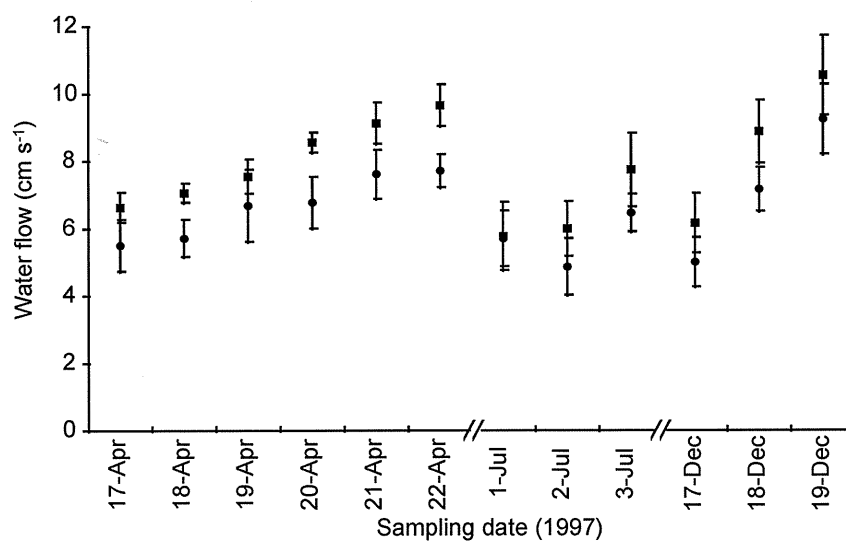
Source of variation	DON				DOP			
	df	MS ( $\times 10^{-4}$ )	F	p	df	MS ( $\times 10^{-4}$ )	F	p
Reef	2	85.7	1.02	ns	2	1.4	0.05	ns
Location(R)	6	83.7	0.51	ns	6	31.2	0.76	ns
Season	1	3.9	0.01	ns	1	116.3	3.38	ns
Trip(S)	7	698.7	4.25	**	5	34.4	0.84	ns
R x S	2	253.7	1.54	ns	2	47.9	1.17	ns
R x T(S)	14	164.6	1.74	ns	10	40.9	1.48	ns
Residual	48	94.7	-	-	36	27.7	-	-

### **Water flow rates**

The average values of the water flow rates for each sampling day are shown in Fig. 4. ANOVA indicated significant variation between the sampling days (Factor *Day*, Table 8). Highly significant differences also existed between the two zones measured (Table 8). The flow rates were consistently higher on the coral zone of the reef flat (mean:  $7.80 \text{ cm s}^{-1}$ , SE=  $0.16$ , range:  $5.77 - 10.53 \text{ cm s}^{-1}$ ) than in the seaweed zone (mean=  $5.53 \text{ cm s}^{-1}$ , SE=  $0.14$ , range:  $4.86 - 9.24 \text{ cm s}^{-1}$ ). No correlations were found between any tidal parameters (tidal range, maximum tide height and minimum tide height, data not shown) and the water flow. Water flow values appeared to be dependent on wind speed and wind direction. During the April 1997 field trip, the south-east winds increased steadily from about 10 kn on the first day to 25-30 kn on the sixth day. This increase was reflected in the increasing water flow rates, although the sampling location is partially protected from S-E winds. Wind speeds in December 1997 were only between 10 and 15 kn, but the wind direction was north to north-east. Cannon Bay is not protected in this wind direction, and thus relatively low wind speeds resulted in the highest observed water flow rates at the last day measured in December.

**Table 8.** ANOVA for water flow rates at Great Palm Island. Data were log-transformed. For significance levels and abbreviations: see Table 2.

Source of variation	df	MS ( $\times 10^{-4}$ )	F	p
Zone	1	0.2447	13.75	**
Location (Z)	4	0.0178	5.24	***
Day	11	0.0983	28.91	***
Z x D	11	0.0026	0.76	ns
D x L (Z)	44	0.0034	3.52	***
Residual	144	0.0009	-	-

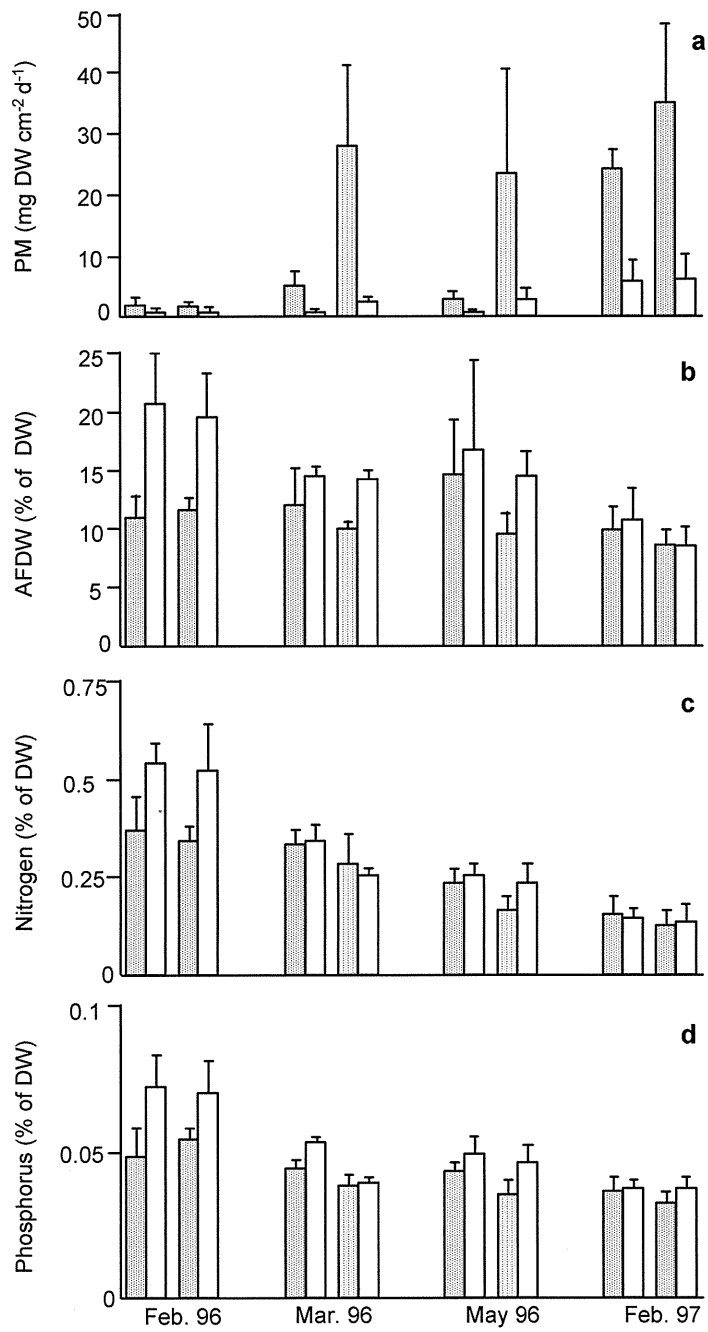


**Figure 4.** Water flow rates (mean values  $\pm$  SE) at Great Palm Island measured with erosive blocks at several occasions during three field trips in 1997. Black circles represent samples from the seaweed zone, black squares samples from the hard coral zone.

### **Particle deposition rates**

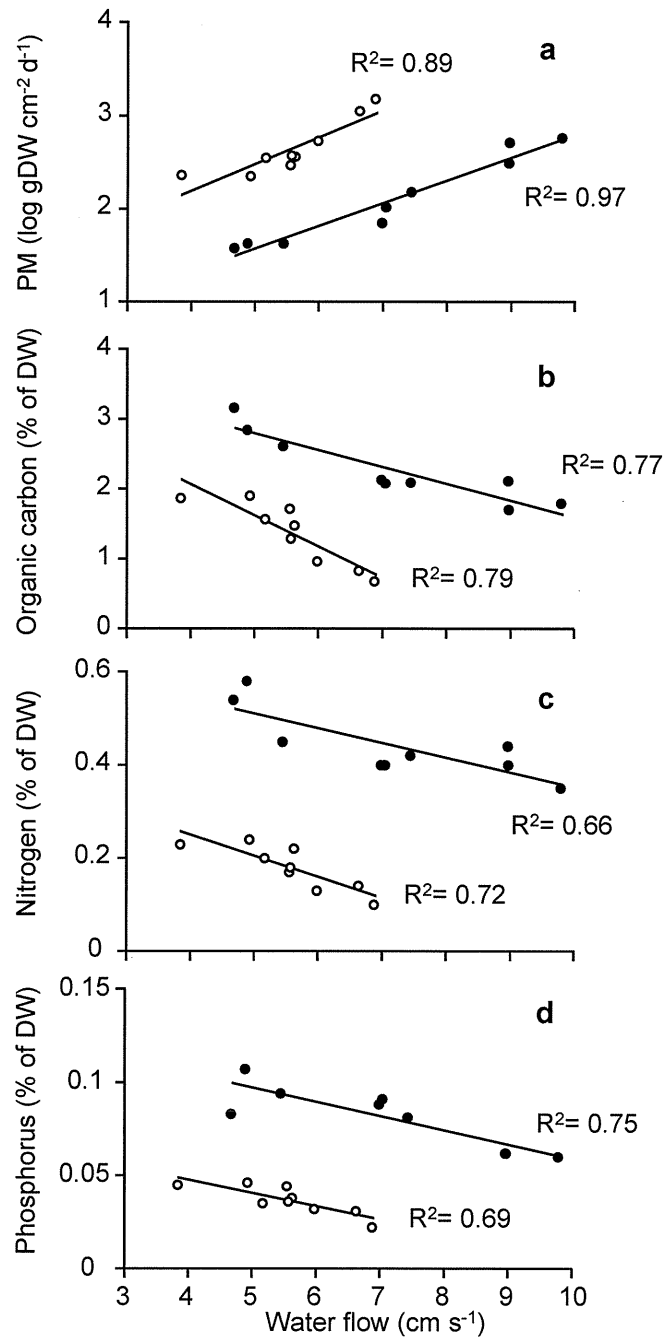
The amount of particulate matter (PM) collected in sediment traps in the seaweed or in the coral zone on the reef flat at Great Palm Island varied considerably between the zones as well as between sampling occasions (Fig. 5). The mean amount of PM collected in the seaweed zone ( $519.3 \text{ mg DW trap}^{-1} \text{ d}^{-1}$ ,  $\text{SE} = 80.8$ ) was more than five times higher (factor *Zone*, Table 9) than that collected simultaneously in the coral zone ( $90.1 \text{ mg trap}^{-1} \text{ DW d}^{-1}$ ,  $\text{SE} = 14.3$ ). These values are equivalent to areal deposition rates of  $15.6 \text{ mg DW cm}^{-2} \text{ d}^{-1}$  in the seaweed zone and  $2.7 \text{ mg DW cm}^{-2} \text{ d}^{-1}$  in the coral zone. Temporal differences between the sampling months were also significant (factor *Month*, Table 9). The post hoc comparison of means showed that the samples from February 1997 were significantly higher than those from February 1996. The mean organic content of the PM, measured as AFDW, and the N and P contents were significantly higher in the coral zone than in the seaweed zone (Fig. 5, Table 9). The significant differences in the factor *Month* (Table 9) were qualified by the post hoc test that showed significantly higher AFDW contents in February and May 1996 than in February 1997. The nitrogen levels in the collected PM were significantly different between all sampling months (Table 9), with highest values in February 1996 and lowest in February 1997 (Tukey HSD,  $p < 0.05$ ). The P content in the PM was significantly higher in February 1996 than in the samples from the other months (Tukey HSD,  $p < 0.05$ ). The mean nitrogen content over all sampling times was  $0.31$  ( $\text{SE}: 0.02$ ) % DW in the coral zone and  $0.26$  ( $\text{SE} = 0.01$ ) % DW in the seaweed zone. The respective overall means for the phosphorus contents were  $0.052$  ( $\text{SE} = 0.002$ ) % DW and  $0.042$  ( $\text{SE} = 0.001$ ) % DW. The average C:N:P ratio of the deposited PM (76:12:1) was somewhat lower than the Redfield ratio.

In July and December 1997, PM was collected in sediment traps in the seaweed zone of Great Palm Island and simultaneous water flow measurements were carried out (see section 3.2.2). The large differences between the sampling days in the PM parameters collected were best explained by the different water flow conditions. Correlation analyses showed a significant positive linear relationship between water flow rates and the amount of PM collected in sediment traps (Fig. 6) at the three sampling stations in the seaweed zone. The nutrient content of the collected PM ( $C_{\text{org}}$ , N, and P) had a significant negative linear relationship with water flow (Fig. 6). Due to the overall higher amount of particle deposition on days with a high water flow, however, the overall nutrient deposition was higher on such days despite the lower relative nutrient content.



**Figure 5.** Total amount and composition of particulate matter (PM) collected in sediment traps in the seaweed zone (grey bars) and in the hard coral zone (white bars) at Great Palm Island. Data are means  $\pm$  SE.





**Figure 6.** Correlations of water flow rates and (a) total amount of particulate matter (PM), (b) organic carbon-, (c) nitrogen-, and (d) phosphorus content of PM collected in sediment traps in the seaweed zone at Great Palm Island. White symbols represent samples from July 1997, black symbols samples from December 1997.  $R^2$ : Pearson product moment correlation coefficients.

**Table 9.** ANOVA for total amount and composition of particulate matter (PM) collected in sediment traps in two zones on the reef flat of Great Palm Island. Data for Total PM were log-transformed, other data were arcsine-transformed. Significance levels and abbreviations: see Table 2.

Source of variation	df	Total PM			Ash-free DW			Nitrogen			Phosphorus		
		MS	F	p	MS (x 10 <sup>-2</sup> )	F	p	MS (x 10 <sup>-2</sup> )	F	p	MS (x 10 <sup>-3</sup> )	F	p
Zone	1	8.92	17.25	***	3.37	24.02	***	6.53	10.00	**	1.8	18.30	***
Month	3	3.14	6.07	**	1.43	10.22	***	38.31	58.66	***	2.4	23.86	***
Z x M	3	0.27	0.51	ns	0.64	4.57	**	4.76	7.28	**	0.3	2.69	ns
Day (Z x M)	8	0.52	15.38	***	0.14	1.64	ns	0.65	2.36	**	0.1	3.66	***
Residual	64	0.034			0.09			0.28			0.027		

## Parameters integrating nutrient availability

### Sediment quality

#### Nitrogen, organic and inorganic carbon concentrations

The concentrations of nitrogen in the sediments of the three nearshore reefs showed a tendency toward higher values during the summer months (Fig. 7a). This, however, was not statistically significant (factor *Season*, Table 10). The values between reefs were significantly different (Table 10). The post hoc comparison of means showed that the nitrogen concentrations at Brook Island (0.025% DW, SE= 0.001) and at Fantome Island 2 (0.023% DW, SE= 0.0006) were significantly higher ( $p < 0.05$ ) than the mean concentration measured at Great Palm Island (0.017% DW, SE= 0.0006).

The concentrations of organic carbon in the sediments also showed a small trend towards higher values during the summer months (Fig. 7b). The ANOVA (Table 10) confirmed that the mean values in summer (0.22% DW, SE: 0.008) were significantly higher ( $p < 0.1$ ) than the winter means (0.19% DW, SE= 0.005). The differences in organic carbon concentration were also significant between the reefs sampled (Table 10). The mean values at Brook Island (0.23% DW, SE= 0.005) and at Fantome Island (0.20% DW, SE= 0.005) were significantly higher than at Great Palm Island (0.17% DW, SE= 0.009).

The concentrations of inorganic carbon showed little variation over the course of the study and the values at Great Palm Island reef flat were on a lower level compared to the other islands (Fig. 7b). Highly significant differences between the reefs were indicated by ANOVA (Table 10) and post hoc comparison confirmed that the values at Fantome Island (9.84% DW, SE= 0.18, equivalent 82% CaCO<sub>3</sub>) and Brook Island (9.58% DW, SE= 0.28, equivalent 80% CaCO<sub>3</sub>) were significantly higher than at Great Palm Island (6.66% DW, SE= 0.24, equivalent to 56% CaCO<sub>3</sub>).

**Table 10.** ANOVA for organic carbon, nitrogen and inorganic carbon concentrations in sediments at three nearshore reefs. Data were log transformed. For significance levels and abbreviations see Table 2.

Source of variation	df	Organic carbon			Nitrogen			Inorganic carbon		
		MS (x 10 <sup>-7</sup> )	F	p	MS (x 10 <sup>-7</sup> )	F	p	MS (x 10 <sup>-4</sup> )	F	p
Reef	2	275.1	18.97	**	461.8	13.91	**	2757.8	39.28	***
Location(R)	6	14.5	0.89	ns	33.2	1.81	ns	70.2	0.92	ns
Season	1	199.5	4.41	*	115.1	1.64	ns	36.2	0.29	ns
Trip(S)	7	45.2	2.76	*	70.4	3.85	**	123.5	1.62	ns
R x S	2	21.0	1.28	ns	4.5	0.25	ns	107.8	1.42	ns
R x T(S)	14	16.4	4.00	***	18.32	1.60	ns	76.1	2.48	**
Residual	48	4.1	-	-	11.6	-	-	30.6	-	-

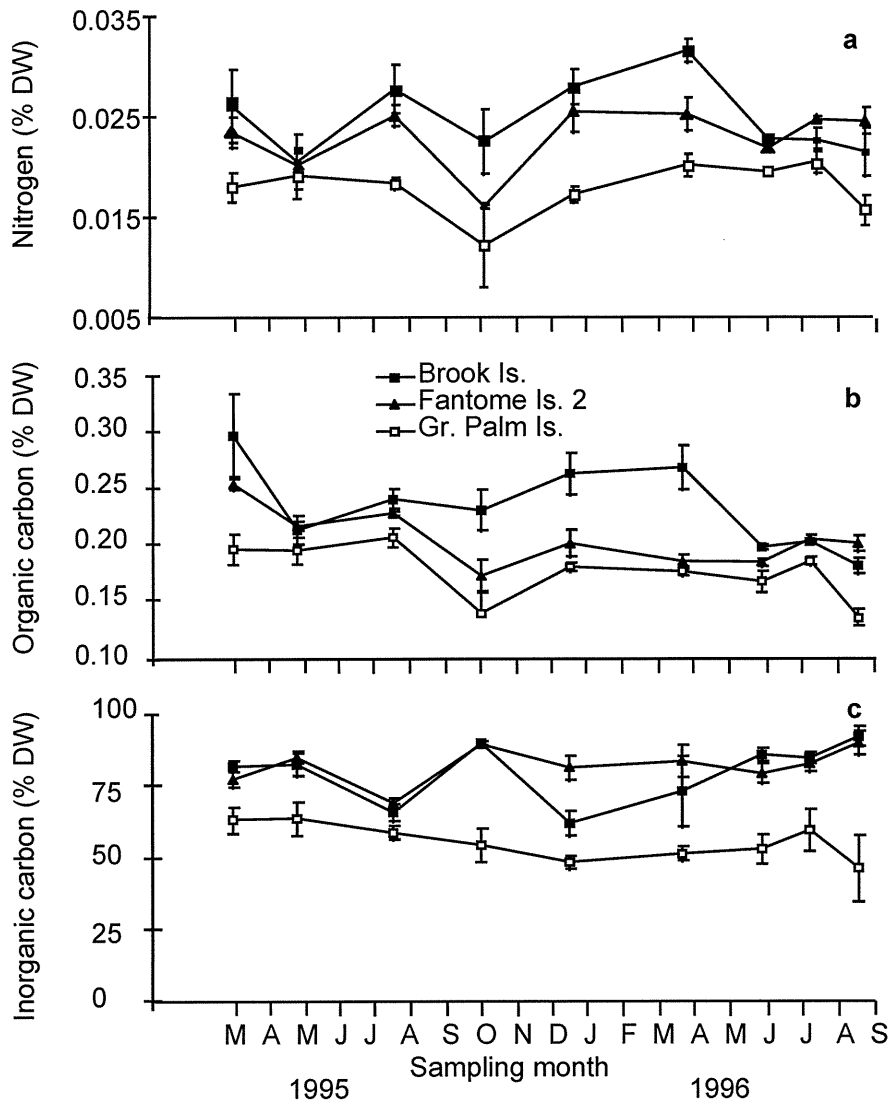
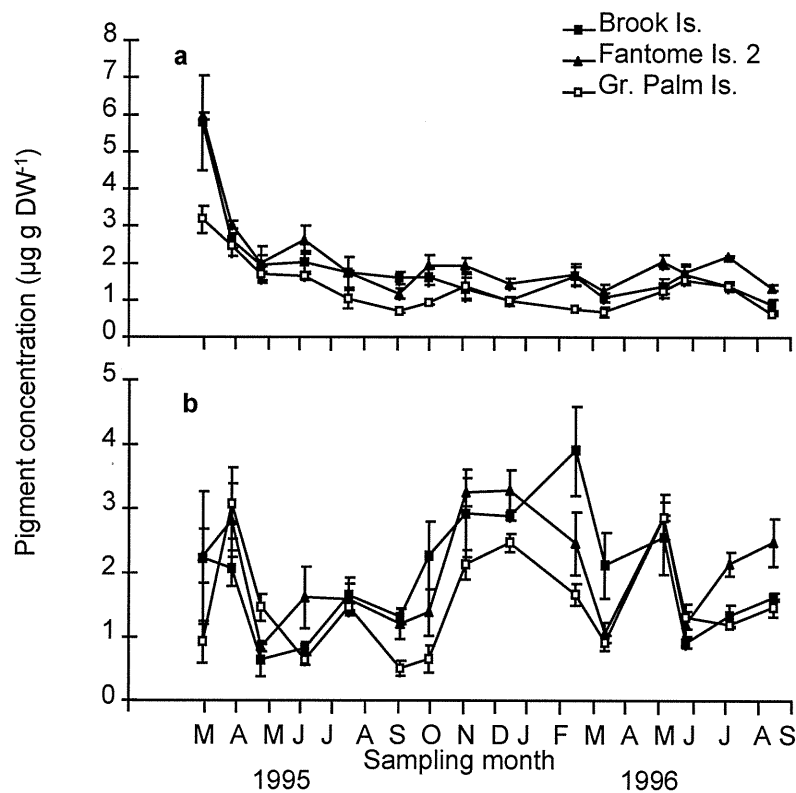


Figure 7. Concentrations (mean values  $\pm$  SE) of nitrogen (a), organic carbon (b), and calcium carbonate (c) in the surface layer of sediments of three nearshore reefs in the central section of the GBR.

### Chlorophyll *a* and phaeophytin

With the exception of the first two sampling dates in the summer of 1995, the chlorophyll *a* concentration in the upper 5 mm of the sediments was relatively stable over time (Fig. 8a). No significant differences were detected between the two seasons, whereas the variation between field trips was significant (Table 11). The differences between the reefs were also significant (Table 11) and the post hoc comparison showed that the mean values at Brook Island ( $1.85 \mu\text{g g DW}^{-1}$ ,  $\text{SE} = 0.019$ ) and at Fantome Island ( $2.14 \mu\text{g g DW}^{-1}$ ,  $\text{SE} = 0.17$ ) were significantly higher ( $p < 0.05$ ) than at Great Palm Island ( $1.36 \mu\text{g g DW}^{-1}$ ,  $\text{SE} = 0.11$ ).



**Figure 8.** Concentrations ( $\pm$  SE) of chlorophyll *a* (a) and phaeophytin (b) in the surface layer of sediments at three nearshore reefs in the central section of the GBR.

Although the seasonal component of the phaeophytin concentration in the sediments appears distinct, with summer values being higher than winter values (Fig. 8b), the ANOVA showed no statistically significant difference between the two seasons (Table 11). This is probably due to the large amount of variation attributed to differences between sampling dates. No differences in phaeophytin concentrations were detected between the reefs (Table 11).

**Table 11.** ANOVA for chlorophyll *a* and phaeophytin concentrations in sediments at three nearshore reefs. Data were log transformed. For significance levels and abbreviations: see Table 2.

Source of variation	df	Chlorophyll <i>a</i>			Phaeophytin		
		MS ( $\times 10^{-4}$ )	F	p	MS ( $\times 10^{-4}$ )	F	p
Reef	2	1641.0	7.18	**	785.8	2.07	ns
Location(R)	6	228.6	3.93	***	378.9	1.94	ns
Season	1	1370.0	1.08	ns	2455.3	2.50	ns
Trip(S)	13	1264.2	21.76	***	983.4	5.02	***
R $\times$ S	2	1.6	0.03	ns	152.3	0.78	ns
R $\times$ T(S)	26	58.1	2.43	**	195.7	3.98	***
Residual	84	23.9	-	-	49.2	-	-

### **Nutrients in macroalgal tissue**

The tissue N values of *Sargassum baccularia* were variable during the sampling period at all three study locations (Fig. 9a). The ANOVA indicated significant differences between the sampled reefs (Table 12). The values collected in samples at Brook Island (1.02% DW, SE= 0.03) were significantly higher ( $p < 0.05$ ) than those at Great Palm Island (0.88% DW, SE= 0.01). Tissue nitrogen concentrations in algae at Fantome Island 1 were intermediate (0.94% DW, SE= 0.02). There was also a significant seasonal difference in tissue N values (factor *Season*, Table 12), with higher values in the summer samples (1.00% DW, SE= 0.02) than in those collected in winter (0.88% DW, SE= 0.02).

The P levels in *Sargassum baccularia* tissue showed much less variation over the sampling period than the tissue N values (Fig. 9b). The ANOVA detected significant differences in tissue P levels between the reefs (Table 12). The values at Brook Island (0.098% DW, SE= 0.002) were significantly higher (Tukey HSD,  $p < 0.05$ ) compared to values in samples from Great Palm Island (0.076% DW, SE= 0.001) and Fantome Island 1 (0.071% DW, SE= 0.002).

**Table 12.** ANOVA for nitrogen and phosphorus concentrations in tissue of *Sargassum baccularia* at three nearshore reefs. Data were arcsine transformed. For significance levels and abbreviations see Table 2.

Source of variation	Df	Tissue nitrogen			Tissue phosphorus		
		MS	F	p	MS ( $\times 10^{-3}$ )	F	p
Reef	2	0.36	5.77	***	11.6	21.97	***
Season	1	.64	10.21	***	0.013	0.025	ns
R $\times$ S	2	0.13	2.12	ns	0.7	1.40	ns
Trip (R $\times$ S)	31	0.06	4.87	***	0.5	4.94	***
Residual	131	0.01	-	-	0.107	-	-

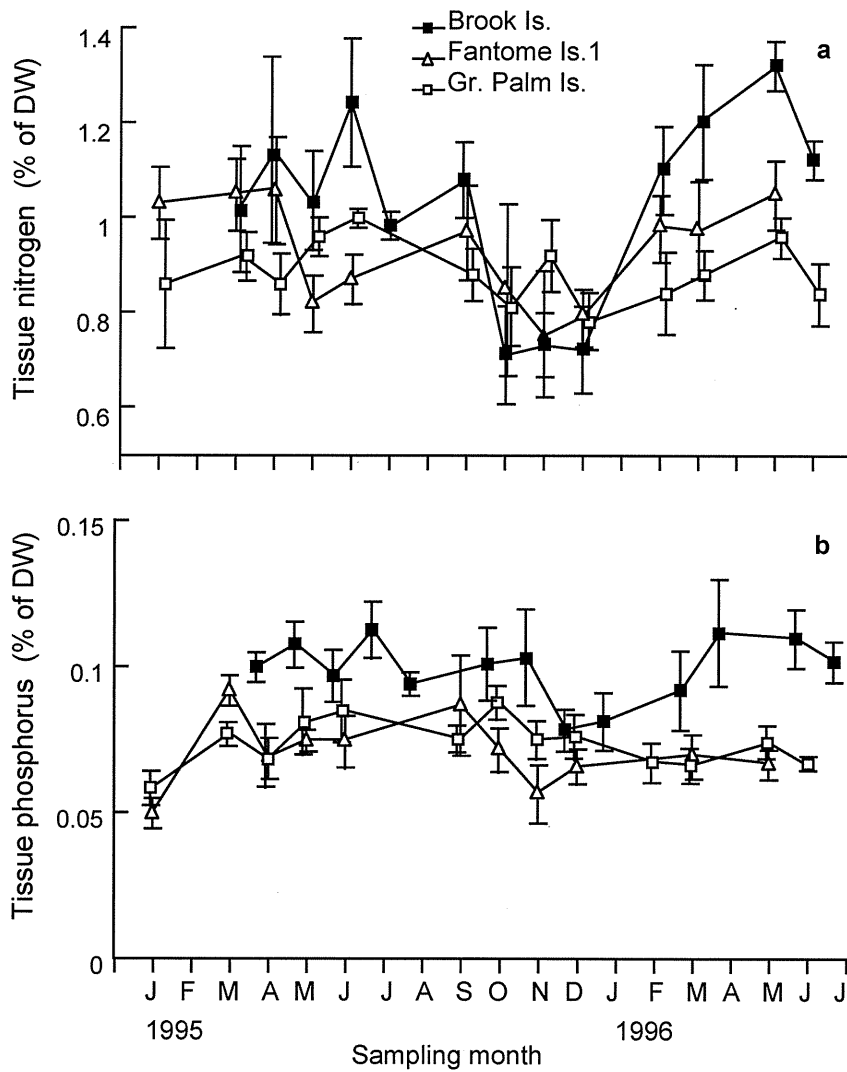


Figure 9. Nitrogen (a) and phosphorus (b) content (mean values  $\pm$  SE) in *Sargassum baccularia* tissue collected at three nearshore reefs in the central section of the GBR.

## Biological parameters

### *Diatom and bacteria numbers in reef flat sediments*

Diatom numbers were only counted in sediments sampled during six field trips, thus a statistical comparison was only performed for differences between sampling dates and reefs (Table 13). Samples from December 1995 and March 1996 had the highest diatom numbers and samples of the three winter months in 1996 showed relatively low values (Fig. 10a). The statistical analysis revealed that a significant component of the variation is due to the different sampling months (Table 13), and a post hoc comparison of means showed that the values found in March 1996 were significantly higher than in all other months sampled. Significant differences were also detected between the three reefs (Table 13). The mean number of diatoms at Great Palm Island ( $1.7 \times 10^6 \text{ ml}^{-1}$ ,  $\text{SE} = 0.9 \times 10^5$ ) was significantly smaller than numbers found at Brook Island ( $2.2 \times 10^6 \text{ ml}^{-1}$ ,  $\text{SE} = 1.8 \times 10^5$ ) and at Fantome Island ( $2.4 \times 10^6 \text{ ml}^{-1}$ ,  $\text{SE} = 1.2 \times 10^5$ ).

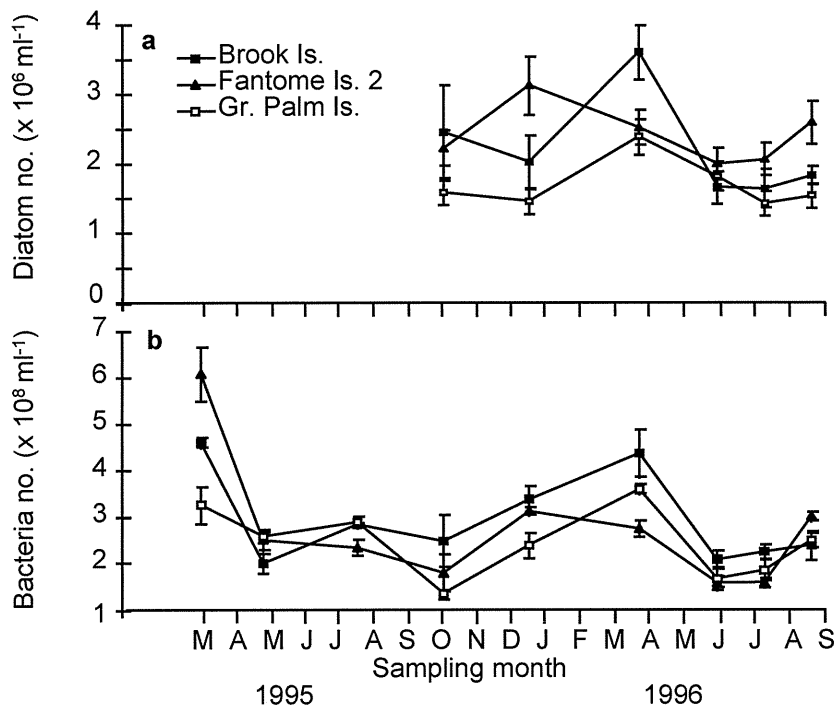


Figure 10. Benthic diatom- (a) and bacteria numbers (b) in the surface layer of sediments of three nearshore reefs in the central section of the GBR. Data are mean values  $\pm$  SE.

Bacteria numbers in the sediment were high during most summer months (Fig. 10b). Although variation was high, the mean number during the summer months ( $3.4 \times 10^8 \text{ ml}^{-1}$ ,  $\text{SE} = 1.4 \times 10^7$ ) was significantly higher (ANOVA, Table 14) than the mean number during winter ( $2.2 \times 10^8 \text{ ml}^{-1}$ ,  $\text{SE} = 1.1 \times 10^7$ ). Differences between the reefs were also significant (Table 14). The lowest bacterial numbers were found at Great Palm Island



( $2.4 \times 10^8 \text{ ml}^{-1}$ ,  $\text{SE} = 1.5 \times 10^7$ ), and these values were found to be significantly lower (Tukey HSD,  $p < 0.05$ ) than those at Brook Island ( $2.9 \times 10^8 \text{ ml}^{-1}$ ,  $\text{SE} = 2.0 \times 10^7$ ), but did not differ from the mean value found at Fantome Island ( $2.8 \times 10^8 \text{ ml}^{-1}$ ,  $\text{SE} = 2.7 \times 10^7$ ).

**Table 13.** ANOVA for diatom numbers in sediments at three nearshore reefs. Data were log transformed. For significance levels and abbreviations see Table 2.

Source of variation	df	MS ( $\times 10^{-4}$ )	F	p
Reef	2	1119.5	23.18	***
Location(R)	6	48.3	0.44	ns
Trip	5	509.3	4.59	***
R x T	10	184.4	1.68	ns
Residual	30	109.7	-	-

**Table 14.** ANOVA of bacterial numbers in sediments at three nearshore reefs. Data were log transformed. For significance levels and abbreviations see Table 2.

Source of variation	df	MS ( $\times 10^{-4}$ )	F	p
Reef	2	367.6	6.60	**
Location(R)	6	55.7	0.25	ns
Season	1	6993.8	6.99	**
Trip(S)	7	1000.5	4.42	***
R x S	2	111.4	0.49	ns
R x T(S)	14	226.5	3.87	***
Residual	48	58.6	-	-

### ***Microbenthos community production***

All parameters related to production measured in situ indicated significant variation among the sampling months (Table 15). Community net and gross production of the microalgal community were positive throughout our study period and showed distinctly reduced values in the two winter months (Table 16). The summer net production values varied only slightly between  $573$  and  $790 \text{ mg C m}^{-2} \text{ d}^{-1}$ , and were about twice as high as the winter values. Assuming that the summer and winter values were each representative of six months of the year, we calculated the average net-carbon fixation as  $461 \text{ mg C m}^{-2} \text{ d}^{-1}$ , equivalent to an annual carbon fixation of approximately  $168 \text{ g C m}^{-2}$ .

The photosynthetic capacity ( $P_{\text{max}}$ ) followed the same seasonal pattern as community net and gross production (Table 16). The ratio of production to respiration (P/R) did not exhibit a seasonal pattern, but stayed on a high level throughout the study period (Table 16).

**Table 15.** ANOVA (factor *Month*) for community net and gross production ( $\text{mg C m}^{-2}\text{d}^{-1}$ ), P/R (dimensionless) and  $P_{\text{max}}$  ( $\text{mg O}_2 \text{min}^{-1} \text{m}^{-2}$ ) of microbenthos communities at Great Palm Island, df = degree of freedom, MS = Mean Square. For significance levels and abbreviations see Table 2.

Independent Variable	Transformation	df	MS	F	p
Net-production	$\sqrt{x+1}$	6	270.5	23.36	***
Error		77	11.6		
Gross-production	$\sqrt{x+1}$	6	225.5	23.98	***
Error		77	9.28		
P/R	none	6	5.91	6.63	***
Error		77	0.89		
$P_{\text{max}}$	$\sqrt{x+1}$	6	1.79	23.21	***
Error		77	0.08		

**Table 16.** Monthly average ( $\pm$  SE) of production parameters from *in situ* measurements of microphytobenthos communities at Great Palm Island.

$P_{\text{max}}$ : photosynthetic capacity, P/R: production to respiration ratio. Means with the same superscript letter were not significantly different (Tukey HSD test).

Month	n	Net production ( $\text{mg C m}^{-2} \text{d}^{-1}$ )	Gross production ( $\text{mg C m}^{-2} \text{d}^{-1}$ )	$P_{\text{max}}$ ( $\text{mg O}_2 \text{m}^{-2} \text{min}^{-1}$ )	P/R
1996: February	9	573.14 <sup>a</sup> (47.40)	913.99 <sup>a</sup> (34.74)	6.14 <sup>a</sup> (0.47)	2.85 <sup>a</sup> (0.27)
March	15	583.65 <sup>a</sup> (43.43)	854.26 <sup>a</sup> (52.12)	5.65 <sup>a</sup> (0.45)	3.24 <sup>a,c</sup> (0.17)
May	16	666.24 <sup>a</sup> (57.36)	983.05 <sup>a</sup> (60.78)	6.72 <sup>a</sup> (0.54)	3.27 <sup>a,c</sup> (0.26)
July	15	269.77 <sup>b</sup> (20.96)	487.97 <sup>b</sup> (28.59)	2.66 <sup>b</sup> (0.18)	2.88 <sup>a</sup> (0.27)
September	10	245.39 <sup>b</sup> (34.19)	484.77 <sup>b</sup> (27.71)	3.26 <sup>b</sup> (0.29)	2.42 <sup>a</sup> (0.34)
December	8	790.01 <sup>a</sup> (27.24)	1035.59 <sup>a</sup> (27.89)	7.16 <sup>a</sup> (0.26)	4.43 <sup>b,c</sup> (0.33)
1997: February	11	708.88 <sup>a</sup> (51.02)	937.62 <sup>a</sup> (59.49)	7.02 <sup>a</sup> (0.41)	4.39 <sup>b,c</sup> (0.33)

**Table 17.** Monthly average values ( $\pm$  SE) of temperature and light from *in situ* measurements of microphytobenthos production at Great Palm Island (n= 4).

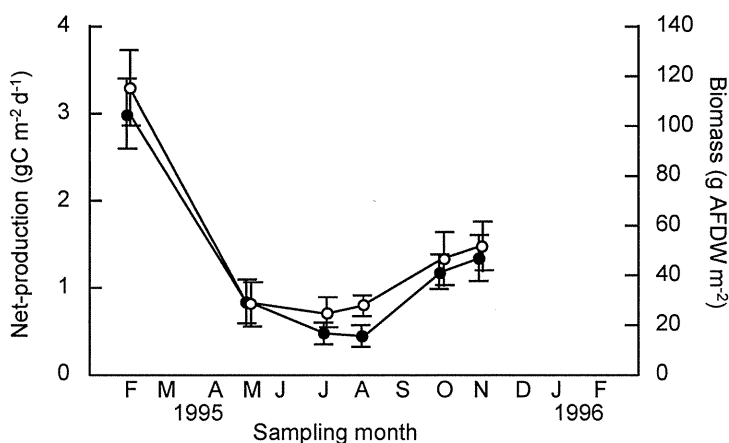
Month	Daily light sum (E m <sup>-2</sup> )	Maximum light ( $\mu$ E s <sup>-1</sup> m <sup>-2</sup> )	Temperature (°C)
1996:			
February	30.7 (7.1)	1318 (238)	30.0 (0.3)
March	27.7 (2.3)	1325 (99)	27.8 (0.3)
May	19.8 (1.3)	999 (19)	27.6 (0.1)
July	22.5 (0.2)	1002 (10)	22.5 (0.2)
September	20.3 (1.1)	1184 (60)	23.1 (0.1)
December	25.0 (4.0)	1342 (86)	28.1 (0.5)
1997:			
February	22.5 (4.3)	1382 (50)	28.7 (0.3)

#### Effects of light and temperature

As expected, both light and temperature showed a maximum in summer and distinctly lower values in July and September (Table 17). The maximum light intensity in winter was about 200 to 300  $\mu$ E m<sup>-2</sup> s<sup>-1</sup> lower than in summer. However, the large difference in the daily light sums between February 1996 and February 1997, indicates that light was also dependent on several other factors such as cloud cover, wave action and turbidity.

#### Production of *Sargassum baccularia*

The net-production rates of *Sargassum baccularia* at Great Palm Island showed significant differences over the sampling period (Fig. 11; 1-factor ANOVA:  $F_{5, 54} = 16.01$ ,  $p < 0.05$ ). Similar to the production rates of the microphytobenthos community, the net production rates of *S. baccularia* were significantly higher in the summer months February, November, and December compared to the winter months, May, July, and August (Tukey HSD  $p < 0.05$ ). The highest production rate was measured in February ( $\sim 3$  g C m<sup>-2</sup> d<sup>-1</sup>) and was associated with maximum biomass values in this month (Fig. 11).



**Figure 11.** Net production (●) and biomass (○) of *Sargassum baccularia* at Great Palm Island. Data are mean values  $\pm$  SE.

## DISCUSSION

### Water column nutrients

The concentrations of the inorganic macro-nutrients in the water column over the coral reef flats of Brook, Fantome and Great Palm Islands (Fig. 2, Table 4) were different to those reported for other water bodies in the GBR (Table 18). The dissolved inorganic nitrogen (DIN) species on the study reefs were higher than concentrations in open waters in the same area, and lower than values from other fringing reefs in the Cairns and Central sections of the GBRWHA (Table 18). Water column nutrients measured at other reef flats of the Palm and Brook Islands in 1992-94 (Klumpp et al. 1999) were similar to values in this study. Several other studies have reported that levels of dissolved inorganic nitrogen compounds on reefs are generally higher compared to water outside the reef tract (Webb & Wiebe 1978, Andrews & Müller 1983, Crossland et al. 1984, Ayukai 1993, Wilkinson et al. 1984). The increased nitrogen concentrations on reefs have been attributed to nitrogen fixation of benthic cyanobacteria (Wilkinson et al. 1984, Wiebe 1985).

The fixed nitrogen may then be cycled through:

- direct excretion by the nitrogen fixers;
- the decomposition of nitrogen fixers; or
- assimilation of the nitrogen fixers by herbivores and subsequent ammonium excretion (D'Elia & Wiebe 1990).

Alternatively, the elevated concentrations of nitrate and nitrite on reef flats may be indicative of bacterial ammonia oxidation and subsequent nitrification (D'Elia & Wiebe 1990), a process which may also explain why most inorganic nitrogen from reef flats is exported in the form of nitrate (Webb & Wiebe 1975).

In contrast to the DIN concentrations, the phosphate values over the study reef flats were three to five times lower than concentrations measured at other open water and reef stations in the GBRWHA (Table 18). Although phosphate concentrations are only slightly altered when water flows over reef flats (Pilson & Betzer 1973), Atkinson (1987) and Atkinson & Smith (1987) demonstrated that reef communities take up phosphate. Pilson & Betzer (1973) measured slight phosphate decreases on transects with high macroalgal biomass. During summer, the reefs of our study area are dominated by large macroalgae with a high biomass (Schaffelke & Klumpp 1997). It is therefore possible that the low phosphate values during summer were caused by the uptake of phosphate by these algae and other primary producers. Due to high growth rates in summer, uptake rates by these algae are high and the demand for inorganic nutrients is higher than the supply, indicating that macroalgal growth at our study area is nutrient-limited during summer (Schaffelke & Klumpp 1998a).

**Table 18.** Summary of dissolved inorganic nutrients ( $\mu\text{M}$ ) in the water column of different water bodies in the GBR region. Values are overall means with ranges of means from different sites and/or seasons. Data sources: <sup>1</sup>compilation of data from various sources in Blake 1994, <sup>2</sup>Furnas et al. 1997, <sup>3</sup>Klumpp et al. 1999, <sup>4</sup>this report, <sup>5</sup>Furnas et al. 1995, <sup>6</sup>Mitchell et al. 1997, <sup>7</sup>Devlin et al. 2001, nd= no data.

Region	Nitrite	Nitrate	Ammonium	DIN	Phosphate
Fringing reefs, Cairns section <sup>1</sup>	0.06 (0.01-0.14)	0.36 (0.21-0.56)	0.66 (0.29-1.29)	1.06 (0.66-1.52)	0.17 (0.14-0.23)
Fringing reefs, Central section <sup>1</sup>	0.03 (0.01-0.05)	0.28 (0.05-0.86)	0.55 (0.22-0.86)	0.85 (0.38-1.34)	0.21 (0.09-0.29)
Open water, inshore Cairns section <sup>2</sup>	0.02 (0.01-0.03)	0.13 (0.03-0.23)	0.09 (0.02-0.15)	0.24 (0.06-0.41)	0.10 (0.08-0.11)
Open water, offshore Cairns section <sup>2</sup>	0.02 (0.01-0.02)	0.07 (0.06-0.07)	0.06 (0.05-0.07)	0.14 (0.13-0.15)	0.11 (0.09-0.12)
Fringing reefs, Herbert River area <sup>3</sup>	0.03 (0.01-0.05)	0.12 (0.01-0.32)	0.62 (0.40-0.89)	0.76 (0.41-1.26)	0.06 (0.04-0.08)
Fringing reefs, Herbert River area <sup>4</sup>	0.04 (0.00-0.09)	0.18 (0.00-0.56)	0.21 (0.00-0.62)	0.44 (0.06-0.91)	0.04 (0.00-0.25)
Herbert River water, non-flood conditions <sup>5</sup>	0.10 (0.05-0.16)	6.67 (1.60-11.36)	1.04 (0.85-1.25)	7.80 (2.66-12.77)	0.06 (0.04-0.09)
Herbert River water, flood conditions <sup>6</sup>	nd	nd	nd	14.5 (3-26.5)	0.5 (0.1-0.7)
Flood plumes in GBR waters <sup>7</sup>	0.51 (0.02-1.20)	6.31 (0.79-17.22)	5.14 (0.44-12.80)	11.40 (1.66-25.26)	0.81 (0.06-2.46)

Concentrations of dissolved organic phosphorus (DOP) and dissolved organic nitrogen (DON) measured in open waters of the inter-reef areas (Furnas et al. 1997) were on a level similar to that over our study reef flats (Fig. 3, Table 4).

Most water column nutrient parameters were lower at Great Palm Island than at Fantome Island and Brook Island (Table 4). Although factors such as different residence times of the water or differing nitrogen fixation rates may apply, it is more likely that the lower values at Great Palm Island result from the greater distance to the mainland and to the Herbert River mouth compared to the two other islands. Large-scale cross-shelf surveys in the vicinity of our study area (Furnas et al. 1995, 1997) indicated that nitrate, nitrite, silicate, and suspended solid concentrations were significantly higher in inshore waters than in offshore lagoonal waters (Table 18). High nutrient concentrations inshore were also found around Magnetic Island (Brodie et al. 1989), in waters off Townsville (Revelante and Gilmartin 1982, Walker & O'Donnell 1981), and around fringing reefs in the Cairns section and the Whitsunday region (Table 18, more detailed data in Blake 1994). As expected, the dissolved inorganic nutrient concentrations in the Herbert River water and in cyclonic flood plumes are much higher than in the receiving marine waters (Table 18).

A useful indicator of biological water column nutrient availability is the ratio between the organic and the inorganic species of both nitrogen and phosphorus (Table 19). The DON to DIN ratios at all our sampling sites were distinctly lower than in offshore open waters of the area (Tully region, calculated from Furnas et al. 1997). The inshore Tully region ratios were similar to the ratios in this study and these values indicate a relatively high availability of inorganic nutrients. Interestingly, the ratios from waters further north are distinctly higher both inshore and offshore, caused by comparably low concentrations of DIN (Furnas et al. 1997). In contrast to the trend for N, the ratios of DOP to PO<sub>4</sub> at our sampling sites were higher than the open water stations of Furnas et al. Inspection of the original data (Table 4, Furnas et al. 1997) showed that this discrepancy is due to lower PO<sub>4</sub> values in our study. The ratios for river and flood plume waters are all very low (Table 19), indicating high inorganic nutrient levels, relative to the organic fraction. The high concentrations of dissolved inorganic nutrients, particularly DIN, on the fringing reefs may be caused by:

- a high rate of N-fixation on the reefs, as has been shown for other GBR reefs (Wilkinson et al. 1984, Wiebe 1985, Ayukai et al. 1993); and
- the seasonal influence of river run-off, which is high in dissolved inorganic nutrients (Table 18).

There is still a considerable gap in the knowledge on nutrient transformation processes, once the land run-off reaches the sea. We assume that it is more likely that N-fixation and other biological processes cause the relatively high availability of dissolved inorganic nutrients on nearshore reefs, and that the seasonal discharge events present discrete nutrient import pulses, which may cause differences in nutrient stocks between reefs.

It is generally perceived that nutrient values in the waters of the GBR are higher during summer due to higher terrigenous run-off during that period (Revelante & Gilmartin 1982, Ayukai 1993, Furnas et al. 1995, Mitchell & Furnas 1997) and higher frequencies of upwelling intrusions (Furnas et al. 1995). In contrast, the inorganic and organic nutrients in the water column at our study reefs were higher during winter, with the exception of nitrate and nitrite. However, these differences were statistically significant only for phosphate. Biological processes may modify the potentially higher nutrient availability during summer.

Especially the higher production of photoautotrophic organisms and the higher macroalgal biomass during summer (see below) may lead to a higher nutrient demand and thus a lower nutrient concentration in the water column. In contrast to our data, nitrate and nitrite values on One Tree Reef were high during winter, and ammonium concentrations were high during spring and summer (Hatcher & Hatcher 1981, Hatcher & Frith 1985). The nutrient concentrations in the water outside One Tree reef did not change with season, and the above authors explained the nutrient variations on the reef by N-fixation and remineralisation processes.

**Table 19.** Ratios of dissolved organic to dissolved inorganic nutrients in the water column of different water bodies in the GBR region. Calculated from: <sup>1</sup>This study, <sup>2</sup>Furnas et al. 1997, <sup>3</sup>Furnas et al. 1995, <sup>4</sup>Mitchell et al. 1997, <sup>5</sup>Devlin et al. 2001.

Area	DON/DIN ratio	DOP/PO <sub>4</sub> ratio
Great Palm Is. <sup>1</sup>	13.6	3.8
Fantome Is. 1 <sup>1</sup>	7.1	2.7
Fantome Is. 2 <sup>1</sup>	8.6	2.1
Brook Is. <sup>1</sup>	10.9	3.8
Cairns region, open water, inshore <sup>2</sup>	95.0	1.4
Cairns region, open water, offshore <sup>2</sup>	42.3	0.9
Tully region, open water, inshore <sup>2</sup>	14.9	2.0
Tully region, open water, offshore <sup>2</sup>	36.7	0.7
Herbert River, non-flood <sup>3</sup>	1.2	0.4
Herbert River, flood <sup>4</sup>	1.1	3.3
Flood plumes <sup>5</sup>	1.5	1.4

The mapping of cyclonic flood plumes from the Herbert and Burdekin Rivers (Wolanski & Van Senden 1983, Steven et al. 1996, Devlin et al. 2001), which are the main rivers in the vicinity of the study area, indicate that Brook Islands have been inundated more often by nutrient-rich flood plumes than the Palm Island Group. The maps of the flood plume monitoring program of the GBRMPA (data collected since 1986, Devlin et al. 2001) may represent only a snapshot in time, usually one day of aerial surveys during a flood event, however they offer a good indication of the spatial extent of cyclonic flood plumes. During the study period two cyclones (Cyclone Violet, March 1995 and cyclone Ethel, March 1996) affected the study area and the associated flood plumes inundated the Brook Islands, but not the Palm Islands (Steven et al. 1996, Devlin et al. 2001). We sampled directly after the flood in early March 1995 (Table 1), however, we were only able to find high water column nutrient concentrations at the coastal side of Fantome Island (station Fantome 1). Although not directly inundated by the flood plume, this site is close to the river mouth, and may have been reached by higher nutrient concentration due to mixing processes. In 1996, we sampled two weeks after the flood associated with cyclone Ethel, however, did not detect a flood plume signal in the water column nutrients.

The hydrodynamic conditions in the GBR coastal zone create a water movement that is directed predominantly north- and shore-ward (Wolanski 1994). Water from the Herbert River mouth reaches the Brook Islands after the passage through the Hinchinbrook Channel, which may be a reason for the generally high values of all parameters at the Brook Island site. The Palm Islands are located south of the Herbert River mouth and it may hence be assumed that these islands are under less influence by this river. Water from the Burdekin River, however, may reach as far north as the Palm Island Group (Wolanski & Jones 1981) and may affect the water climate of those islands. Of our three Palm Islands stations, the two Fantome Island stations were much closer to the mainland coast than the Great Palm Island station. The inner shore area between the coast and the inshore islands is characterised by high resuspension fluxes and generally higher concentrations of suspended particles and water column chlorophyll (Furnas et al. 1995, Brodie et al. 1997). The location of the sampling station at Great Palm Island may be considered to be more oceanic compared to the Fantome Island stations,

indicated by the generally lower concentrations of dissolved inorganic nutrients at this station (Table 4).

### **The water/sediment interface**

Most inorganic nutrients were more concentrated in the interstitial water relative to the overlying water column (Table 5). The highest concentration factors (= the ratio of the average nutrient concentration in the interstitial water to the concentration in the water column) were found for phosphate (71 in summer, 12.5 in winter) and ammonium (21 in summer and 10 in winter). Both DOP (3.2 in summer and 6.3 in winter) and DON (2.2 in summer, 1.8 in winter) were less increased in the interstitial water than the inorganic nutrients. The nutrient concentrations in the interstitial water of our three study reef flats were at the lower end of the range of data reported for coral reef sediments (eg. Entsch et al. 1983, DiSalvo 1974). Samples from reef lagoons may reach values as high as 100  $\mu\text{M}$  ammonium (LIMER Team 1976, Ullman & Sandström 1987, Johnstone et al. 1989). However, these high values were integrated over a larger sediment depth, and ammonium concentrations usually increase with sediment depth (Alongi 1989). Capone et al. (1992) found ammonium values in the interstitial water of the upper two centimetre of coarse sediments on coral reefs of the central GBR in the same range as the values we measured. Entsch et al. (1983) pointed out that samples taken with a syringe may underestimate pore water nutrient concentrations due to possible dilution with water from the overlying water column. To avoid this problem, the sample volume in this study was kept to a minimum, however, a slight dilution of porewater samples cannot be excluded with certainty.

The sediment interstitial is an important site for the regeneration of organic matter and the remineralisation to inorganic nutrients by bacteria (DiSalvo 1974, Entsch et al. 1983). The interstitial nutrients are continuously released into the water column (Ullman & Sandström 1987, Alongi 1989, 1990, Capone et al. 1992), often with higher rates during winter (Furnas et al. 1995). A model calculation showed that the nutrient flux from released porewater into nearshore waters of Cleveland Bay is higher than the combined river inputs (Ullman & Sandström 1987). The porewater release is assumed to be much higher during sediment resuspension events, caused by e.g. currents, wind and swell waves (Fanning et al. 1982, Larcombe et al. 1995). The porewater nutrients released by the activity of bioturbating animals are particularly important on reefs (Massin 1982, Uthicke 1999). Also, the influence of dredging and trawling activities on the benthic nutrient fluxes are assumed to be significant (Alongi 1989). However, reliable estimates of these nutrient fluxes are not available.

The prevalent resuspension and other processes that release sediment components back into the water column make it difficult to estimate the material fluxes that transport organic matter from the water column into the sediment. Deposition rates measured with sediment traps offer only a rough estimate, because they do not distinguish between net deposited and resuspended material (Woolfe & Larcombe 1998). In our measurements a significant water flow dependence was obvious with higher deposition rates and diluted organic content of the deposited particulate matter (PM) during days with high water flow (Fig. 6). It may be assumed that the material collected in sediment traps is resuspended and recycled several times, undergoing a range of biological or biochemical transformations until it may be eventually buried. However, sediment traps have been widely used and enable us to make comparisons, albeit rough, between studies and locations.



The deposition rates and nutrient contents of the particulate matter (PM) collected in sediment traps at Great Palm Island were in most cases higher than at other coral reefs or open water stations further away from the GBR coast (Koop & Larkum 1987, Hansen et al. 1992, Furnas et al. 1995). Comparisons between PM collected in traps and sediment data from the same sites, generally reveal organic carbon ( $C_{org}$ ) and N concentrations about one order of magnitude higher in the water-borne material (Fig. 7, Koop & Larkum 1987, Johnstone et al. 1990, Hansen et al. 1992). Johnstone et al. (1990) attributed this to a fast consumption of the deposited organic matter in a coral reef lagoon with virtually no accumulation over time. The relatively low organic content of sediments may have led to a 'dilution' of trap-samples from the seaweed zone with resuspended matter during days with high water flow.

The origin and composition of the particles deposited on coral reefs varies between locations and reef zones, but is generally believed to be autochthonous (Lewis 1977, Hatcher 1988, Alongi 1988, Alongi 1989, Furnas et al. 1995). To identify the origin with some degree of certainty, it is necessary to analyse stable isotope ratios or signatures of other biochemical markers such as lipids or sterols. Microscopic inspection of the PM revealed mainly an amorphous greyish matrix, with some cyanobacteria and embedded diatoms. The C:N:P ratios of PM in the present study were roughly in the range of the Redfield ratio, and higher than other data reported from the GBR (Koop & Larkum 1987, Hansen et al. 1992, both only C:N; Furnas et al. 1995), but much lower than ratios obtained from detritus collections at Enewetak Atoll and from Western Australia (cited in Hatcher 1983). However, the Redfield-like atomic ratios may not necessarily indicate the planktonic origin of the PM, i.e. the high C:N ratios of macroalgal detritus decrease drastically during decomposition and colonisation with microbes and reach values close to the Redfield ratio (Sharma et al. 1994, Duggins & Eckman 1997).

At the fringing reef stations of this study, the PM settles not only on sediments but also on the surface of benthic organisms such as corals and macroalgae. The standing stocks of particulate organic material deposited on the benthos are  $4.7 \text{ g C m}^{-2}$ ,  $670 \text{ mg N m}^{-2}$ , and  $124 \text{ mg P m}^{-2}$ , calculated using estimates of macroalgal biomass and of the amount and composition of PM settled on macroalgal thalli (Schaffelke & Klumpp 1997, Schaffelke 1999b). In contrast to the general assumption that negative effects by smothering of the benthos will prevail, Anthony (1999) has shown that inshore hard corals use these organic-rich particles as an additional or alternative food source. Similarly, macroalgae use the PM as an alternative nutrient source after the particulate nutrients were presumably remineralised in the boundary layer on the thalli (Schaffelke 1999b).

The composition of suspended particles in the water column was not measured in the context of the present study. As an overview, particle data from different water bodies in the study area are summarised in Table 20. Similar to the dissolved nutrients in the water column, also the particulate nutrients showed distinctly higher concentrations in the Herbert River water and in coastal waters during monsoonal flood events (Table 20).

In the coastal zone of the GBR higher and more variable stocks of particulate matter and higher phytoplankton biomass than further offshore have been measured (Furnas et al. 1995, Brodie et al. 1997). Nutrients from anthropogenic sources comprise a major proportion of the nutrient inputs into the GBRWHA, although they are only a minor component of the total nutrient fluxes (Furnas et al. 1995). However, the GBR coastal

zone is generally subject to higher and seasonally more variable inputs than the shelf waters.

**Table 20.** Summary of suspended particle characteristics in the water column of different water bodies in the GBR region. SS= suspended solids (mg l<sup>-1</sup>), PN= particulate nitrogen, PP= particulate phosphorus (µM). Plant pigments in µg l<sup>-1</sup>. Values in brackets are range of means from different sites and/or seasons or SE. Sources of data: <sup>1</sup>compilation of data from various sources in Blake 1994. <sup>2</sup>Furnas et al. 1995, <sup>3</sup>Fabricius & Dommissse 2000, Anthony & Fabricius 2000, <sup>4</sup>M. Dommissse in prep., <sup>5</sup>Klumpp et al. 1999, <sup>6</sup>Mitchell et al. 1997, <sup>7</sup>Devlin et al. 2001, nd= no data.

Region	SS	PN	PP	Chl <i>a</i>	Phaeophytin
Fringing reefs, Central section <sup>1</sup>	3.35 (2.2-5.3)	nd	nd	1.00 (0.59-1.25)	nd
Open water, inshore Cairns section <sup>2</sup>	1.99 (1.07-3.47)	1.46 (1.2-1.8)	0.14 (0.09-0.19)	0.60 (0.42-0.77)	0.27 (0.20-0.34)
Open water, offshore Cairns section <sup>2</sup>	0.28 (0.16-0.88)	0.95 (0.75-1.13)	0.07 (0.05-0.09)	0.45 (0.34-0.59)	0.23 (0.19-0.27)
Fringing reefs, Herbert River area <sup>3</sup>	1.40 (1.30-1.49)	0.94 (0.38-2.48)	0.05 (0.04-0.07)	0.27 (0.23-0.31)	0.19 (0.15-0.22)
Great Palm Island <sup>4</sup>	2.74 (0.65)	2.6 (0.08)	0.07 (0.001)	nd	nd
Fringing reefs and open waters in Herbert River area <sup>5</sup>	nd	2.06 (1.3-3.1)	0.20 (0.11-0.29)	nd	nd
Herbert River water, non flood <sup>2</sup>	68.9 (63.0-72.0)	9.72 (9.50-10.15)	0.92 (0.77-1.00)	0.90 (0.62-1.05)	1.29 (1.00-1.51)
Herbert River water, flood <sup>6</sup>	156.0 (60-390)	41.1 (18-88)	3.2 (1.0-7.0)	nd	nd
Flood plumes <sup>7</sup>	143.0 (3.0-672)	10.8 (10.3-11.2)	1.1 (0.4-2.3)	6.0 (0.93-17.9)	2.2 (0.8-6.10)

Imported nutrients may be initially utilised by phytoplankton, but may then be recycled and retained in the coastal zone as particles and aggregates composed of dead phytoplankton, bacteria and sediments. The importance of such biological flocculation processes in tropical coastal areas has been recently addresses by Ayukai & Wolanski (1997) and Wolanski et al. (1997, 1998). The aggregates are in turn consumed by of filter feeders or remineralised in microbial loops in the water-column and the benthos. Particle/ detritus-based cycles in coral reefs were virtually ignored until about 15 years ago (Hatcher 1983) and are still largely obscure. However, recent modelling exercises have pointed out their importance in coral reef trophodynamics (Johnson et al. 1995, Arias-González 1997, Arias-González et al. 1997), as opposed to the long-standing dogma of the predominance of grazer-based food webs (e.g. Polunin & Klumpp 1992). In ecosystems with a high abundance of suspended organic particles paired with a low

concentration of dissolved inorganic nutrients, such as the coastal zone of the GBR, the recycling of material via detrital cycles may be of even higher prevalence.

### **Parameters integrating nutrient availability**

Because of the high temporal and spatial variability of water column nutrients, the use of integrative, proxy parameters as indicators for nutrient availability has been favoured (discussed in Steven et al. 1998). With the exception of water column chlorophyll *a* (GBRMPA long-term chlorophyll monitoring program, Brodie & Furnas 1992, Steven et al. 1998), however, very few potential integrative parameters have been measured on a long term basis or on a larger spatial scale. In the present study, we considered as integrative parameters the nutrient and organic content in surface sediments, and the nutrient content in macroalgal tissue.

The bulk of the organic carbon content measured in the sediments is likely to be composed of bacteria, microalgae, and detritus (De Vaugelas & Naim 1981). The total organic carbon content of the surface sediments at our study sites (Fig. 7b) was ~0.2% dry-weight (DW). This is at the lower end of the range of sediment organic carbon values sampled on GBR reefs (Moriarty et al. 1985; Hansen et al. 1987, 1992; Johnstone et al. 1990; Hansen & Skilleter 1994). However, most of the cited studies were performed in coral reef lagoons, which may receive most of the organic matter through the allochthonous input of detritus (Koop & Larkum 1987). Comparative data from the Herbert River region (Table 20) are in a range similar to our samples. The large-scale sampling of Alongi (1989) and Brunskill et al. (2002) of non-reef sediments in this region indicated clear cross-shelf trends in organic carbon, with distinctly higher values closer to the coast and in the Hinchinbrook Channel. Transects from the Johnstone River estuary to ~30 km offshore showed a similar trend (Gagan et al. 1987, Pailles & Moody 1996). Surface sediments along a transect from the coast to some inshore islands in the Whitsunday region were distinctly higher than inshore data from the Herbert River and the Johnstone River region (Table 21).

The range of nitrogen concentrations in the sediments at our study sites (Fig. 7a, 0.017-0.025% DW) was similar to the values from other reefs (Moriarty et al. 1985, Hansen et al. 1987, Johnstone et al. 1990, Hansen & Skilleter 1994), with the exception of sediments from Davies Reef lagoon that had exceptionally high N values (Hansen et al. 1992). Comparative data from the Herbert River region indicate again that the sediment N values at our sites were relatively low (Table 21). Klumpp et al.'s (1999) data, obtained at sampling sites on other reef flats of the Palm and Brook Islands two to three years earlier, are about twice as high as values in the present study. This may indicate a year-to-year variability or spatial difference on an inter-reefal scale. Again, the cross-shelf studies of Alongi (1989) and Brunskill (unpub. data) indicated a clear proximity-to-land signal in the sediment nitrogen content.

The annual average of the atomic organic carbon to nitrogen (C/N) ratio in our sediments ranged from 10.7 to 11.7, depending on sampling location. This is in the range of the data from other studies in the Herbert River region, with the exceptions of very low C/N ratios in Alongi's cross-shelf samples (Alongi 1989). Blake (1997) had some sites in the Whitsunday Islands with very high C/N ratios, caused by very high organic carbon contents in the sediments.

The sediment phosphorus values are difficult to compare between studies (Table 21), because different analytical methods were employed, potentially measuring different P fractions (see Furnas et al. 1995, Pailles & Moody 1995).

Chlorophyll *a* values in the present study (Fig. 8a), as an integrator of microbenthic autotrophic biomass, were in the same range as those from the lagoon of Davies Reef (Hansen et al. 1987, 1992), and slightly lower than those on the reef flat of Lizard Island (Uthicke 1994) or of One Tree Island (Johnstone et al. 1990). Hansen & Skilleter (1994) reported distinctly higher concentrations at One Tree Island.

The amount of phaeophytin, an integrator for dead plant material, was in the same range as the chlorophyll *a* concentrations. This is unusual for coral reef sediments, since most authors found no detectable (Uthicke 1994) or very low (Hansen et al. 1987, 1992; Johnstone et al. 1990) amounts of phaeophytin. The relatively high phaeophytin concentrations may be an indication that the sediments of the three reefs studied received a large proportion of dead plant material, which is likely to result from the high biomass of macroalgae in the area. Freshly dead diatom cells and other microalgae (of planktonic and benthic origin) may also contribute to the phaeophytin pool.

With the exception of phaeophytin, all sediment parameters were distinctly lower at Great Palm Island than at the other sampling stations. Winter values of organic carbon, nitrogen, bacteria and phaeophytin were all lower than summer values. However, probably due to the large variations between sampling occasions, the differences were only significant for bacteria and marginally significant for total organic carbon. Seasonal differences in the function of coral reefs have not been considered until recently (D'Elia & Wiebe 1990), and there are hardly any data available for comparison. We found high values of sediment organic carbon, nitrogen, and chlorophyll *a* directly after cyclonic flood events, especially at Brook Island.

**Table 21.** Summary of sediment components (organic carbon: mmol g<sup>-1</sup>, nutrients: μmol g<sup>-1</sup>) in the GBR region. Values in brackets are range of means from different sites and/or seasons. Data sources: <sup>1</sup>this report, <sup>2</sup>Klumpp et al. 1999, <sup>3</sup>Brunskill et al. (2002) and G. Brunskill, AIMS (unpub. data), <sup>4</sup>Alongi 1989, <sup>5</sup>Pailles & Moody 1996, <sup>6</sup>Blake 1997, nd= no data.

Region	Organic carbon	Nitrogen	Phosphorus
Herbert River region, fringing reef flats <sup>1</sup>	0.14-0.2	12-18	nd
Herbert River region, fringing reef flats <sup>2</sup>	nd	35-39	6-8
Herbert River region, off fringing reefs <sup>3</sup>	0.2-0.5	20-40	12-14
Herbert River region, cross-shelf transect, non-reef sites <sup>4</sup>	0.04-0.6	14-93	8-16
Johnstone River, cross-shelf transect, non-reef sites <sup>5</sup>	0-0.8	nd	4-11
Whitsunday region, coastal transect <sup>6</sup>	0.2-1.7	20-38	20-33

However, due to the longer sampling intervals for most of the sediment parameters, we cannot resolve whether these peaks are directly caused by the flood plumes, or whether they are part of the general trend for higher values during summer.

The nutrient content in macroalgal tissue has long been recognised as a transient nutrient store in environments with periodic nutrient supply, as well as both an integrator for the nutritional history of the plants and a bioindicator for water quality (Rosenberg & Ramus 1982, Björnsäter & Wheeler 1990, Lyngby 1990, Lyngby et al. 1994, Lapointe et al. 1992, Fong et al. 1994, 1998, Jones et al. 1996). Our results indicate higher N and P nutrient stores in *Sargassum baccularia* tissue at Brook Island than at the Palm Island sampling sites (Fig. 9). The tissue N values in late summer were higher than values in winter and spring. This indicates a higher availability to the plants during the main wet season months, presumably caused by increased riverine inputs. It must be kept in mind that tissue nutrients are composed of essential cell components plus stored nutrients that are surplus to the immediate requirements for growth. If the growth rates were high during times of high nutrient availability, a high nutrient storage level would not be expected.

Detailed studies indicated that *Sargassum baccularia* is nutrient-limited in the field, which means that maximum growth is not attained, especially at the beginning of the growth season in spring (Schaffelke & Klumpp 1998a). *S. baccularia* and a number of other macroalgal species can efficiently use transient nutrient pulses and show increased growth or production following this (Schaffelke & Klumpp 1998b, Schaffelke 1999a). This mechanism may be especially important during summer, when nutrient inputs are high and pulse-like, and the nutrient demand in *Sargassum* species is high because this is the time of the seasonal growth maximum of this species (Schaffelke & Klumpp 1997, 1998a).

### **Biological parameters**

A step towards indicators that integrate even further the nutrient availability are biological parameters, which take the response of whole organisms into account. We concentrated on the estimation of benthic biological parameters, the abundance of bacteria and diatoms, and the production of the microbenthic community and the dominant *Sargassum* species at our study sites.

Bacterial numbers were found in the order of  $10^8$  cells per ml sediment (Fig. 10b), which is on the lower end of the range reported from other coral reef sediments (Sorokin 1974, Moriarty et al. 1985, Hansen & Skilleter 1994, Uthicke 1994, Torrèton et al. 1997). It is likely that bacteria counts are relatively low due to the low organic carbon values, because there is usually a positive correlation between these two parameters (Torrèton et al. 1997, Uthicke unpub. data). Particularly high bacterial numbers were found directly after cyclonic flood events in the area, however, as for sediment nutrients, we cannot resolve a causal relationship between the two factors.

The microalgal numbers in the sediments (Fig. 10a) confirmed that benthic diatoms constitute the bulk of the autotrophic biomass with about  $10^6$  cells per ml of sediment.

Similar to the bacterial biomass and total organic carbon, all parameters that express the production of the microalgal community [community net- and gross-production, photosynthetic capacity ( $P_{max}$ )] were 50 to 60% lower during the winter months compared to all sampling months in the summer (Table 15). For logistic reasons, the

production measurements were only performed at Great Palm Island, thus a spatial comparison is not possible. During the whole study period the microbenthos community was strongly autotrophic with production to respiration (P/R) ratios between 2.8 and 4.4. The monthly averages for net-carbon fixation ranged from 250 to 790 g C m<sup>-2</sup> d<sup>-1</sup>. The extrapolated annual community carbon fixation is approximately 170 g C m<sup>-2</sup> for the sediment communities on studied the reef flat at Great Palm Island. This value is similar to the net-community production on Ningaloo Reef, Western Australia (210 g C m<sup>-2</sup> a<sup>-1</sup>; Masini 1990) and on sediments of Lizard Island, northern GBR (70 to 350 mg C m<sup>-2</sup> d<sup>-1</sup>, <sup>14</sup>C technique, Moriarty et al. 1985). Higher values were measured on some atolls (430 to 1330 g C m<sup>-2</sup> a<sup>-1</sup>, Sournia 1976; 300 g C m<sup>-2</sup> a<sup>-1</sup>, Sorokin 1978). On shallow sediments of Davies Reef, central GBR, community net-production was found to be negative (P/R < 1), but on deeper sediments (16-26 m), positive production rates between 40 and 180 mg C m<sup>-2</sup> d<sup>-1</sup> were measured (Hansen et al. 1987). Low community net-production values and P/R ratios close to unity were found at One Tree Island, southern GBR (-3 to 50 mg C m<sup>-2</sup> d<sup>-1</sup>, Johnstone et al. 1990). However, Uthicke & Klumpp (1998) suggested that Johnstone et al.'s low values were not caused by low primary production but by a high proportion of this production being directly assimilated by bacteria and infauna.

Benthic community structure of nearshore coral reefs has been described to be different to those of coral reefs further offshore (Morrissey 1980, Done 1982, Klumpp *et al.* in press, McCook *et al.* 1997). The high abundance of large Fucales in certain zones on nearshore reefs of the GBR has been quantified by Morrissey (1980), Martin-Smith (1993), Vuki & Price (1994), and Schaffelke & Klumpp (1997). All three study reefs had distinct zones with a high biomass of macrophytes. In these zones 59 conspicuous macroalgae and seagrass taxa are identified (Schaffelke & Klumpp 1997). Large Fucales were particularly abundant and we measured high production rates for the dominant species, *Sargassum baccularia*.

The areal net-production of *Sargassum baccularia* stands was between 0.4 and 3.0 g C m<sup>-2</sup> day<sup>-1</sup>, reflecting seasonal changes of both biomass and biomass specific net production (Schaffelke & Klumpp 1997). Our data were in a range similar to production rates of other tropical *Sargassum* species (Morrissey 1985, Klumpp *et al.* in press) and also of coral-reef epilithic algal communities (EAC) measured over a large spatial scale on the GBR with the same technique (Klumpp & McKinnon 1989, 1992). An average EAC production of about 0.4 g C m<sup>-2</sup> day<sup>-1</sup> was measured on the inshore Pandora Reef (calculated from data in Klumpp & McKinnon 1992); this value is equivalent to the low winter production rates of *S. baccularia*. These results imply that the general view that EAC, and in particular turf algae, are the most important primary producers on coral reefs (eg. Larkum 1983) may not be applicable to nearshore fringing reefs with abundant macrophytes.

After fertility in late summer, nearly the entire biomass of the *Sargassum* beds is shed (Martin-Smith 1993, Vuki & Price 1994, Schaffelke pers. obs.) and enters the detrital cycle. In autumn, accumulations of floating *Sargassum* thalli are often observable as 'rafts' in inshore GBR waters. The biomass of the annual 'bloom' of ephemeral algae in spring (Rogers (1997, Schaffelke & Klumpp 1997) may have a similar fate. High biomass is accumulated for a period of about ten weeks, then the algae disappear and presumably disintegrate (pers. observations, Klumpp *et al.* in press).

Coral reefs with a high cover of large Phaeophyta have been regarded as detritus-driven ecosystems (Crossland *et al.* 1984, Hatcher 1983b, Marsh 1976). The trophic structure of

nearshore coral reefs, at least in the well defined macroalgal zones, may be similar to that of temperate kelp beds. About 90% of macroalgal biomass is recycled through detrital pathways in these temperate systems (e.g. Mann 1982). In contrast, on many offshore coral reefs, where grazing pressure by herbivorous fish is high enough to prevent substantial algal stands (McCook 1996), 50 to 70% of plant biomass is directly consumed by grazers (Hatcher 1982, Carpenter 1986, Klumpp & Polunin 1990, Polunin & Klumpp 1992). On nearshore reefs of the GBR, a high turnover of macrophyte biomass, due to the continuous and seasonal disintegration of tissue, may result in high fluxes and high availability of detrital compounds in the water column and the sediments.

### **Method assessment and recommendations**

In the present study we measured a suite of direct and proxy parameters at four nearshore sites to detect seasonal or inter-reefal differences in nutrient availability. Direct measures for nutrient availability are water column and porewater nutrients, although the latter are also influenced by bacterial activity, and nutrients in macroalgal tissue. Although the connection between nutrient availability and the proxy parameters is still largely unknown it may be assumed that higher nutrient availability results in a higher production of photoautotrophic biomass. The following parameters are directly generated by autotrophic organisms: sediment pigments, diatom numbers, microphytobenthos production, *Sargassum* production. The proxy parameters that depend on both nutrient availability and autotrophic biomass are: particle deposition, bacteria numbers, C/N ratio in the sediments, and nutrients in macroalgal tissue.

We detected statistical differences in all parameter groups between reefs, and some parameters between seasons. The main trend our data indicated was that the nutrient availability was highest at Brook Island and lowest at Great Palm Island. The directly measured nutrients in the water column showed a very high variability on all scales (between replicates, sites, reefs, months). The statistical differences between reefs and seasons detected in the dissolved nutrient parameters ranged from 21 to 83% of the respective maximum values, and the coefficient of variance was higher than 100 for most dissolved nutrient species. Although differences between reefs and seasons were detected (data in section 4.1.1), the use of water column nutrients is suggested to be too costly and too variable to be employed as indicators for changes over time scales of years to decades. Only one species ( $\text{NH}_4$ ) of the porewater dissolved nutrients showed a statistical difference between reefs. The sediment quality parameters, except for phaeophytin, and the *Sargassum* tissue nutrients were significantly higher at Brook Island than at Great Palm Island. The statistical differences we detected between the means of these parameters ranged from 14 to 36%, and the coefficient of variance was less than 60 for all parameters. Hence, the integrative parameters showed a much lower variability and may be considered a parameter more robust with regard to biological patchiness and methodological error. Statistically significant differences between reefs or seasons were obtained with fewer replicate samples for the sediment parameters and *Sargassum* tissue nutrients compared to water column nutrient concentrations.

In many parts of the world increased nutrient inputs have caused eutrophication of waterbodies. Eutrophication has been defined as a sequence of stages (GESAMP 1990), involving increased primary production that leads to higher availability of organic material. This may cause changes in benthic community composition as well as changes in biochemical cycles due to accumulation of organic material in the sediments. In serious cases of eutrophication, benthic anoxia was observed with severe repercussions

for the ecosystem as a whole (Justic 1987, Koop et al. 1990). The work of Alongi (1989), Brunskill et al. (2002), and Brunskill (unpub. data) in the Herbert River region indicate distinct proximity-to-land signals in both sediment organic carbon and nitrogen. In the future, continuing anthropogenic nutrient inputs may result in increased primary production and increased availability of organic material in the coastal zone. We suggest sediment organic carbon, nitrogen, and bacteria numbers to be suitable indicators to detect long-term changes in the trophic status of the GBR coastal zone, as they were the most robust proxy parameters for nutrient availability in the present study.

Algal tissue nutrients have been used as sensitive bioindicators for nutrient availability in short-term bioassays with uniform plant material (Lyngby 1990, Lyngby et al. 1994, Jones et al. 1996, Fong et al. 1998). To obtain meaningful results using of field collected material, however, tissue nutrient levels have to be supported by measurements of production or growth, because the nutrient stores are dynamic and are quickly metabolised to produce new biomass (Schaffelke & Klumpp 1998a). This would make this variable potentially too costly for routine use.

The measurement of primary production of selected organisms is a useful indicator for nutrient availability, if measured over at least 24 h periods, like in the present study, to accommodate metabolic variability due to changes in net photosynthesis and respiration. Primary production, however, is a rather costly variable to measure and sufficient replication on a temporal and spatial is difficult to attain. Modern techniques such as pulse amplitude modulated (PAM) fluorometry enable instantaneous measurements of production, however have to be carefully calibrated against other techniques to yield ecologically meaningful data (Cunningham et al. 1996, Dennison et al. 1997).

The long-term chlorophyll monitoring program in the GBR lagoon (since 1992, Brodie & Furnas 1992, Steven et al. 1998) combines cost effectiveness with a reasonably sensitive indicator of nutrient availability. However, temporal trends in chlorophyll concentrations from an existing dataset were not detected over the past 20 years in the central midshelf GBR lagoon, due to the high temporal and spatial variability of this parameter (Brodie et al. 1997). This may be alleviated by using shorter sampling intervals (one week), which has been possible so far only for one cross-shelf transect. Gabric et al. (1998) and McEwan et al. (1998) combined chlorophyll monitoring with satellite imagery and mathematical modelling and were able to show that inner shore areas of Moreton Bay are strongly affected by point-source wastewater discharges, and their hindcasting model suggests a ten-fold increase of algal production since European settlement.

The increased growth for several weeks of fringing reef macroalgae after exposure to short nutrient spikes (Schaffelke & Klumpp 1998b) indicates that monthly or even weekly protocols of monitoring chlorophyll and nutrient concentrations in the water column may miss key events of nutrient pulses e.g. during the wet season. A yet-to-be-developed biological system, more useful to indicate changes in water quality over time scales from years to decades, would integrate nutrient availability over longer periods and provide clearer indications of the consequent changes in benthic communities

Preliminary analyses of large-scale survey data suggest a relationship between soft coral (De'ath & Fabricius 2000) and macroalgal (L. McCook, AIMS, in prep.) community structure and distance from the coast and distance to river mouths. Whether other



organisms are influenced in the same way is subject of current studies, which involve comprehensive analyses of survey data in conjunction with environmental data (ongoing CRC Reef research). Although biological monitoring is a costly endeavour, results of such spatial analyses may be used to improve the effectiveness of programs already in place.

### **Synthesis and outlook**

Although this study was not primarily designed to investigate differences between reefs as a function of distance from the coast (and thus of potential anthropogenic inputs), the consistency of lower nutrient values in conjunction with lower sediment quality data at the island furthest away from the mainland (Great Palm Island) suggests that such a gradient exists.

A cross-shelf gradient has also been recognised for a range of variables indicating nutrient availability (nutrients: Furnas et al. 1997, chlorophyll *a*: Brodie et al. 1997,  $C_{org}$ : Alongi 1989, Gagan et al. 1987, Brunskill et al. 2002, Brunskill unpub. data). This emphasises that the material exported into the coastal zone will most strongly affect the ecosystems of the coast itself and of the nearshore islands.

In this study, most variables indicated a higher nutrient availability at Brook Island compared to the sea-ward site at Great Palm Island, with the two Fantome Island sites being intermediate. We suggest that this is the result of:

- the greater distance of the Great Palm Island site to the nutrient-rich coastal mixing zone close to the mainland; and
- the more frequent inundation of the Brook Islands with Herbert River water due to the north-ward transport of flood plumes.

Flood plumes have been identified as the major means by which terrestrial material is exported to the GBRWHA. These flood plumes are composed of freshwater, dissolved and particulate nutrients, organic compounds, and other associated contaminants (e.g. Devlin et al. 2001). There are significant gaps in the knowledge of the interactive effect of the three main components of flood plumes (nutrients, particles, freshwater) on inshore benthic organisms. The impact of flood plumes on benthic communities can be classified as a combination of three factors:

- short-term (days) spikes in dissolved inorganic and organic nutrients;
- medium-term (days to weeks) decreases in salinity; and
- long-term (weeks to months) increase in suspended solids (particulate organic matter and sediment).

The expected effects of flood plumes on the biota in the GBR coastal zone are accordingly:

- immediate effects, such as the mortality of some groups (e.g. corals killed by fresh water, Van Woesik et al. 1995), and the proliferation of others (e.g. diatoms, Revelante & Gilmartin 1982);

- medium-term effects, such as the increased growth of macroalgae in response to nutrient spikes (Schaffelke & Klumpp 1998b, Schaffelke 1999a, Russ & McCook 1999); and
- long-term effects, such as replacement of sediment- or freshwater-sensitive assemblages by more persistent taxa.

A number of experimental studies from the GBR region have addressed the nature and magnitude of potential effects of single components of terrigenous run-off on benthic biota. Increased concentrations of dissolved inorganic nutrients increase the growth and productivity of different macroalgae (Schaffelke & Klumpp 1998a, b; Schaffelke 1999a) and of microphytobenthos (Uthicke & Klumpp 1998), or decrease the recruitment success of hard corals (Ward & Harrison 1997). Increased supply of ammonium also increased the number of zooxanthellae in corals and giant clams, the ecological effects of this remain obscure (Hoegh-Guldberg 1994, Ambariyanto & Hoegh-Guldberg 1997). Suspended particles increase the growth of some macroalgae (Schaffelke 1999b) and corals (Anthony 1999, Anthony & Fabricius 2000.), although accumulated sediment deposits decrease the growth and recruitment of corals (Dodge & Vaisnys 1977, Bak 1978, Rogers 1990) and of some inshore macroalgae (Umar et al. 1998).

It is assumed that sediment carried by run-off is not transported far beyond the coastal fringe, ie. to the 20 m isobath (sedimentology data: Larcombe & Woolfe 1999, biomarkers: Currie & Johns 1989). Studies on turbidity and sediment transport on the inner shelf of the Central Section of the GBRWHA have shown that very little net sediment accumulation occurs and advocates that coral reefs have been exposed and have adapted to high turbidity since ~ 5000 years (Larcombe et al. 1995, Woolfe & Larcombe 1998, Larcombe & Woolfe 1999).

These studies however, have not considered;

- fine sediment accumulation at a reef or single coral colony scale, facilitated by a water flow baffling effect of the corals (Woolfe & Larcombe 1998); and
- the composition of the sediment, especially the organic and nutrient content. Risk et al. (1994) found organic carbon from terrestrial origin in corals up to 110 km offshore, which indicates that fine particles may indeed be transported over larger areas across the shelf.

There is a large body of evidence showing that suspended solids in the GBR coastal are high in organic content. A mass balance study showed that most of the organic carbon exported by the Herbert River is transported through the Hinchinbrook Channel into Rockingham Bay, additionally mangrove detritus is exported from Hinchinbrook Channel (Alongi et al. 1998, Wolanski et al. 1998). During mixing processes in estuaries, organic aggregates of fine sediments are formed by microbial colonisation (Ayukai & Wolanski 1997, Wolanski et al. 1997). Also, planktonic biomass stays in the water column as detrital particles, the amount of which is possibly enhanced after nutrient-induced plankton blooms. The bulk of the fine suspended matter in Bowling Green Bay and Lizard Island lagoon was of unidentified origin and appeared to be highly processed and rich in bacteria (Currie & Johns 1988). Suspended solids may remain and be transported in the coastal zone for periods of weeks to months due to recycling and resuspension processes (Wolanski 1994, Furnas et al. 1995). Temporarily deposited fine particles may repeatedly smother benthic organisms, potentially causing damage by

anoxia or depletion of light or nutrients. The smothering by particles rich in organic compounds and subsequent bacterial colonisation is assumed to be much more detrimental than by sediment per se (Hodgson 1990).

Reefs were, since geological times, subject to natural cycles of flood, storm, and high temperature events and biological disturbances such as crown-of-thorns outbreaks (Done 1997). These cycles on a decadal scale promoted the establishment of resilient, adapted benthic communities (Done 1997). Veron (1995) described particularly species-rich coral communities in very turbid coastal waters. However, since white settlement the quality of flood events may have been modified by increased concentrations of nutrients and particles in land run-off. Resilience to disturbance, hence, may be limited to a certain threshold when communities cannot recover quickly enough before the next disturbance event strikes (Done 1982). In such cases the benthic communities change their species composition drastically or even collapse entirely (Smith et al. 1981, Done 1982). Especially slow growing organisms, such as large *Porites* colonies may be incapable of recovering to their previous state after disturbance (Done 1982, Van Woesik & Done 1997).

Probably the largest problem in assessing effects of land run-off and impaired water quality on the nearshore benthic and pelagic communities is the unknown carrying capacity of the GBR lagoon to buffer the cumulative inputs. Physical dilution and biological transformation processes still effectively remove nutrients, particles, and other contaminants out of the water column, however, with every molecule that is exported into GBR waters, the nutrient stocks are likely to slowly increase (Furnas et al. 1995).

To date, science has been unable to prove that large-scale changes in the nearshore areas of the GBR have occurred. This is mainly due to the lack of long-term data series, that permit the delimitation of natural variability and anthropogenic impacts. Nevertheless, there are enough examples on hand from other geographical regions to illustrate that environmental changes did and will occur (GESAMP 1990). The implementation of every measure possible to improve upstream land use practices and waste water treatment is vital to ensure the long-term health of the GBRWHA. We do not know, however, how much change is required to revert impacts of the past and when we could expect to see results of such change (Wasson 1996).

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