Marine Biology 113, 363–372 (1992)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Detrital pathways in a coral reef lagoon

II. Detritus deposition, benthic microbial biomass and production*

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Date of final manuscript acceptance: March 6, 1992. Communicated by G. F. Humphrey, Sydney

Abstract. Coral reef lagoons have generally been regarded as sinks for organic matter exported from more productive reef front and reef flat zones. The object of this study was to examine the importance of detritus as a carbon source for benthic communities in the lagoon at Davies Reef, central Great Barrier Reef. We report the results of seasonal measurements, taken in 1986, of bacterial numbers and production, protozoan numbers, community primary production and respiration in the sediments of Davies Reef lagoon. Deposition rates of organic matter in the lagoon were also measured. Deposition rates (±1 SE) of carbon ranged from 9.2 (±1.5) to 140.7 (±10.3) mg C m^{-2} d^{-1}. Deposition rates were highest in winter and spring, lowest in summer. Rates of bacterial production ranged from 4.7 (±0.2) pmol thymidine incorporated g^{-1} dry wt (DW) h^{-1} in winter to 23.5 (±1.0) pmol thymidine incorporated g^{-1} DW h^{-1} in spring. The number of ciliates ranged from 65 (±10) to 356 (±50) cm^{-3} through the year and the number of large (≥20 μm) flagellates from 38 (±7) to 108 (±16) cm^{-3}. There were no clear relationships between the sediment organic content, detrital input or temperature and the rates of bacterial processes, community metabolism or the standing stocks of microbes in the lagoon. The relative significance of detritus and *in situ* primary production as sources of carbon in the lagoon varied with season. In summer and autumn, detritus was less important than primary production as a source of carbon (4 to 27% of total carbon input). In winter and spring, detritus input became more significant in supply of carbon to the sediments (32 to 67% of the total carbon input). The lagoon does not simply act as a sink for carbon exported from the reef flat. We calculate that only 5% of the net reef flat primary production reached lagoon sediments in summer, but nearly 40% in winter.

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Introduction

The lagoons of coral reefs have generally been regarded as sinks for detritus exported from more productive reef front and reef flat zones (Kinsey 1979, 1985a). Detrital particles derived from turf algal communities, coral mucus and other material may be exported to the lagoon to serve as the major source of organic matter supporting heterotrophic processes (Lewis 1980, Hatcher 1983a, Alongi 1989). However, the early models of coral reef ecosystems (Odum and Odum 1955, Johannes et al. 1972) assumed that water flow is primarily unidirectional with upstream export to downstream communities, and may be too simplistic. Other sources of carbon such as primary production in lagoon sediments may be equally important to benthic communities. At Davies Reef, in the central Great Barrier Reef, there was considerable primary production in lagoon sediments in winter due to the presence of microalgal mats (Hansen et al. 1987). Detritus may be less significant as a source of organic matter to lagoon communities if water flow through the lagoon is rapid with little subsequent sedimentation of the particulate matter (Kinsey 1985a). The relative importance of *in situ* primary production and detrital input to the support of lagoon communities may change with seasonal or hydrographic conditions (Alongi 1989).

This report is the second from a multidisciplinary study of the sediment communities in Davies Reef lagoon. The object of the study was to examine the importance of detritus in food chains in the lagoon at Davies Reef. The study included seasonal measurements of benthic community metabolism and estimates of biomass and production of microbial, meiofaunal and macrofaunal communities, coupled with measures of organic matter deposition in the lagoon. The macrofaunal biomass and estimates of production were reported earlier (Riddle et al. 1990).

Here we present the results of seasonal measurements of bacterial numbers and production, protozoan numbers, community primary production and respiration in

the sediments of Davies Reef lagoon. Deposition rates of organic matter in the lagoon were also measured.

Materials and methods

The investigation was carried out in 1986 at Davies Reef (18°51'S, 147°39'E), a platform reef (6.2 × 3.2 km), in the central section of the Great Barrier Reef (Fig. 1). The windward reef flat is about 300 m wide and oriented towards the predominant southeast trade winds. The semi-enclosed lagoon is largely open to the leeward side. Sampling sites were located in the lagoon behind the windward reef flat and in the deeper water in the mid lagoon.

Sediment traps were constructed as shown in Fig. 2. Sedimented material collected at the base of the trap in a funnel, the end of which was threaded to accept a glass collecting jar. Two sets of paired traps were deployed at each of the sampling sites, placed at mid-depth in the water column. Traps were left for two to four consecutive days on each sampling trip. Collecting jars were exchanged every 24 h by divers. The samples from the traps were filtered onto pre-ashed (480 °C for 12 h) GF/F filters (Whatman), rinsed with distilled water and frozen until further analysis. On return to the laboratory, samples were dried at 60 °C, weighed, decalcified and then reweighed. The samples were decalcified by suspending the filters on stainless steel pins, adding concentrated hydrochloric acid (Aristar) (three drops was usually sufficient), and left for 1 h. The samples were then redried and analysed using a Perkin Elmer CHN analyser. The standard used to generate the curves from which nitrogen and carbon concentrations were extrapolated was ethylenediaminetetraacetic acid (EDTA). Blanks (acid-treated GF/F filters) were subtracted from sample values. Because the sampling intensity for sedimentation rates varied from season to season, to analyse for differences in deposition rates by analysis of variance (ANOVA), the data from two days' sampling from each season were picked randomly so that the ANOVA model was balanced.

Rates of benthic community metabolism were measured as oxygen fluxes in cylindrical chambers enclosing a portion of the sediment surface. A total of six chambers were deployed at each location. The chambers were constructed of perspex with a volume of 3.4 liters and a base area of 283 cm^2. Each chamber had two sampling ports sealed with rubber stoppers through which a syringe needle could be inserted for withdrawal of water samples. Duplicate samples were withdrawn from each chamber for measurement of oxygen concentrations. The changes in oxygen concentration were measured over a 4-h period at midday (10:00 to 14:00 hrs) and at night. Water in the chambers was mixed by gently double syringe pumping prior to sampling. Oxygen concentrations were measured using a polarographic oxygen probe (Syland, Model 4000). The probe was calibrated with air-saturated and deoxygenated (sodium dithionate) seawater. Gross primary production and respiration rates were calculated based on equations of Kinsey (1978). From previous studies of community metabolism in lagoon sediments (Hansen et al. 1987, Hansen unpublished data) production over the midday period represents ca. 50% (range: 44 to 67%) of the total daily production, and estimates of gross daily production were corrected for this. Production and respiration rates were converted from oxygen to carbon equivalents using a PQ and RQ of 1, which is reasonable for these sediments (Kinsey 1979).

Bacterial abundance was determined by direct counts of acridine-orange-stained cells and epifluorescence microscopy (Hobbie et al. 1977). Three sediment cores (0.5 cm inner diameter, 1 cm deep) were collected at each site and preserved in 4% formalin-seawater. The sediments were treated with 10% acetic acid (v/v in distilled water) overnight to dissolve the carbonate sediment, then homogenised for 3.5 min with a laboratory disperser (Ystral, Germany). Cell biovolumes were determined by microscopy. Carbon content was assumed to be 220 fg C μm^{-3} (Bratbak and Dundas 1984).

Bacterial production rates were measured as the incorporation of tritiated thymidine into DNA as described by Pollard (1987). The principle of the procedure is discussed in Moriarty (1986). Isotope dilution curves showed that addition of 3 nmol thymidine was sufficient to overcome any dilution effects (Pollard and Moriarty 1984). To determine the rate of thymidine uptake, five 0.6 cm^3 sediment samples were collected at each sampling site. Each core was incubated in a tube with 48 µl of 16 Ci/mmol [methyl-^{3}H]

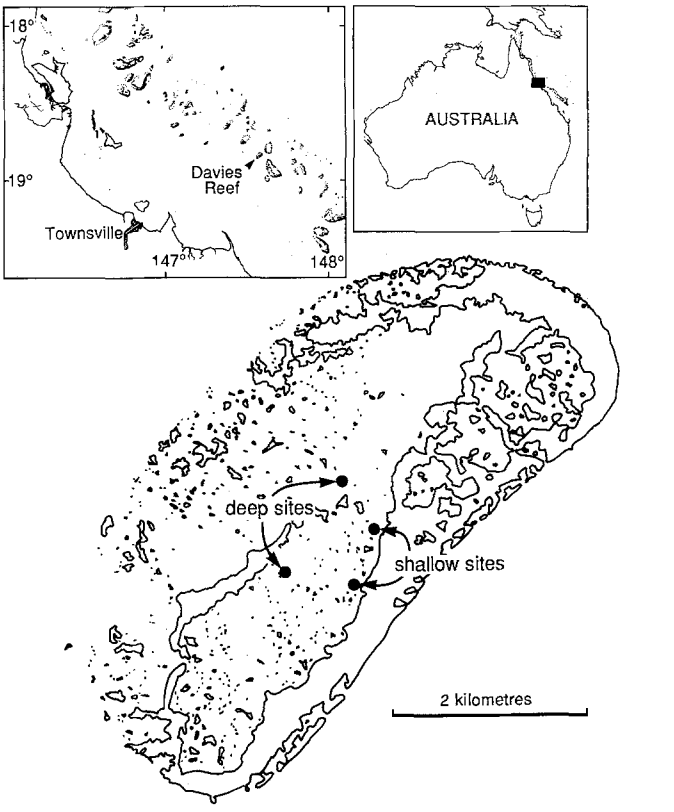

Fig. 1. Location of Davies Reef in relation to the Australian coast and location of sampling sites within Davies Reef lagoon

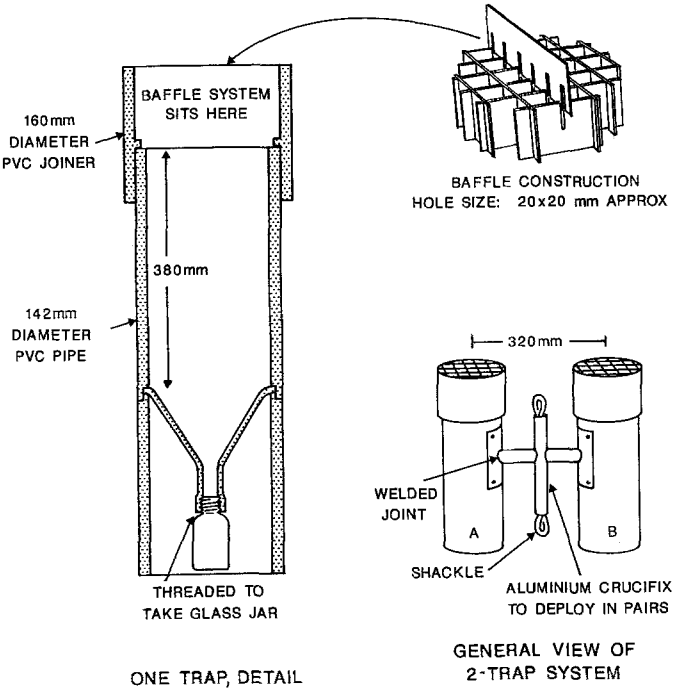

Fig. 2. Design of sediment traps deployed in Davies Reef lagoon

thymidine for 10 min at *in situ* temperature. Incubations were terminated with 10 ml 90% ethanol. Replicates in which ethanol was added immediately after isotope addition served as a control. Sediments were unavoidably disturbed, which may affect incorporation rates (Dobbs et al. 1989), but previous studies have indicated that disturbance effects are not evident for incubation times less than 15 min (Findlay et al. 1985, Moriarty and Pollard 1990). A conversion factor of 1×10^{18} cell divisions mol^{-1} thymidine incorporated was used in calculating bacterial production (Moriarty 1988).

Protozoa were extracted from five replicate cores (1.1 cm inner diameter, 1 cm deep) using the silica gel Percoll (Alongi 1986). Each core was centrifuged at low speed ($490 \times g$) for 20 min in a 30 ml centrifuge tube containing 10 ml of a Percoll-sorbitol mixture. The procedure was repeated three times. Ciliates and flagellates (≥ 20 µm) were counted in a petri dish with the glass bottom lined into 1 cm^2 grids.

Chlorophyll and phaeopigments were estimated from three to five replicate cores of sediment (1.1 cm inner diameter, 1 cm deep) per site by extraction with acetone (90% v/v with water) using the method of Lorenzen (1967). After extraction in the dark overnight at 0 °C, samples were centrifuged to remove particulates. Absorbance of the extracts before and after acidification was measured at 665 and 750 nm on a Varian spectrophotometer.

Total organic carbon and nitrogen were measured from three replicate sediment cores per site. Sediments were dried at 60 °C to constant weight, then ground to a powder. Total nitrogen was determined by combustion of sediments in a Perkin Elmer CHN analyser as described above. Total organic carbon was measured on a Beckman TOC analyser as described by Sandstrom et al. (1985).

Grain size analysis of sediments followed methods described in Folk (1974). Two replicate cores of surface sediments were collected at each site. Percent silt and clay were estimated by sieve and pipette analysis. The sand fraction was dry-sifted and weighed to determine particle size distribution.

Data were analysed using mixed-model nested (hierarchical) analyses of variance (ANOVA). Seasons and habitats (shallow and deep) were treated as fixed factors. We sampled for bacterial production and numbers at four times during a given day; time of day was treated as a fixed factor. For deposition rate of particulate material in sediment traps, the factor of time was the days within each season that the traps were sampled; time was therefore a random factor. All other levels were fully nested within habitats and were therefore treated as random factors. To investigate differences among means *a posteriori*, Student-Newman-Keuls multiple comparison tests (SNK) were used. Cochran's test was used to test for heterogeneity of variances and variance-stabilising transformations were used where necessary (Winer 1971).

Results

General sediment characteristics

Sediment grain size was similar between stations, comprising medium to fine sands (Table 1). The organic carbon and nitrogen concentrations in the sediments were low at all sampling times. Over the year organic carbon values ranged from 2.1 (± 0.01) to 3.2 (± 0.01) mg g^{-1} dry wt (DW). Sediment nitrogen values ranged from 0.5 (± 0.1) to 1.3 (± 0.1) mg g^{-1} DW. Chlorophyll and pheopigment concentrations were very patchy within each sampling site. Water temperatures in the lagoon ranged from 23 °C in winter to 26 °C in summer.

Deposition rates

The dry weight of particulate material deposited seasonally in the lagoon is shown in Table 2. There was large day-to-day variation within each site; the deposition rate varied by up to a factor of 4 over several days. There was no clear difference between rates of deposition in shallow or deep sites.

Rates of deposition of organic carbon in the lagoon at each of the four sites over 2 to 4 d during each sampling season are shown in Fig. 3. Carbon deposition rates (± 1 SE) ranged from 9.2 (± 1.5) mg C m^{-2} d^{-1} in summer to 140.7 (± 10.3) mg C m^{-2} d^{-1} in spring. There was a significant season × time interaction (Table 3). Deposition rates were significantly lower in summer than at other times of the year [SNK: Winter (W) = Spring (SP) > Autumn (AU) > Summer (S)]. The atomic car-

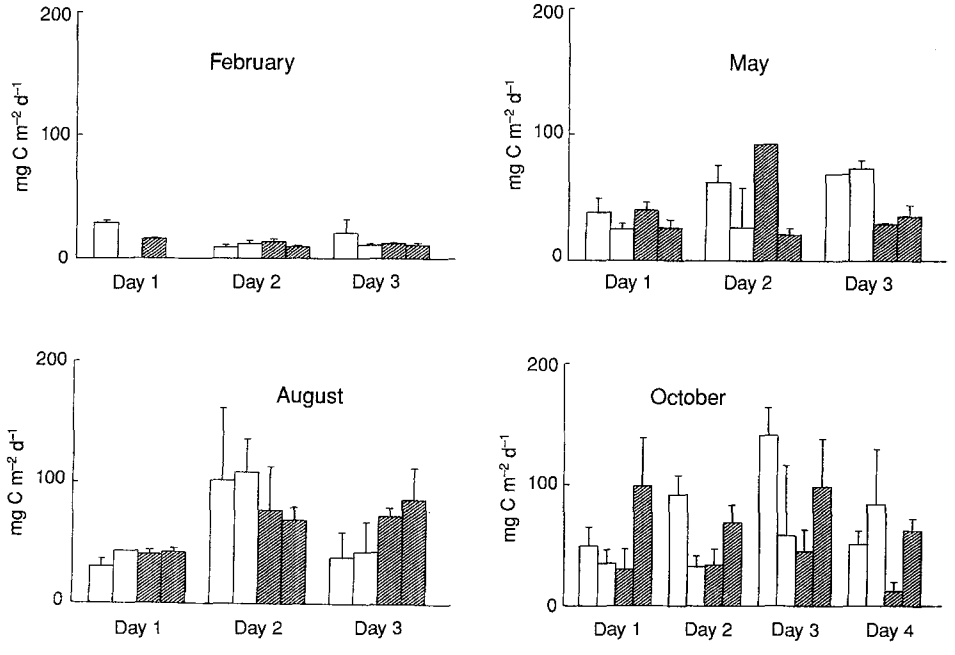

Fig. 3. Deposition of organic carbon in Davies Reef lagoon in shallow (open bars) and deep (hatched bars) sites at different times of year. Vertical bars are +1 SE. Days of sampling and numbers of replicates correspond to those listed in Table 2

Table 1. Sediment characteristics in Davies Lagoon at shallow and deep sites during four seasons in 1986. Means (±1 SE) are shown. DW: dry weight

Season	Habitat	Location	% Sand +gravel	% Silt +clay	Median grain size (μm)	Total organic carbon (mg/g DW)	Total nitrogen (mg/g DW)	Chlorophyll (μg/g DW)	Pheopigments (μg/g DW)
Summer	Shallow	1	96.0	4.0	274	3.2 (0.01)	0.6 (0.1)	2.8 (1.1)	2.4 (1.0)
		2	95.4	4.7	230	2.3 (0.01)	1.0 (0.1)	2.9 (0.3)	0.5 (0.4)
	Deep	1	87.9	12.2	198	2.2 (0.01)	0.6 (0.2)	2.8 (0.9)	0.9 (0.6)
		2	93.5	6.6	209	2.5 (0.01)	1.2 (0.1)	3.0 (1.2)	1.1 (1.0)
Autumn	Shallow	1	95.8	4.2	194	2.9 (0.02)	1.3 (0.1)	7.7 (1.6)	0.2 (0.1)
		2	95.3	4.7	273	2.4 (0.01)	0.8 (0.1)	5.3 (0.6)	0.7 (0.7)
	Deep	1	89.6	10.5	139	2.6 (0.01)	1.0 (0.03)	7.1 (1.5)	0.9 (0.9)
		2	93.4	6.6	181	2.6 (0.01)	0.9 (0.2)	5.7 (0.8)	0.3 (0.1)
Winter	Shallow	1	94.7	5.3	118	2.7 (0.01)	0.8 (0.1)	2.9 (2.1)	6.2 (3.2)
		2	95.2	4.8	293	2.7 (0.04)	0.9 (0.1)	7.8 (1.8)	2.0 (1.0)
	Deep	1	85.0	15.1	180	2.4 (0.02)	1.0 (0.1)	3.2 (2.1)	7.4 (3.2)
		2	93.8	6.3	198	2.6 (0.01)	0.8 (0)	0.8 (0.6)	1.2 (1.2)
Spring	Shallow	1	92.7	7.4	152	2.3 (0.01)	0.5 (0.1)	0.9 (0.9)	8.9 (2.0)
		2	92.2	7.9	221	2.1 (0.01)	0.8 (0.1)	6.9 (2.5)	3.0 (2.2)
	Deep	1	83.9	16.4	194	2.3 (0.01)	0.5 (0.1)	0.8 (0.8)	6.7 (1.3)
		2	93.4	6.6	214	2.5 (0.01)	0.8 (0.1)	1.9 (1.7)	6.4 (1.8)

Table 2. Deposition (g dry wt m^{-2} d^{-1}) of particulate matter at shallow and deep sites during four seasons in Davies Reef lagoon in 1986. Means (±1 SE) are for four traps at each site unless noted otherwise in brackets [ ]. nd: no data. Also shown are atomic carbon:nitrogen values of the particulate matter

Season	Date	Shallow		Deep	
		Site 1	Site 2	Site 1	Site 2
Deposition:					
Summer	11 Feb	1.43 (0.15)	nd	0.94 (0.04)	nd
	12 Feb	0.36 (0.03)	0.54 (0.05)	0.55 (0.07)	0.35 (0.03) [3]
	15 Feb	0.81 (0.02)	0.60 (0.02)	0.73 (0.04)	0.66 (0.05)
Autumn	25 May	2.05 (0.44)	1.55 (0.09)	2.62 (0.73)	1.11 (0.21)
	26 May	3.43 (0.74)	1.08 (0.17)	6.71 (3.20)	1.22 (0.22)
	28 May	3.80 (1.09)	3.29 (1.39)	1.55 [1]	1.41 (0.19)
Winter	12 Aug	1.60 (0.48)	2.39 (0.12)	1.52 (0.01) [2]	1.45 (0.57)
	13 Aug	3.82 (0.19)	2.96 (0.90)	2.41 (0.14) [2]	2.09 (0.43)
	14 Aug	2.24 (1.11)	1.64 (0.68)	2.79 (0.72) [2]	3.00 (0.93)
Spring	23 Oct	1.86 (0.65)	1.39 (0.76)	1.09 (0.36)	5.19 (2.14)
	24 Oct	3.30 (0.51) [3]	1.04 (0.45)	1.23 (0.41)	2.99 (0.72)
	25 Oct	6.70 (1.97)	1.33 (0.94)	1.30 (0.58)	2.70 (0.93)
	26 Oct	2.55 (0.70)	2.81 (1.51)	0.54 (0.34)	2.12 [1]
C:N values:					
Summer		4	3	4	3
Autumn		7	6	12	5
Winter		7	6	6	7
Spring		12	4	7	11

bon:nitrogen values of the particulate material in the traps ranged from 3 to 12 (Table 2).

Community metabolism

There were significant differences between seasons and between habitat types for both gross primary production and respiration rates in lagoon sediments (Table 3, Fig. 4). Rates of gross primary production were significantly higher in summer and autumn than in winter and spring (SNK: S = Au > W = Sp). The rates of respiration were highest in summer and lowest in winter (SNK: S > Au > Sp > W). There was also an effect of habitat with higher rates of respiration and gross primary production at the shallow sites.

Table 3. Summary of analyses of variance of protozoan and bacterial abundances and rates of particulate deposition, respiration, community gross primary production, and bacterial production. Significance levels: * $0.05>p>0.01$; ** $0.01>p>0.001$; *** $p<0.001$; ns: $p>0.05$

Source of variation	Ciliates	Flagellates	Respiration	Gross primary production
Season	ns	*	***	***
Habitat	ns	ns	**	*
Season × Habitat	***	ns	ns	ns
Location (Season × Habitat)	ns	*	ns	**

	Bacterial production	Particulate deposition rate
Season	***	***
Habitat	ns	ns
Time	ns	ns
Season × Habitat	ns	ns
Season × Time	ns	*
Habitat × Time	ns	ns
Season × Habitat × Time	ns	ns
Location (Season × Habitat × Time)	***	ns

	Bacterial numbers
Season	***
Habitat	**
Time	ns
Season × Habitat	*
Season × Time	ns
Habitat × Time	ns
Season × Habitat × Time	ns
Location (Season × Habitat × Time)	***
Core (Location × Season × Habitat × Time)	***
Slide (Core × Location × Season × Habitat × Time)	ns

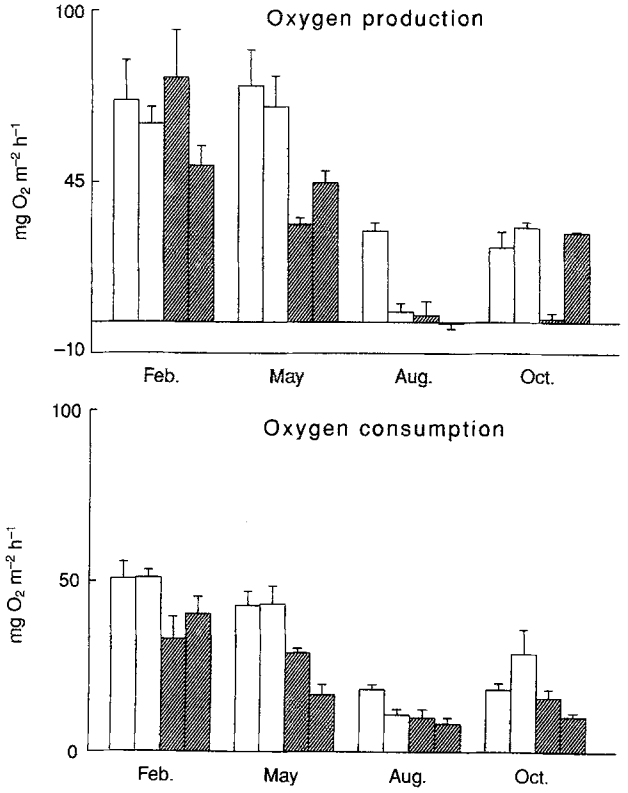

Fig. 4. Rates of benthic community gross primary production (upper panel) and respiration (oxygen consumption; lower panel) in sediments at Davies Reef lagoon during four seasons at shallow (open bars) and deep (hatched bars) sites

Bacterial production and numbers

Rates of bacterial production were significantly different at locations within habitats (Table 3, Fig. 5). Although the variation at the level of individual sites was significant, there was also significant variation in rates of bacterial production related to season. Bacterial production was lowest in winter, highest in spring, and rates in summer and autumn were not significantly different (SNK: Sp > S = Au > W). Rates of bacterial production (±1 SE) ranged from 4.7 (±0.2) pmol thymidine (Tdr) incorporated g^{-1} DW h^{-1} in winter to 23.5 (±1.0) pmol Tdr incorporated g^{-1} DW h^{-1} in spring.

Bacterial numbers showed significant small scale variation at the level of cores and locations within habitats (Table 3, Fig. 6). However, there was also a significant season × habitat interaction. At the shallow sites, bacterial numbers were lowest in winter and summer, and higher in spring and autumn. Bacterial numbers ranged from 4.0×10^8 to 8.9×10^8 cells g^{-1} DW. At deep sites there was no significant difference in bacterial numbers between seasons except in winter when numbers were lower. Bacterial numbers ranged from 3.1×10^8 to 12.0×10^8 cells g^{-1} DW. Neither changes in bacterial numbers nor production showed a consistent pattern related to the daily time of sampling.

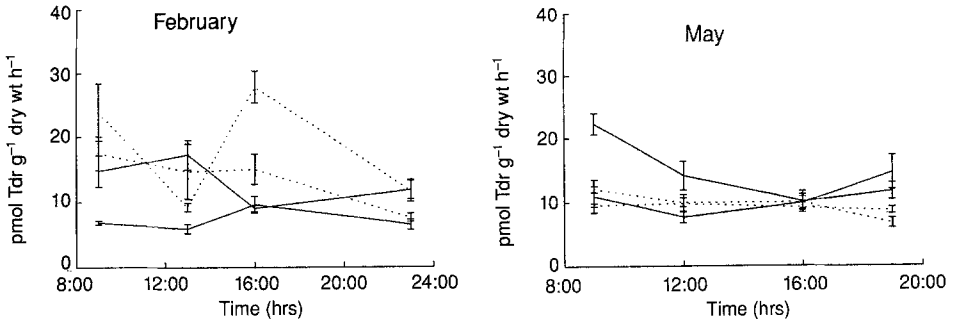

Fig. 5. Bacterial production, measured as thymidine (Tdr) incorporation rates at shallow (continuous line) and deep (dotted line) sites in Davies Reef lagoon during four seasons. Vertical bars are ±1 SE

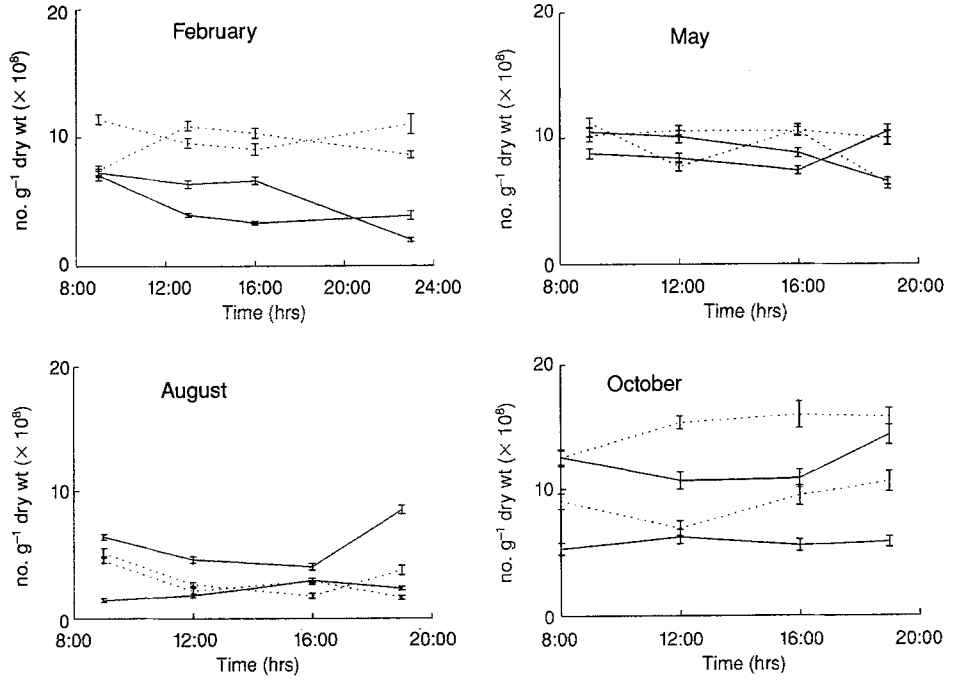

Fig. 6. Diel variation in bacterial densities at shallow (continuous line) and deep (dotted line) sites in Davies Reef lagoon during four seasons. Vertical bars are ±1 SE

Protozoans

Hypotrich ciliates, dinoflagellates and cryptomonads were common at the sampling sites. Nearly all the flagellates were pigmented dinoflagellates. There was a significant interaction between season and habitat for ciliate numbers (Table 3, Fig. 7). At shallow sites, ciliate numbers did not differ significantly with season. At deep sites, there were no seasonal differences in ciliate numbers except in spring, when they were higher than at other seasons. Ciliate numbers did not differ significantly between shallow and deep sites except in spring, when number of ciliates in deep sites exceeded those in shallow sites.

Numbers of flagellates were not significantly different with respect to deep or shallow sites in the lagoon. There were significant differences between seasons; numbers in spring were significantly higher than in autumn. Numbers in other seasons were not significantly different (SNK: Sp > Au, Sp = S = W, S = W = Au).

Discussion

Organic matter input to lagoon sediments

The rate of deposition of organic carbon in Davies Reef lagoon is relatively low when compared to rates of or-

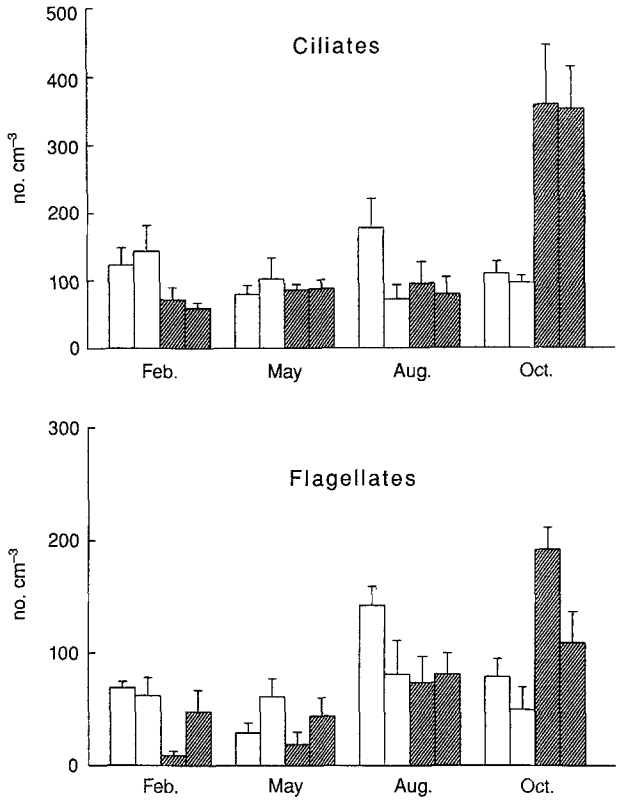

Fig. 7. Ciliate and flagellate densities in Davies Reef lagoon sediments at shallow (open bars) and deep (hatched bars) sites during different seasons. Vertical bars are +1 SE

ganic matter production on the reef. There were large day-to-day variations in deposition rates within the lagoon, but these did not appear to be directly linked to any obvious environmental variables such as turbulence, strong winds or other factors which might be expected to increase the rate of erosion and/or advection of particulate matter from reef flat communities. There was no significant difference in the amount of deposition in shallow or deep sites within the lagoon. Lagoon sites closer to the reef flat did not receive a larger input of detrital material.

It is likely that most of the detritus reaching the lagoon is derived from the turf algal communities, either directly from fragmentation and erosion, or after grazing and export as fecal or other particulate matter. Detritus input from other sources such as from surrounding ocean waters is probably less significant. Plankton advected onto the reef from surrounding oceanic waters are largely consumed at the reef front (Hamner et al. 1988). Coral mucus may be another source of detritus to the lagoon, but its contribution to the total detritus pool may be small due to low rates of fluid mucus production by common corals (Coffroth 1990). The particulate organic matter in the water column at Davies lagoon is dominated by detritus rather than phytoplankton (Roman et al. 1990), but direct identification of the detritus is difficult. The bulk of the particulate matter examined in this study was largely amorphous, although some filamentous algae were identifiable.

If much of the detritus is derived from reef-flat epilithic algal communities (EAC), then factors affecting the rate of supply of detritus to the lagoon would be (1) the rate of production of the EAC and (2) its rate of utilisation (e.g. grazing, fragmentation). The amount of detritus sedimenting into the lagoon does not appear to be linked to the periods of peak primary production of the EAC. In fact, deposition rates were significantly lower in summer, when EAC primary production rates are highest (Barnes 1989, Klumpp and McKinnon 1989). However, the rate of grazing on the reef also increases in summer, so that a smaller fraction of the total EAC is available for export from the reef flat in summer relative to winter months. Klumpp and Polunin (1990) estimated that in summer 72% of the net reef flat primary production was grazed by fish and invertebrates, and in winter 42%. This may be a factor affecting the lower deposition rates in the lagoon at Davies in summer.

There are few other measurements of deposition in coral reef lagoons with which to compare the rate of deposition at Davies Reef (review of Hatcher 1983a, Koop and Larkum 1987). Rates of particulate matter deposition at One Tree Reef lagoon in the southern Great Barrier Reef (Koop and Larkum 1987) were over ten times greater (1 500 mg C m^{-2} d^{-1}) than at Davies Reef lagoon. However, the lagoon at One Tree Island Reef is shallow (ca. 6 m) and fully enclosed with an emergent reef crest, which may result in a longer turnover time of the lagoon water and more material being retained within the reef to eventually reach the lagoon sediments.

The average carbon:nitrogen ratio of organic matter in the sediments (3.2) was lower than that of the particulate matter in sediment traps (7.6), which was in turn lower than that of epilithic algal material derived from the reef flat (14; Klumpp and Polunin 1989). The relative nitrogen concentration in the organic matter thus becomes higher as the material settles out of the water column and into the sediments. This suggests that more labile carbon compounds may be rapidly utilised in the detrital material, with the remaining nitrogen compounds composed of largely refractory material that is concentrated as the material decomposes, or that there is an increasing proportion of nitrogen-rich microbiota (Rice and Tenore 1981, Tenore et al. 1984).

The major carbon sources to lagoon benthic communities are detrital import and *in situ* primary production. In Table 4, we summarise carbon inputs at two depths in the Davies Reef lagoon at four seasons. It shows that the sum of carbon input from particulate deposition and gross primary production virtually balance carbon consumption as measured by community respiration. This, coupled with the low levels of organic matter in the sediments, indicates that organic matter reaching lagoon sediments is rapidly utilised. The relative significance of detritus input and benthic primary production in the lagoon changes with season. In summer and autumn, primary production in the sediments represents a much greater source of carbon than does detritus supply. In winter and spring, detritus input becomes much more significant in supply of carbon to the sediments.

Table 4. Comparison of rates (mg C m^{-2} d^{-1}) of detrital deposition, primary and bacterial production, and community respiration at four seasons and two habitats in Davies Reef lagoon in 1986. Conversion factors for calculation of daily rates of bacterial and primary production are discussed in "Materials and methods". Means (±1 SE) are shown

Season	Habitat	Particulate deposition	Gross primary production	Community respiration	Bacterial production
Summer	Shallow	16 (3)	373 (20)	458 (23)	105 (9)
	Deep	12 (1)	320 (37)	331 (36)	177 (16)
Autumn	Shallow	58 (12)	365 (27)	389 (29)	121 (8)
	Deep	73 (34)	193 (9)	208 (22)	96 (3)
Winter	Shallow	69 (15)	98 (17)	133 (14)	81 (3)
	Deep	66 (7)	32 (6)	84 (13)	46 (3)
Spring	Shallow	78 (17)	161 (16)	214 (35)	240 (19)
	Deep	72 (19)	89 (11)	119 (15)	238 (32)

Table 5. Proportion of net daily reef flat primary production reaching the lagoon as detritus at Davies Reef

	Winter	Summer
Algal net primary production (mg C m^{-2} d^{-1})[a]	1 157	1 851
Detritus deposition rate (mg C m^{-2} d^{-1})	67.5	14
Algal net primary production (g C m^{-1} d^{-1})[b]	521	833
Detritus deposition rate (g C m^{-1} d^{-1})[c]	204	42
Proportion algal net primary production deposited in lagoon (% d^{-1})	39	5

[a] Rates from Klumpp and Pulfrich (1989) and Klumpp and McKinnon (1989)
[b] Lineal rate calculated from estimated reef flat width of 450 m
[c] Lineal rate calculated from estimated lagoon width of 3 000 m

Role of bacteria

It has been previously assumed that detrital input must be important in supporting growth of benthic bacterial populations based on the relative rates of bacterial production and benthic primary production in coral reef sediments (Moriarty et al. 1985, Hansen et al. 1987). In those studies it was found that benthic primary production in lagoon sediments was not high enough to provide the fixed carbon required to support the observed production rates of bacteria. It was suggested that detrital input must make up the balance.

If we assume a conversion efficiency of 50% for the bacteria (Ducklow 1983, Williams 1984), bacterial populations in Davies Reef lagoon sediments, depending on season and location, could require from 54 to >100% of the total daily carbon input for growth and respiration (Table 4). It therefore appears that year round, bacteria are the major consumers of carbon in the lagoon sediments. Without accurate information on conversion efficiencies of bacteria it is not possible to define their role more precisely. Additionally, the relationship between primary productivity and bacterial productivity is not easily calculated (Strayer 1988, Moriarty 1989). When production rates are being compared, the bacterial production should be compared to net primary productivity in a closed system where all production is recycled after accounting for all export or loss to grazers (Moriarty 1989). Information is needed on losses of bacteria due to export or grazing, as well as algal respiration, in order to determine the relationship of bacterial productivity to primary productivity in lagoon sediments.

Relationships between variables measured

There are no clear relationships between the sediment organic content, detrital input or temperature and the rates of bacterial processes, community metabolism or the standing stocks of microbes in the lagoon. Only the rates of benthic primary production and respiration showed a seasonal pattern, with highest rates in summer and low rates in winter. Seasonal patterns of primary production on reefs have been noted in other studies (Kinsey 1985b).

In order to understand the relationships between the microbial and faunal groups and environmental variables, much more detailed studies over shorter time scales within each season are required, as well as direct experimental manipulation. There may be lag times in response of changes in conditions that were not possible to detect in a study such as this one.

Detritus vs grazing pathways on coral reefs

On coral reefs, primary production of epilithic algal communities is the major component of whole reef production (Barnes 1983, Kinsey 1985b) and a major source of fixed carbon to nonsymbiotic consumers (Hatcher 1983b, Russ 1987, Klumpp and Polunin 1990). At Davies Reef in summer, the EAC contributes 28% of total reef gross primary production, but nearly all of the reef flat net primary production (Klumpp and McKinnon 1989). There has been much speculation on the fate of the EAC, whether the major portion of it is consumed directly by grazers or exported from the reef flat as detritus. Previous estimates indicate that from 10 to 80% of the net production of the reef flat communities may be exported as detritus (review of Hatcher 1983b). From the deposition rates measured in this study and primary production values from Klumpp and Pulfrich (1989), we calculate that, in winter, ca. 39% of the net daily reef flat primary production is exported to the lagoon benthos. In summer the amount is much lower, about 5% (see estimates in Table 5).

The amount of detrital material reaching the lagoon benthos is much lower than the total amount of detrital material in the pool of material potentially available for export. From the difference in measured rates of grazing

and primary production of the EAC, Klumpp and Polunin (1990) calculated that 30% of EAC net production in summer and 60% in winter can go directly into the detrital food web; the balance is grazed on the reef flat by fish and invertebrates. However, the actual amount would be much greater, as the grazed material is not totally assimilated by consumers and most will eventually find its way into the detritus food web as fecal material. The fate of the remaining material is as yet undetermined. It may be utilised on the reef flat by detritivores and filter feeders or by organisms in the water column over the reef, or be exported from the reef to surrounding waters.

Acknowledgements. We thank the Masters and crews of the R. V. "Lady Basten" and R. V. "The Harry Messel" for their help. We thank P. Daniel and D. McKinnon for field and lab assistance and J. Jeffrey for figure drawing. Contribution No. 642 from the Australian Institute of Marine Science.

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