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Microbial-meiofaunal interrelationships in some tropical intertidal sediments

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ABSTRACT

Interrelationships among microbial and meiofaunal communities were examined for one year at four intertidal mangrove and sandflat habitats in tropical northeastern Australia. None of the microbial and meiofaunal communities correlated with physical factors over the year as densities of most microbial and meiofaunal groups, bacterial productivity and specific growth rates (μ) of bacteria fluctuated significantly over time at each habitat with no distinct seasonality. However, over a tidal cycle, bacterial growth rates were significantly affected by tidal flooding and exposure on the sandflat; bacterial growth rates increased with increasing sediment temperatures upon exposure during daylight. Protozoan and meiofaunal abundances generally did not change significantly over tidal cycles.

There were few significant correlations and no time lags of bacterial growth rates, and bacterial and microalgal (as chlorophyll *a*) densities with protozoans and meiobenthos (including nematode species and trophic groups) over the year or during tidal cycles. In concert with the very high rates of bacterial productivity ($\bar{x}$ = 475 mgC · m^{-2} d^{-1}; range; 45-1725 mgC · m^{-2} d^{-1}) measured in these tropical sediments, the results suggest that protozoan and meiofaunal communities may not be tightly coupled to the dynamics of bacterial and microalgal communities in some tropical intertidal habitats.

1. Introduction

Trophic interactions among benthic microbes and meiofauna are poorly understood. Most benthic research has emphasized the role of bacteria and microalgae as food for meiofauna (see reviews of Hicks and Coull, 1983; Heip *et al.*, 1985). Meiofauna feed primarily on bacteria, microalgae, small detrital particles (Alongi and Tietjen, 1980; Tietjen, 1980; Montagna, 1984) and perhaps protozoa (Hicks and Coull, 1983), but interactions among these organisms are complex and incorporate a variety of mechanisms in addition to predation (Coull, 1973; Lee, 1980; Alongi, 1988b). Competitive and cooperative relationships are known but have been rarely documented (see review of Lee, 1980). For example, Muller and Lee (1977) observed competitive interactions between the nematode, *Chromadorina germanica,* and the hypotrich ciliate, *Euplotes vannus,* when grown on mixed bacterial diets in the laboratory. Alongi (1985) found that laboratory populations of the ciliate, *Aspidisca* sp. and microflagellates were

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either more abundant or unaffected by the presence of meiofauna. It is evident from these laboratory studies that trophic interactions between meiofauna and microbes, particularly with protozoans, has been neglected.

Only Montagna *et al.* (1983) and Montagna (1984) have attempted to relate microbial (bacteria and diatoms) and meiofaunal densities over an annual period and to estimate *in situ* grazing by meiofauna on bacterial and diatom standing stocks. In North Inlet estuary in South Carolina, Montagna *et al.* (1983) found that meiofaunal densities correlated only with diatom abundances in temperate intertidal mud and sand sediments. Depending upon grazing pressure, however, consumers can significantly affect growth rates and turnover of prey populations without necessarily affecting prey standing stock (Valiela, 1984). Moreover, the effects of meiofaunal grazing on bacteria and microalgae can be obscured by interactions between protozoans and meiofauna, even in laboratory microcosms (Alongi, 1985; Alongi and Hanson, 1985). The present study was conducted to address the following question: Is there *in situ* evidence for interrelationships among microbes (bacteria, protozoans and microalgae) and meiofauna in tropical intertidal sediments, either on a scale of weeks to months or over a tidal cycle?

2. Materials and methods

a. Study sites. This study was conducted from April 1985 to May 1986 at Chunda Bay near the Australian Institute of Marine Science (19°17'S, 147°03'E) in tropical North Queensland, Australia. Chunda Bay is part of a larger marine coastal embayment (Bowling Green Bay) and is bordered by mangrove forests with extensive (~15 km^2) sandflats. Tides are diurnal with an annual tidal range of 3.8 m. Mangrove detritus composed of leaf litter, propagules and small pieces of wood and bark, is transported from the adjacent forests and deposited as beach wrack along the northwestern edge of Chunda Bay.

Four intertidal sites were examined. Station 1 was located in the high intertidal zone (*in sensu* Hedgepeth, 1957) among thickets of the mangroves, *Avicennia marina* and *Ceriops tagal.* The sediment has low water content (generally < 25% by weight) and is flooded only at very high (> 3.3 m) spring tides. Station 2 was located on a low intertidal bank among pneumatophores (breathing roots) of the grey mangrove *Avicennia marina* and near stilt roots of the red mangrove, *Rhizophora stylosa.* Station 3 was situated within the beach wrack described above. Station 4 was located on a sandflat ~1 km southeast of the beach wrack deposits.

b. Sampling scheme. Each station was sampled fortnightly initially, then over longer periods of time (2-6 weeks), to coincide with occurrence of low tide at mid-morning. Sampling during the same time of day and tide was considered critical because of possible diel variations and changes induced by tides. Each station was sampled at low tide between 0800 and 1200 h.

To examine the effect of tidal flooding and exposure on microbial and meiofaunal numbers and bacterial growth rates, sediment cores were collected every 3 h over a tidal cycle during daylight (between 0500–1800) on the sandflat (station 4) during austral winter and summer. During each season, two tidal cycles were examined in which either high or low tide occurred at noon.

c. Physical and chemical analyses. At each study site, interstitial temperature (°C), salinity, redox potential (E_h), pH and sediment granulometry were measured from replicate cores taken to a depth of 5 cm using techniques described in Alongi (1987a). Organic carbon and nitrogen, and total phosphorus were also determined from milled, freeze-dried (5 cm) cores. Organic carbon was measured on a BECKMAN Total Carbon Analyzer. Total nitrogen was measured from the same samples on a LECO Model 600 CHN Analyzer. Total phosphorus was measured on a Spectrametrics V plasma emission spectrometer following a perchloric acid digestion of a finely ground sample (Allen *et al.*, 1974).

d. Microbial and meiofaunal analyses. Bacterial numbers were estimated by epifluorescence microscopy (Hobbie *et al.*, 1977) as described in Alongi (1988a). Protozoa and soft-bodied meiofauna were extracted from 3 replicate cores (1.1 cm and 2.64 cm inner diameters, respectively; 5 cm deep) per site using the silica gel Percoll (Alongi, 1986). Briefly, each core is centrifuged at low speed (490 × g) for 20 min in a 30 ml centrifuge tube containing 10 ml of a Percoll-sorbitol mixture (Alongi, 1986). Meiofauna, ciliates and large (> 20 μm) flagellates in the supernatant were counted in a Petri dish with the glass bottom lined into 1 cm^2 grids. A fixed number of grids (n = 15 of 65) were counted randomly and the numbers extrapolated to per m^2. Small (< 20 μm) flagellates were enumerated from a separate 1 ml portion of the supernatant using the method of Sherr *et al.* (1983). Flagellates were preserved in acid Lugol's solution and counted on a haemocytometer. Percoll recovers > 85–95% of the protozoa in sediments (Alongi, 1986). Chlorophyll *a* was extracted from replicate syringe samples (2.64 cm^2 surface area) taken to depth of 5 cm using a 90% (v/v with water) acetone solution and assayed by the spectrophotometric method of Lorenzen (1967).

Bacterial production was measured by the rate of [^{3}H-methyl] thymidine incorporation into DNA (Moriarty and Pollard, 1981; Pollard and Moriarty, 1984; Alongi, 1988a). Sediment cores (0.78 cc) were taken to a depth of 5 cm using 1 ml Terumo syringes with the luer end cut off. Each core was dispensed into a separate, acid-washed test tube with replicate (n = 9) samples per site. Duplicate control samples were killed with 10% sodium-tetraborate buffered formaldehyde. 45–50 μCi of [3H-methyl] thymidine (specific activity: 45-48 Ci · $mmol^{-1}$) with 500 μl of sterile seawater was added to each tube, shaken momentarily to achieve even distribution of thymidine, and incubated under shaded conditions or in the dark at *in situ* temperature

for 10 min. Sample processing was completed following the extraction procedures of Pollard and Moriarty (1984).

Recovery of DNA, measured with ^{14}C-DNA, was 88 ± 7%. Recovery-corrected production estimates were calculated using a conversion factor of 2.0×10^{18} cells dividing · mol^{-1} thymidine incorporated (Moriarty and Pollard, 1981; Pollard and Moriarty, 1984) and the carbon/cell conversion factor of Rublee (1982). Specific growth rate of bacteria, $\mu(d^{-1})$, was calculated by dividing the mean ($n = 9$) bacterial production estimate (mgC · $m^{-2}d^{-1}$) by the mean ($n = 5$) direct-count, standing crop (mgC · m^{-2}) estimate for each of the 16 sampling periods of each station. This results in a mean estimate of bacterial growth rate for each station of each sampling interval over the study period.

Three plastic cores (6.6 cm^2 surface area) were taken for hard-bodied (chitinous) meiofauna to a depth of 5 cm at each site. Each core was preserved in a 1:500 (v/v) buffered seawater formalin (5%) mixture with Rose Bengal (0.5 g · l^{-1}). Preliminary sampling at low and high tide to a depth of 1 m indicated that > 75–90% of the meiofauna was found with the top 5 cm in each intertidal zone. In the laboratory, sediments were passed through a set of two sieves, the top one with a mesh opening of 500 μm and the bottom screen with a mesh size of 45 μm. Animals retained on the 45 μm mesh were enumerated under a dissecting microscope. Nematodes were identified to species level when possible and classified for feeding type by the scheme of Wieser (1953).

e. Data analyses. Differences over time within and between stations in environmental factors, microbes and meiofauna were tested using one-way (for within station tests) and two-way (for between station tests) repeated-measures ANOVA'S (Winer, 1971; Edwards, 1985) with time as the repeated measure. Each ANOVA was followed by a Student-Newman-Keuls (SNK) multiple comparisons test if a significant temporal or station effect was found. Microbial and meiofaunal densities were log $(x + 1)$ transformed and environmental factors were arcsine transformed when homogeneity of variance was rejected by an F_{MAX} test.

Pearson's partial product-moment correlation analysis (Legendre and Legendre, 1983) was used initially to examine relationships among microbes and meiofauna and with environmental factors. However, because no x and y variable combinations tested were significantly correlated with the same third (z) variable, all values presented herein are simple (nonpartial) correlations.

In the correlation analyses, the mean bacterial growth rate values for each site and sampling period ($n = 16$ for each site) were tested against the mean of each of the other variables (also as n of 16). Because of the large number of correlation tests, the probability of a Type I error (rejecting a true null hypothesis) occurring is high. The data were tested for time lags to a maximum period of 8 weeks using the graphical analysis method of Wood and Foot (1981). The significance level for all analyses was 0.05 except where specified.

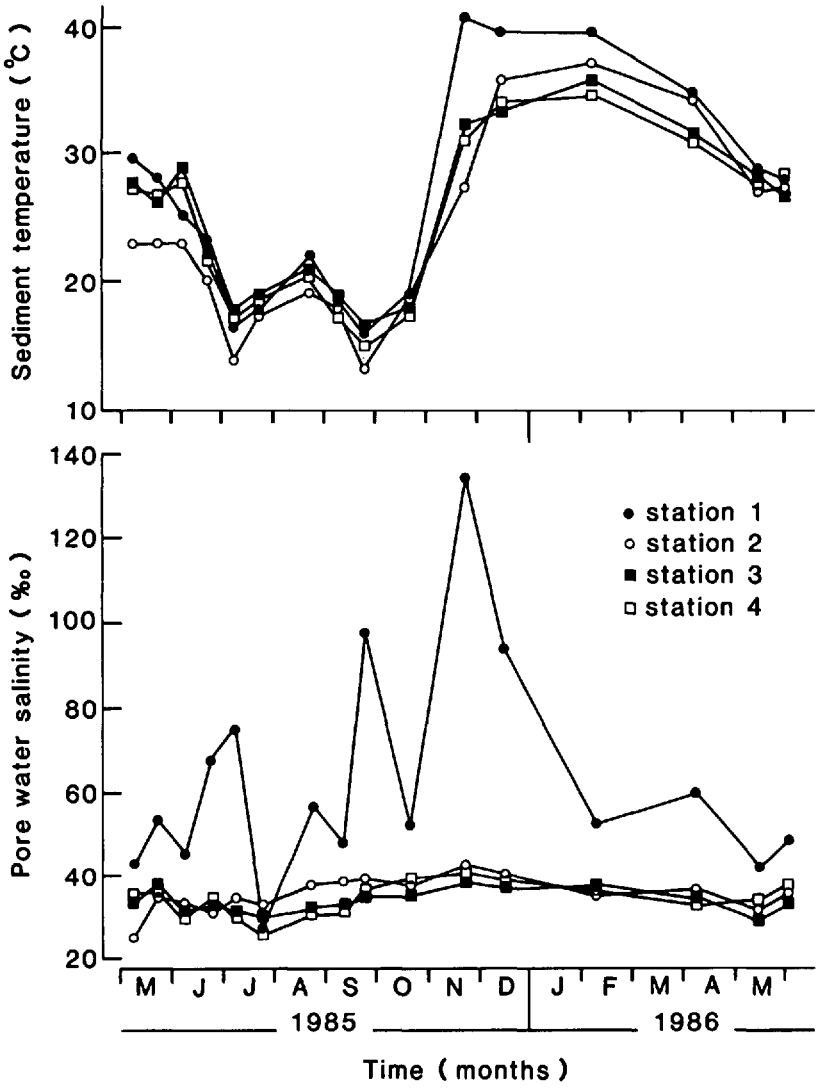

Figure 1. Temporal changes in sediment temperature and pore water salinity at each station.

3. Results

a. Physicochemical factors. Sediment temperatures varied seasonally at each station and ranged from 14 to 30°C during austral autumn and winter (April–September) and exceeded 30°C during austral spring and summer at all four sites (Fig. 1). Pore water salinities fluctuated only in the high intertidal (Station 1) ranging from 27 to 135‰. At the other sites, salinities ranged from 25 to 41‰. Granulometry (grain size, sorting, percent sand, silt and clay), pH, Eh and nutrients (POC, PON, Total P) did not vary significantly with time at any of the four stations (Table 1).

Table 1. Sediment granulometry, pH, Eh, particulate organic carbon and nitrogen, and total phosphorus concentrations in Chunda Bay intertidal sediments during 1985–86 study period. Values depict mean ± 1 standard error with range in parentheses.

Station	Mean grain size (mm)	Sorting Coefficient	% Sand	% Silt-Clay	pH	Eh(mV)	POC(%)	PON(%)	Total Phosphorus ($\mu g/g^{-1}$ DW)
1	0.09 ± 0.002 (0.04–0.11)	1.1 ± 0.13 (0.39–2.6)	74.7 ± 1.4 (58.2-80.4)	25.3 ± 1.5 (17.5–46.2)	7.4 ± 0.1 (6.5–8.0)	+165.4 ± 22.3 (−102–+240)	2.0 ± 0.51 (0.3–8.2)	0.12 ± 0.011 (0.08–0.22)	243 ± 38
2	0.20 ± 0.04 (0.15–0.36)	1.5 ± 0.07 (1.21–2.15)	92.9 ± 0.7 (89.1–97.0)	7.1 ± 0.7 (3.0–10.9)	7.3 ± 0.07 (6.6–7.7)	+193.8 ± 12.7 (+78–294)	1.2 ± 0.08 (0.75–1.95)	0.10 ± 0.006 (0.06–0.14)	168 ± 24
3	0.11 ± 0.03 (0.10–0.13)	0.47 ± 0.02 (0.29–0.60)	97.4 ± 0.5 (90.6–99.3)	2.4 ± 0.6 (0.7–9.3)	7.7 ± 0.09 (6.9–8.2)	+265.8 ± 19.6 (+143–427)	2.2 ± 0.52 (0.4–8.5)	0.097 ± 0.012 0.05–0.22	233 ± 62
4	0.13 ± 0.07 (0.10–0.17)	0.84 ± 0.06 (0.32–1.01)	98.8 ± 0.06 (98.4–99.3)	1.2 ± 0.06 (0.7–1.6)	7.7 ± 0.12 (6.1–8.1)	+271 ± 14.2 (+180–370)	0.63 ± 0.05 (0.32–0.91)	0.055 ± 0.003 (0.03–0.075)	174 ± 14

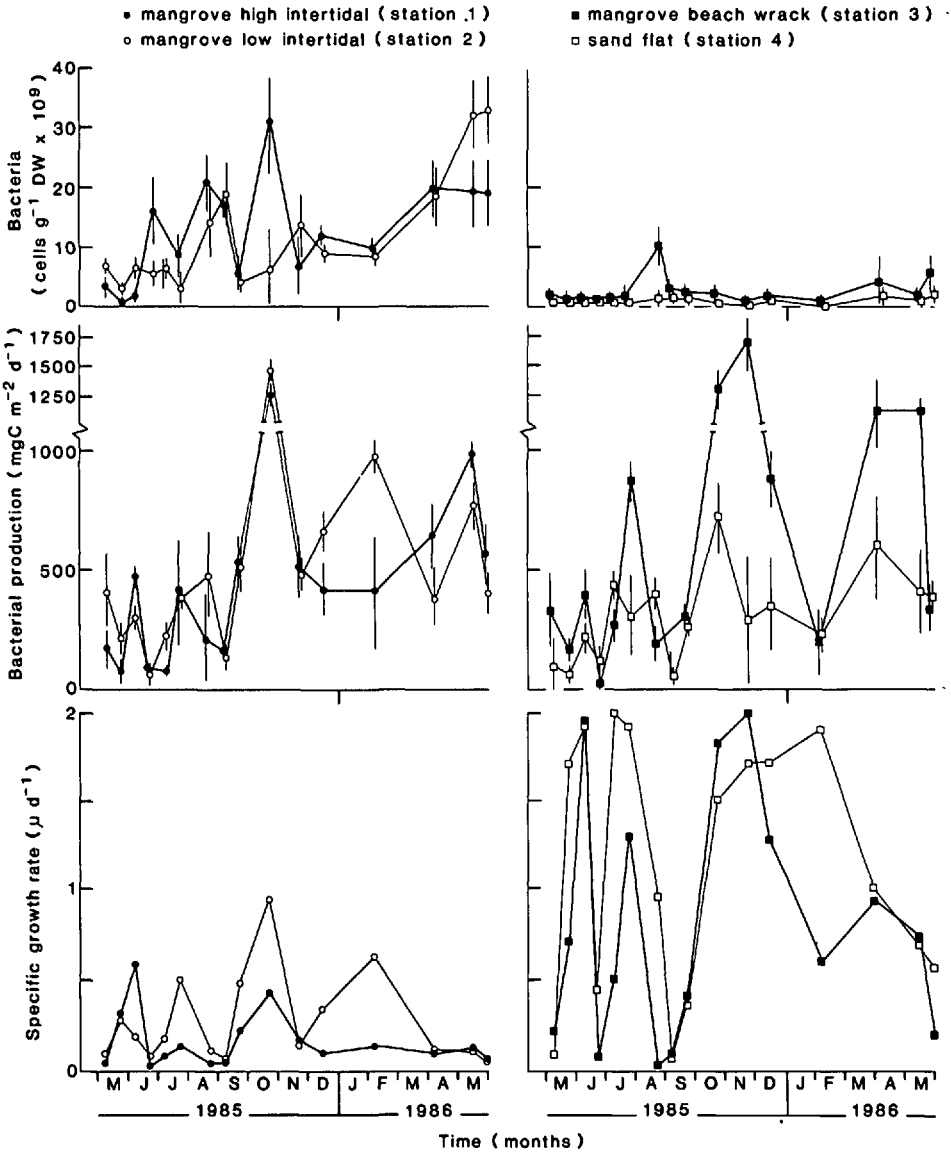

Figure 2. Temporal changes in bacterial numbers, productivity and specific growth rates in sediments at each station. Mangrove stations 1 and 2 are presented in left-hand column from top to bottom; beach wrack and sandflat stations (3 and 4) are depicted in right-hand column from top to bottom.

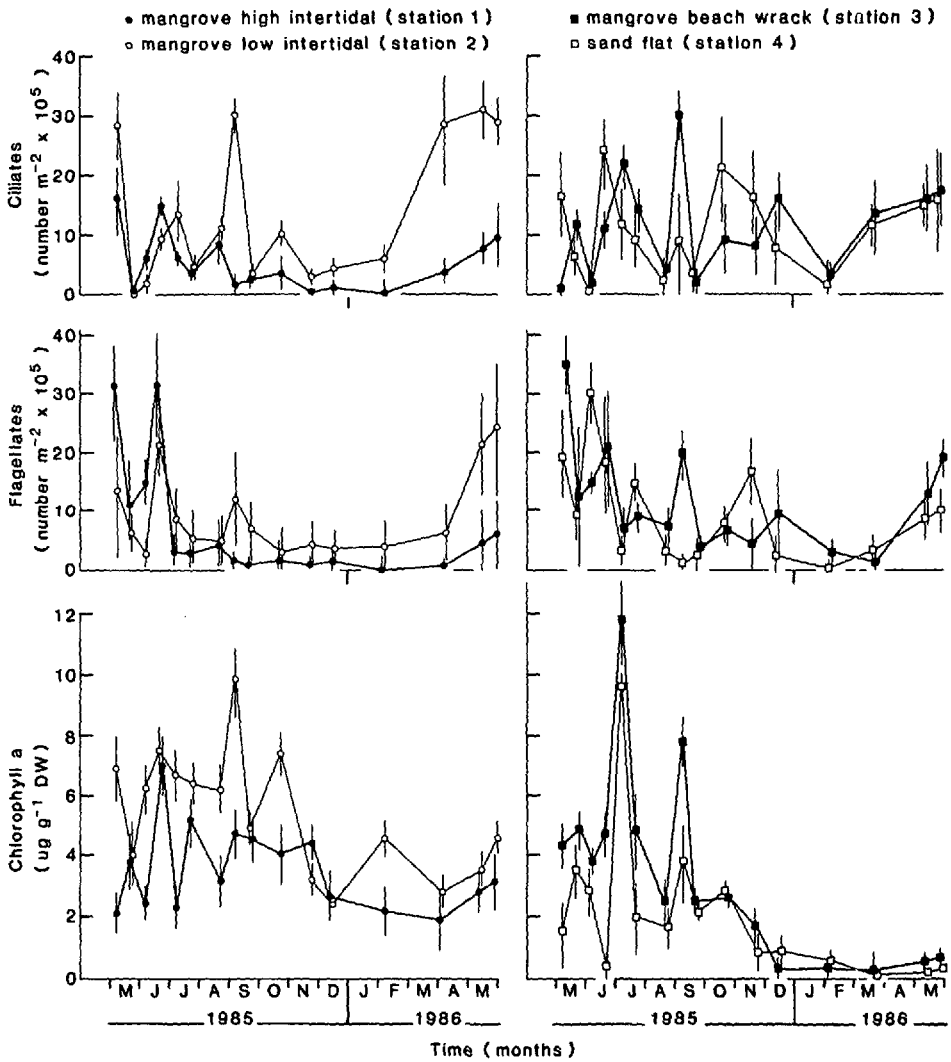

Figure 3. Temporal changes in densities of ciliates, flagellates and chlorophyll *a* in sediments at the mangrove stations (left-hand column; top to bottom) and at the beach wrack and sandflat sites (right-hand column; top to bottom).

b. Community dynamics of microbes and meiofauna. With the exception of bacterial densities at sites 3 and 4 (Fig. 2), bacterial and protozoan numbers (Figs. 2 and 3) bacterial production and growth rates (Fig. 2), and chlorophyll *a* concentrations (Fig. 3) fluctuated significantly over time at each site with no distinct seasonality. Bacterial numbers were significantly greater, and specific growth rates lower, at both mangrove sites (stations 1 and 2) than at the beach wrack (station 3) and sandflat (station 4) habitats. Bacterial production, protozoan numbers and standing amounts of chloro-

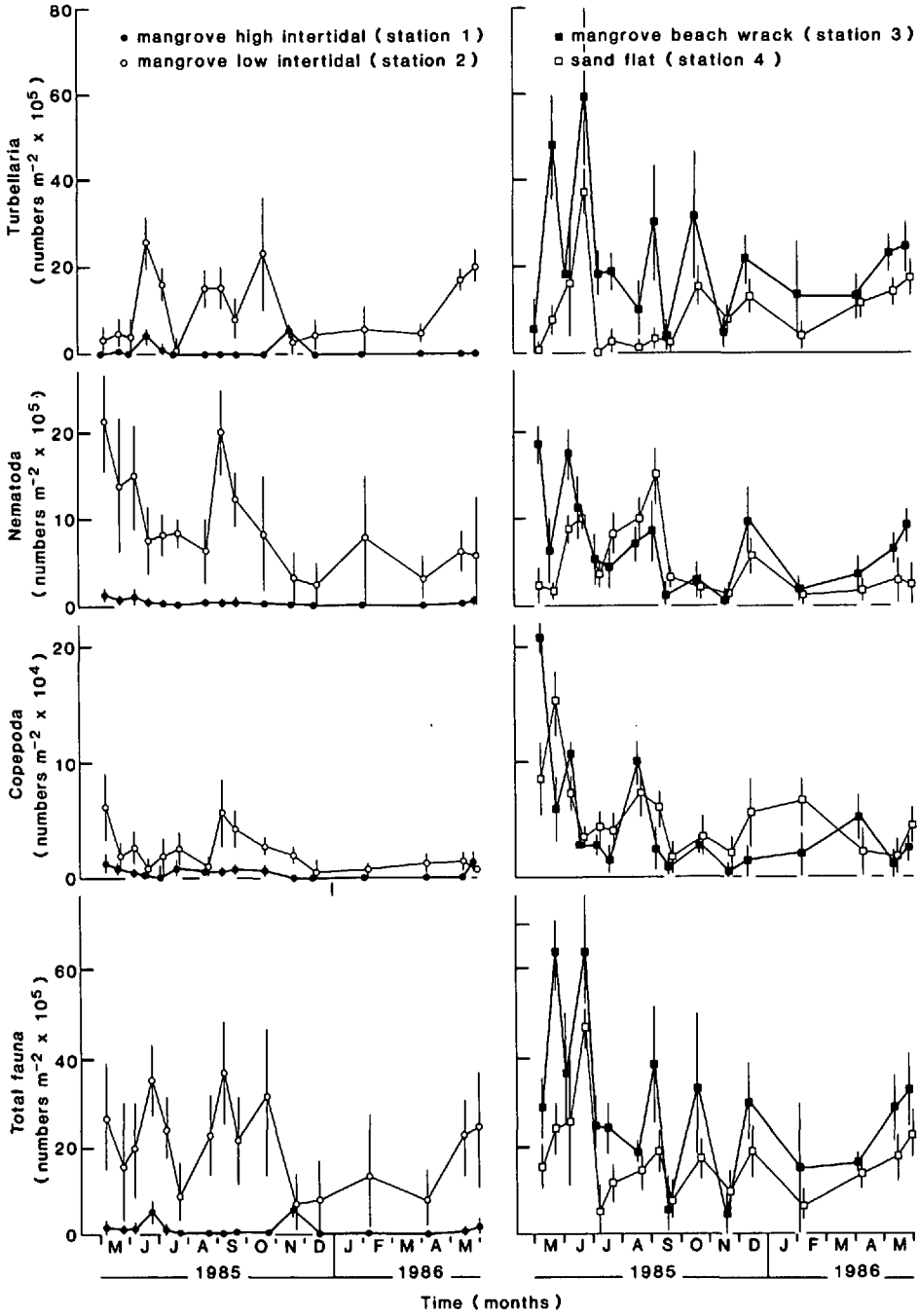

Figure 4. Temporal changes in densities of turbellarians, nematodes, harpacticoid copepods and total meiofauna at the mangrove stations (left-hand column; top to bottom) and at the beach wrack and sandflat sites (right-hand column; top to bottom).

phyll *a* were not signficantly different among sites. There were no significant correlations between microbes and physicochemical factors at any of the four stations. Protozoan densities correlated significantly with bacterial numbers and growth rates only at Station 2; no time lags were found.

Meiofaunal densities also fluctuated significantly over time at each habitat (except for station 1) with highest densities generally occurring in austral autumn and winter, and lowest densities occurring in austral spring and summer (Fig. 4). Abundance of each taxon and of total fauna were not significantly different among the low intertidal habitats (stations 2, 3 and 4) but were significantly less in the high intertidal mangroves (station 1). Meiofaunal taxa and physicochemical factors were not correlated at any of the four sites. There was a distinct lack of significant correlations (with no time lags) between meiofaunal taxa and microbes at all four habitats. Nearly all of these correlations (n = 9 of 12) were among meiofaunal taxa and protozoans.

c. Nematode trophic group patterns. None of the three feeding groups (Fig. 5) or 131 nematode species identified in this study correlated significantly with, or lagged, any of the physicochemical factors. Only at stations 1 and 3 were a few significant correlations (none with time lags) found among microbes and nematode species or trophic groups. At station 1, the dominant species, *Terschellingia longicaudata* correlated positively with bacterial growth rates, whereas the total deposit-feeding fauna correlated positively with bacterial growth rates and inversely with bacterial densities. Within the mangrove beach wrack (station 3), the omnivore/predator, *Oncholaimus brachycercus* correlated positively with flagellates, whereas the total epigrowth-feeding fauna correlated positively with chlorophyll *a*; the total deposit-feeding fauna, comprising 43 species, correlated negatively with bacterial numbers and growth rates.

d. Effect of tidal cycles. In winter on the sandflat, microbial and meiofaunal densities did not change significantly over a tidal cycle (Fig. 6). However, bacterial growth rates nearly doubled from morning (0530 hrs) to early afternoon (Fig. 6 upper graphs) especially when sediments became exposed by noon (Fig. 6 upper right graph).

In summer on the sandflat (Fig. 7), bacterial densities were similarly unaffected over a tidal cycle, but meiofaunal and protozoan densities decreased signficantly when the morning tide receded (0600–0900 hrs) and sediment temperatures approached 40°C (Fig. 7 lower right graph). Bacterial growth rates tripled from day break to mid-morning on the sandflat in summer regardless of tidal state (Fig. 7 upper graphs). When the morning tide was receding (0600–0900 hrs), growth rates quadrupled (Fig. 7 upper right graph) then decreased thereafter upon exposure to hot (40°C) early afternoon temperatures. Combining data from both seasons, the Pearson's correlation between sediment temperature and bacterial growth rates over the tidal cycles was very highly significant (r = 0.86; $P < 0.001$); bacterial growth rates did not correlate

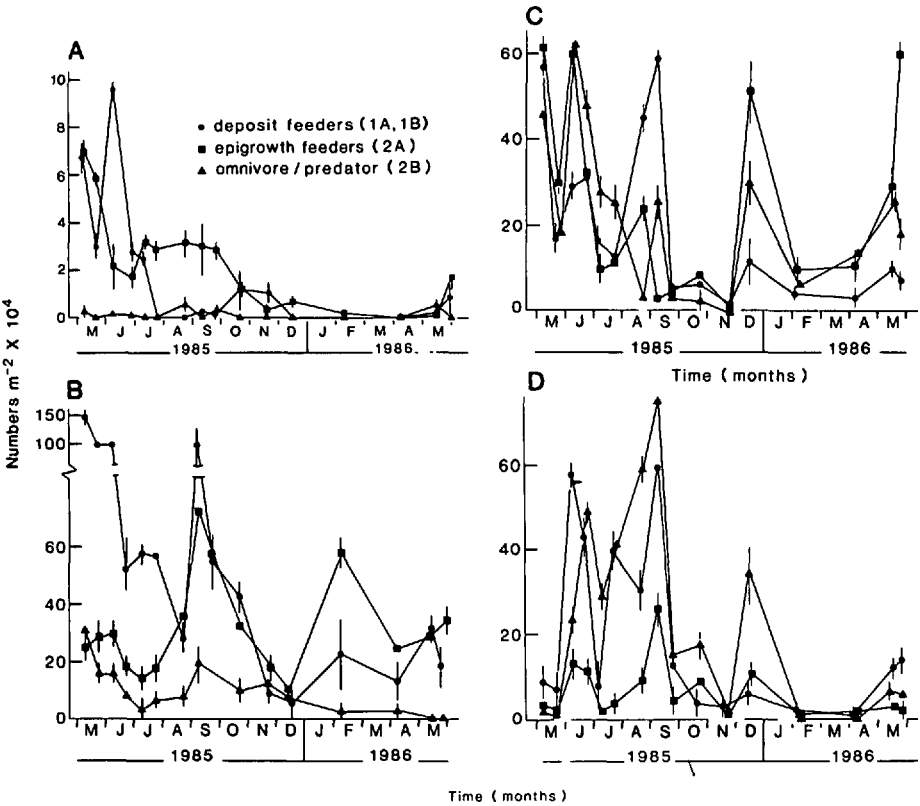

Figure 5. Temporal patterns of the nematode trophic groups at (A) mangrove high intertidal station 1, (B) mangrove low intertidal station 2, (C) mangrove beach wrack station 3 and (D) sandflat station 4.

significantly with any other factor. During both seasons, there were no significant changes in other physicochemical factors or in particulate nutrients over the tidal cycles.

4. Discussion

On a scale of weeks to months and over tidal cycles, there was little evidence to suggest that temporal changes in bacterial and microalgal standing stocks and bacterial growth rates were closely linked to temporal variations in protozoan and meiofaunal densities in these tropical sediments. The few significant correlations calculated for the annual data must be viewed with great caution considering the high probability of Type I errors due to the large number of correlation tests. In addition, the lack of strong correlations among microbes and meiofauna over the annual period were evidently not due to time lags.

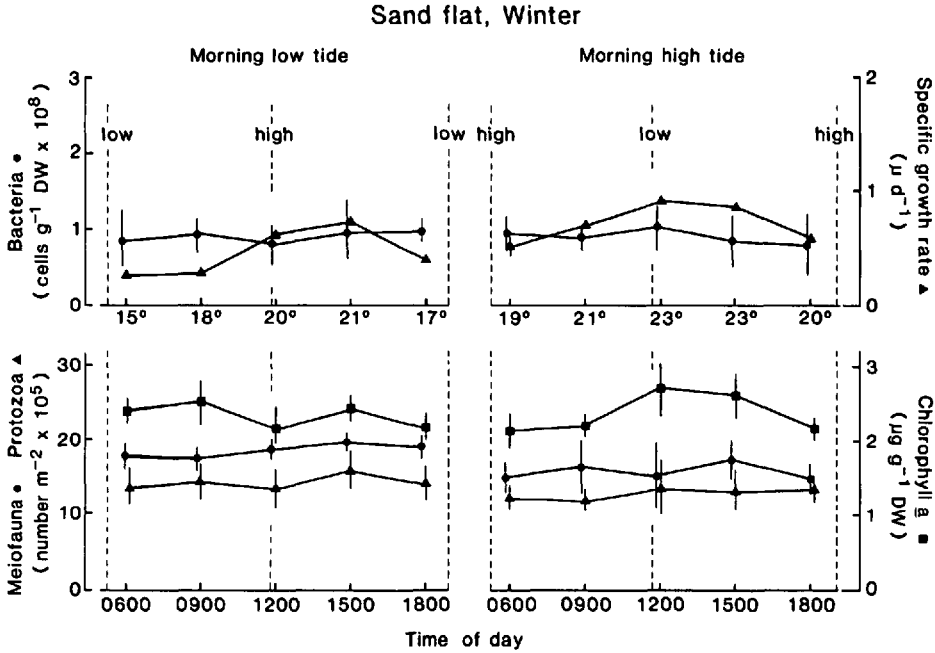

Figure 6. Effect of tidal flooding and exposure in sandflat sediments (station 4) on bacterial numbers (●) and growth rates (▲) (upper left and upper right graphs), protozoan (▲) and meiofaunal (●) densities and microalgal biomass (■) (lower left and lower right graphs) in austral winter. Values for samples taken over a tidal cycle starting at low tide in morning are in left-hand column; right-hand column depicts sample values over a tidal cycle starting at high tide in morning. Sediment temperatures are presented between upper and lower graphs in each column.

Although it is plausible that the lack of significant correlations among microbes and meiofauna was due to sampling intervals longer than their generation times, the data obtained over 3-hour intervals on the sandflat show that changes in tidal state affected only bacterial growth rates. Temperature was the most probable cause indicating that, on a scale of hours, bacterial growth rates in these sediments are affected more by temperature changes associated with tidal flooding and exposure than grazing by protozoans and meiofauna.

In five mangrove estuaries north of this study, Alongi (1988a) similarly found that benthic bacterial biomass and growth rates were regulated primarily by physicochemical factors and by tidal flushing and exposure, not correlating with protozoan and meiofaunal densities. Temperature changes were also cited as the main factor affecting bacterial growth as tidal changes had a significant effect on bacterial productivity in the low intertidal forests.

Further support for the hypothesis that bacterial growth in tropical intertidal sediments is regulated primarily by abiotic factors is provided by the study of Stanley

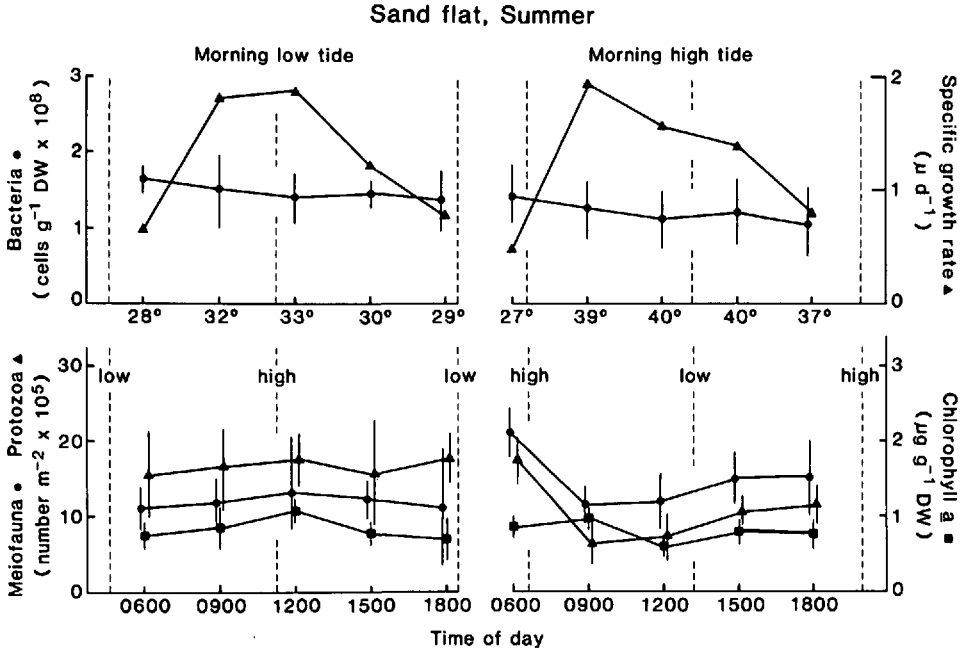

Figure 7. Effect of tidal flooding and exposure in sandflat sediments (station 4) on bacterial numbers (●) and growth rates (▲) (upper left and upper right graphs), protozoan (▲) and meiofaunal (●) densities and microalgal biomass (■) (lower left and lower right graphs) in austral summer. Values for samples taken over a tidal cycle starting at low tide in morning are in left-hand column; right-hand column depicts sample values over a tidal cycle starting at high tide in morning. Sediment temperatures are presented between upper and lower graphs in each column.

et al. (1987). In mangrove sediments at Hinchinbrook Island (ca. 175 km north of Chunda Bay), Stanley *et al.* (1987) found that bacterial growth rates correlated significantly with total dissolved free amino acid concentrations to a sediment depth of 1 m. Flux chamber experiments conducted simultaneously with bacterial productivity measurements revealed that amino acid fluxes could account for between 9 to 38% and 5 to 19% of the nitrogen and carbon required to support the high levels of bacterial productivity (1.0–1.8 gC · $m^{-2}d^{-1}$) measured in surface (0–1 cm) sediments.

Considering the very high rates of bacterial productivity and the close coupling between dissolved nutrients and bacterial growth rates described above in a very similar system, it is plausible that protozoan and meiofaunal communities were not able to affect the dynamics of bacterial and microalgal populations at Chunda Bay. Recent work has indicated that some benthic consumers may not always graze down bacterial populations because rates of bacterial productivity are usually several times greater than maximal ingestion rates of consumers (Alongi, 1985; Alongi and Hanson, 1985; Moriarty *et al.*, 1985; Hansen *et al.*, 1987; Kemp, 1987). For example, in the

laboratory, bacterial growth rates in coral reef sediments were enhanced by protozoans and meiofauna only when twice the natural densities of these organisms were used (Moriarty *et al.*, 1985). Alongi (1985) similarly found that bacterial numbers, productivity and growth rates were little affected by the presence of protozoans or meiobenthos in laboratory microcosms and concluded that the outcome of microbe-meiofauna interactions is dependent upon nutrient factors regulating growth rates of bacteria.

Indeed, in the high intertidal habitat in Chunda Bay where the mean growth rates of bacteria over the study period were slowest (mean $\mu = 0.3$; range = 0.04–1.1; Fig. 2. bottom left graph), nematode deposit feeders correlated positively with bacterial growth rates and inversely with bacterial abundances. However, at the sandflat habitat, where mean bacterial growth rates were fastest (mean μ:1.2; range = 0.21–4.1; Fig. 2, bottom right graph) over the study period, none of the consumer groups correlated with rates of bacterial growth and only copepods correlated with bacterial numbers.

As pointed out by Kemp (1987), the role of protozoans and meiofauna as grazers is likely to be complex and variable between habitats. However, the lack of *in situ* evidence for protozoan and meiofaunal control of microbial communities does not necessarily preclude that meiofauna are not food limited as concluded by Montagna *et al.* (1983) and Montagna (1984). Their conclusion assumes that meiofauna feed only on bacteria and microalgae. In fact, meiofauna eat a variety of other foods such as fungi (Heip *et al.*, 1985), small (< 3 μm) detrital aggregates (Alongi and Tietjen, 1980) and protozoa and other meiofauna (McIntyre, 1969) in order to maintain a balanced diet.

Evidence for trophic interactions could have been obscured or dampened by a variety of factors not examined including densities of macrofauna (Dye and Lasiak, 1986; Poovachironan *et al.*, 1986) and, at the three mangrove-associated sites, soluble tannins leached from mangrove roots and debris (Alongi, 1987b). Large populations (up to 7000 individuals $\cdot$ m^{-2}) of the amphipod *Parhyale hawaienis* (Poovachiranon *et al.*, 1986) occur at the beach wrack site (station 3). Macrofaunal densities on the sandflat (station 4) and at the high intertidal site (station 1) were very low (< 10 individuals $\cdot$ m^{-2}; unpublished data), but dense populations of the fiddler crabs *Uca vocans* and *Uca polita* inhabit the creek bank (station 2) and may have a significant effect on microbial-meiofaunal food chains (Dye and Lasiak, 1986).

Abundances of meiofaunal consumers relative to microbial prey, rates of nutrient supply, and species composition of consumer groups are only a few of the factors probably determining the extent of microbe-meiofauna interactions. On the basis of the present findings, it is reasonably clear that Gerlach's (1978) hypothesis that meiofauna stimulate bacterial productivity is not readily applicable to microbial-meiofaunal food chains in tropical mangroves and sandflats in northern Australia. Many attributes of the benthos described here and in other tropical ecosystems

(Alongi, 1988b) have little parallel in temperate communities used as the basis for Gerlach's calculations: (1) very fast (>0.5 μ (d^{-1}) rates of bacterial growth and very high rates of bacterial productivity (45-1725 mgC · $m^{-2}d^{-1}$)), (2) low densities of hard bodied meiofauna ($10^2 - 10^5 \cdot m^{-2}$), (3) very low (generally < 5 μg Chl *a* · g^{-1} DW sediment) microalgal standing stocks, (4) lack of tidal migration, (5) numerical dominance of turbellarians and (6) lack of seasonality in most populations.

Generalizations made based on temperate work may not necessarily be relevant to tropical inhabitants (Alongi, 1988b). Future studies should focus on quantifying ingestion rates of bacteria and other food resources by protozoans and meiofauna, and on obtaining estimates of protozoan and meiofaunal productivity to properly assess the role of microbial-meiofaunal food chains in temperate and tropical benthic environments.

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