

Benthic infauna and organism-sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance

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ABSTRACT: Sediment infauna and sedimentary structures within the shallow (≤ 15 m depth) inshore of the central Great Barrier Reef lagoon were examined seasonally for 1 yr to relate benthic faunal abundance, community composition and biogenic activity to outwelling of mangrove detritus and natural physical disturbance. Standing amounts of mangrove litter exceeded 4000 g dry weight (DW) m^{-2} in a semi-enclosed area and declined to 3.5 g DW m^{-2} at the inshore-middle shelf boundary. Macroinfaunal densities (mean = 1452; range = 308 to 3950 ind. m^{-2}) and biomass (ash-free dry weight = 0.17 to 6.31 g m^{-2}) varied greatly among sites and seasons, with densities correlating negatively with detritus standing stocks; biomass did not relate to outwelling. Total meiofaunal densities (mean = 715; range = 295 to 1568 ind. 10cm^{-2}) varied significantly among sites and seasons, but only turbellarians correlated positively to standing amounts of mangrove litter. Classification and ordination of nematode communities separated stations mainly on the basis of detrital loading. Species diversity (H') and evenness (J') correlated negatively with detritus standing stocks and extractable tannins derived from the litter. X-radiographs of sediment cores revealed sedimentary facies characterized by low to moderate rates of sedimentation, large patches of buried litter and bioturbation mainly in the upper 5 to 6 cm at the muddiest sites. X-radiographs also showed that these inshore sediments are devoid of large, equilibrium species, but subjected to episodes of scouring and resuspension by large tides and climatic disturbances. The poor nutritional quality of mangrove detritus and intermittent physical disturbances appear to be the major factors preventing the establishment of equilibrium communities and perpetuating the dominance of pioneering infaunal assemblages in this shallow, tropical inshore region.

INTRODUCTION

Coastal benthic communities are fueled by a heterogeneous pool of organic detritus derived from different sources (Tenore et al. 1982, Tenore 1988). In temperate areas, coastal sediments receive organic matter derived mainly from phytoplankton blooms (Graf et al. 1983, 1984), vascular plant debris exported from tidal wetlands and estuaries (Hanson et al. 1981, Hopkinson 1985), winter blooms of seaweeds (e.g. kelp, Duggins et al. 1989) and, depending upon water depth and clarity, *in situ* microalgal production (Tenore 1988 and references therein). Most of the vascular plant detritus advected to adjacent subtidal

sediments is derived from salt marshes, the actual amount exported being dependent upon factors such as areal extent of marsh, tidal amplitude and season.

Coastal sediments in the tropics similarly receive various types and amounts of plant-derived detritus, although the actual components are different to those in higher latitudes. Plankton production in the tropics appears to be less seasonal compared to temperate waters and dominated by the nano- and pico-size fractions (see review of Furnas 1990). It is therefore likely that most of this production is recycled in the water column rather than deposited onto the coastal seabed, as supported by the low amounts of chlorophyll *a*, degraded pigments and *in situ* primary

production (excluding seagrass beds and some semi-enclosed coastal lagoons) measured in most subtidal sediments in the tropics (see review of Alongi 1990a).

Outwelling of leaves, bark, roots and other tree-components derived from mangroves thus appears to be the main source of plant detritus for benthic food chains in most tropical coastal areas (Boto & Bunt 1981, Twilley 1985; but see Fleming et al. 1990). Despite their potential importance as a source of detritus, the role of mangrove forests as regions of outwelling, particularly the actual amounts of litter exported and actual linkages to coastal food webs, has been documented for only a few regions (Rodelli et al. 1984, Flores-Verdugo et al. 1987).

In the central Great Barrier Reef (hereafter GBR) lagoon, it is estimated that the extensive mangrove forests bordering the coast export a substantial amount of litter to the adjacent nearshore (Robertson et al. 1988). Previous studies within the GBR lagoon have focused on outwelling from the mangroves of Missionary Bay off northern Hinchinbrook Island, one of the largest forests in the region (Boto & Bunt 1981, Boto & Wellington 1988, Alongi et al. 1989, 1992, Alongi 1990b, c, 1992, Daniel & Robertson 1990). There are also extensive mangrove forests lining the Hinchinbrook Channel which contribute an equal amount of litter to the adjacent coastal sediments (Robertson et al. 1988).

This organic loading drives an abundant and productive bacterial community in these inshore sediments (Alongi et al. 1989, Alongi 1992) and enriches bulk concentrations of particulate carbon and nitrogen (Alongi 1990b). Variations in the distribution and abundance of epibenthos of the region relate positively to variations in the quantity of exported detritus, particularly for taxa such as penaeid shrimps which may use clumps of deposited litter as refugia from predatory fish (Daniel & Robertson 1990).

In this companion paper we describe the effects of various amounts of mangrove detritus (pieces ≥ 0.5 mm) deposited onto this shallow inshore area on the distribution and abundance of macroinfauna and meiobenthos and on nematode community structure. We also assess the sedimentary facies at these same locations in order to determine the influence of this deposited litter and the effects of natural physical disturbance (tidal scouring, wind waves) on the sedimentary fabric and organism-sediment relations.

MATERIAL AND METHODS

Study area and sediment characteristics. A complete description of the study area and sediment characteristics has been provided in the earlier companion papers (Alongi et al. 1989, Alongi 1990b, c, 1992).

Briefly, 6 stations were established in the Missionary Bay-Murray River-Hinchinbrook Channel region along the north Queensland coast (Fig. 1). Stns MB1 to MB3 are a transect from the shallow subtidal of Missionary Bay off the northern end of Hinchinbrook Island out to the Brook Islands. Stns MB4 and MB5 are near the mouth of the Murray River, which is lined with fringing mangrove forests. Stn MB6 is near the mouth of the Herbert River in the middle of the extensive, deltaic forests of Hinchinbrook Channel.

Geological and hydrographic conditions in this area have been studied earlier by Wolanski et al. (1980), Belperio (1983), Torgersen & Chivas (1985) and Wolanski et al. (1990). Sediments of the stations have been classified as either very fine to medium sands (Stns MB1, MB3, MB4) or coarse silts (Stns MB2, MB5, MB6), moderately reducing, with low to moderate water content, and low to moderate concentrations of calcium carbonate (Alongi et al. 1989, Alongi 1990b, 1992). Organic carbon and total nitrogen concentrations range from 0.2 to 3.9 % and 0.01 to 0.18 % by sediment dry weight (DW), respectively, and are

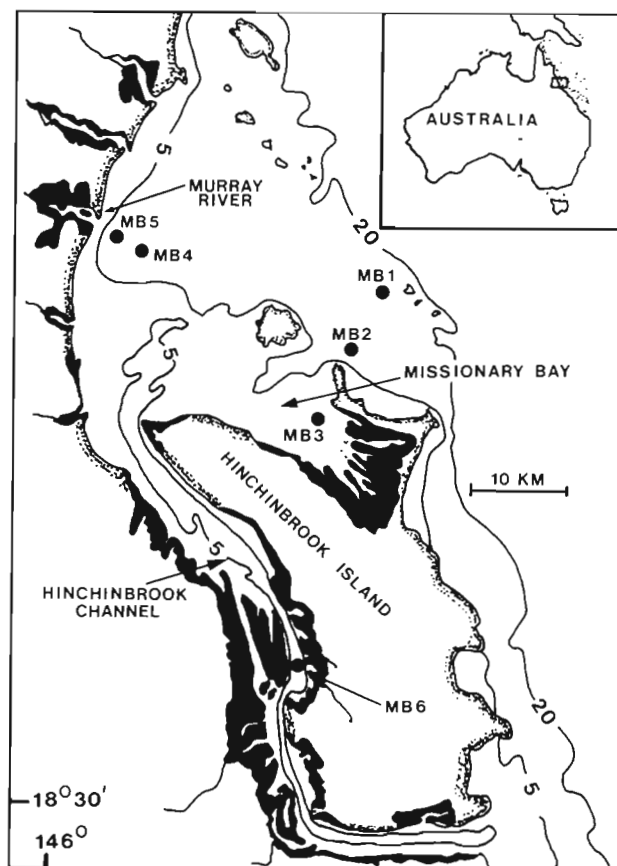


Fig. 1. Location of the 6 benthic stations in the vicinity of Hinchinbrook Island, central GBR lagoon. Darkened areas depict mangrove forests. Isobaths are in meters

highest at stations receiving the greatest input of mangrove detritus (Alongi 1990b). Total phosphorus concentrations range from 0.013 to 0.048 % by DW, but do not relate to outwelling. C:N:P ratios range from 29:6:1 at Stn MB1, which receives the least amount of litter, to a high of 397:17:1 at Stn MB6, which receives the most detritus.

Porewater nutrient concentrations are low (within the μM range) at all stations and not directly related to outwelling (Alongi 1990b). Interstitial ammonium (range: 10 to 310 μM) and silicate (range: 10 to 315 μM) are present in greatest concentration, with lesser amounts of phosphate (range: 1 to 12 μM) and nitrite+nitrate (range: 0.07 to 6.0 μM). Vertical profiles of both particulate and dissolved nutrients are irregular at all 6 stations. Solid-phase iron and manganese concentrations range from 8.9 to 40.0 mg g^{-1} and 107 to 496 $\mu\text{g g}^{-1}$ sediment DW and are irregular with sediment depth, as are low concentrations of porewater Fe and Mn solutes (Alongi et al. 1992).

Bacterial cell counts are high, ranging in surface sediments (top 1 cm) from 0.5 to 20.8 $\times 10^{10}$ cells g^{-1} DW; bacterial productivity and daily specific growth rates range from 0.02 to 5.7 $\text{g C m}^{-2} \text{d}^{-1}$ and from 0.004 to 1.3 d^{-1} , respectively (Alongi et al. 1989, Alongi 1992). Enhancement of bacterial activity and benthic respiration is apparent only at Stn MB6, the site of highest litter deposition. Benthic protozoan densities are low, with ciliate and flagellate numbers ranging from 23 to 511 cells cm^{-3} and 40 to 806 cells cm^{-3} , respectively (Alongi 1990c). Their densities do not relate to the amounts of deposited litter (see Table 1 for summary of station positions, sedimentary and microbial characteristics).

Field sampling and laboratory procedures. Replicate 0.027 m^2 modified Bouma boxcores were taken for detritus, infauna and X-radiographic samples at each station. Cores for X-radiographs were taken in January–February 1988. Samples for mangrove litter and macroinfauna were taken in February, May and August 1987 and January–February 1988. Meiofauna cores were taken on these dates and in October 1987.

Samples for chitinous meiofauna were taken with 3 plastic subcores (6.6 cm^2 surface area) inserted to a depth of 10 cm from 1 or 2 undisturbed boxcores per site. Sampling during the first 2 cruises indicated a sample precision of $\pm 40\%$ (1 standard error) of total mean faunal densities using 3 cores. To increase precision to $\pm 20\%$ of the mean would have required more than 30 samples per site. As this is impractical, a sample precision of $\pm 40\%$ was considered adequate on subsequent cruises in order to determine station and seasonal differences, and to minimize extensive sorting and identification. Each sample was preserved in a 5 % formalin-seawater mixture containing Rose Bengal (0.5 g l^{-1}). In the laboratory, sediments were washed through a nest of 2 sieves, the larger with a mesh opening of 500 μm and the smaller with a mesh opening of 45 μm . Animals that passed through the larger sieve and were retained on the smaller mesh were considered meiofauna. Animals were sorted and major taxa enumerated. Nematodes from the August 1987 (winter) and January–February 1988 (summer) samples were identified to species level when possible, and classified for feeding type (selective/non-selective deposit-feeder, epigrowth feeder or omnivore/predator) using the scheme of Wieser (1953). Non-chitinous meiofauna were estimated from the same

Table 1. Station positions, water depths and mean sedimentologic and microbial characteristics (summarized from Alongi et al. 1989, Alongi 1990b, c). DW: dry weight; POC: particulate organic carbon; TN: total nitrogen

Variable	Station					
	MB1	MB2	MB3	MB4	MB5	MB6
Latitude (S)	18° 08'	18° 10'	18° 14'	18° 07'	18° 07'	18° 24'
Longitude (E)	146° 15'	146° 14'	146° 12'	146° 04'	146° 03'	146° 12'
Depth (m)	15	13	4	8	8	6
Eh (mV)	+228	+86	+7	+76	+42	+31
Grain size (mm)	0.30	0.06	0.16	0.11	0.06	0.04
Sorting (σ_1)	1.97	1.76	2.79	1.90	2.72	2.77
% Sand-gravel	74.2	21.5	53.8	50.9	32.0	52.6
% Silt-clay	25.8	78.5	46.2	49.1	68.0	47.4
Tannins (% DW)	0.002	0.008	0.014	0.009	0.013	0.033
POC (% DW)	0.22	0.70	1.32	0.82	1.41	2.60
TN (% DW)	0.04	0.08	0.08	0.09	0.12	0.12
C:N:P	29:6:1	43:6:1	138:7:1	63:5:1	100:6:1	397:17:1
Chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$ DW)	0.7	1.1	1.4	1.2	1.9	1.0
Phaeopigments ($\mu\text{g g}^{-1}$ DW)	3.7	3.9	3.3	3.1	8.4	7.8
Bacteria (cells $\times 10^{10} \text{g}^{-1}$ DW)	3.0	5.4	4.7	6.9	10.7	6.2
Ciliates (cells cm^{-3})	270	60	221	70	102	221
Flagellates (cells cm^{-3})	83	239	115	180	289	207

cores taken for protozoa and subjected to the Percoll-sorbitol extraction procedure (Alongi 1990c), which is very efficient for harvesting small invertebrates (Schwinghamer 1981).

Three boxcores per station were used to estimate macroinfaunal numbers and biomass, and detritus standing stocks. Each boxcore was sieved (0.5 mm) and preserved in 10 % buffered formalin with Rose Bengal. The animals were sorted to major taxa, enumerated and patted dry, and their preserved wet weight determined; they were then dried (80 °C for 16 to 18 h) and ashed (450 °C for 6 h) to estimate ash-free dry weight (AFDW). Shell-bearing organisms were decalcified in dilute (5 %) phosphoric acid prior to biomass analysis. The litter was captured by continued decantation onto a 0.5 mm sieve until the sediment was visibly clear. The material was then dried (80 °C for 24 h) and weighed. A small sample of the litter was retained during sieving and frozen for later C and N analysis.

Sediment radiographs were made from cores taken by inserting (as gently as possible) at least 2 Plexiglas liners (30 cm long, 2.5 cm thick, 19 cm wide) into 1 or 2 undisturbed boxcores at each station. The cores were then processed for x-rays and dissected using the procedures outlined in Alongi (1989). Primary and biogenic structures were examined using criteria outlined by Collinson & Thompson (1989).

Data analysis. Variations in faunal numbers and biomass and in standing stocks of mangrove detritus among stations and seasons were examined using standard 2-way analysis of variance (Sokal & Rohlf 1981). Each ANOVA was followed by a Student-Newman-Keuls (SNK) multiple comparisons test if a significant ($p < 0.05$) temporal or spatial effect was found (2-tailed test). All data was $\log(x + 1)$ transformed before analysis because prior F_{\max} tests indicated heteroscedasticity. Simple correlations (r) between faunal densities and the other variables (litter, sediment carbon, etc.) were determined using Pearson's product-moment coefficient. In some instances (e.g. correlations with species diversity, H') where a third highly intercorrelated variable was found, partial product-moment correlations were calculated where the relationship between the x and y variable was examined with the third variable, z , held constant (Legendre & Legendre 1983).

Species diversity (H') of nematodes was measured by the Shannon-Wiener information function using \log_2 (Pielou 1975), evenness (J') was calculated after Pielou (1975) and species richness (SR) was estimated using Margalef's (1958) formula. Classification of sites and nematode assemblages was done using the Bray-Curtis similarity measure (Bray & Curtis 1957) with flexible sorting and the cluster intensity coefficient (β)

set at -0.25 (Clifford & Stephenson 1975). Nodal analysis, a cross relation between normal (stations) and inverse (species) classifications (Lambert & Williams 1962), was performed to describe the stations on the basis of their dominant species and the species on their patterns of occurrence among stations. Comparisons of coincidence are expressed in terms of constancy, the degree to which a species is consistently found in a habitat, and fidelity, the degree to which a species selects or is relegated to a habitat. The equations for both terms are given in Tietjen (1984).

Detrended correspondence analysis (DCA) was performed to ordinate the stations using all nematode species identified. The technique is described by Hill & Gauch (1980). The classification and ordination analyses were run combining the data sets for both seasons because of the small sample number (3 cores per station per season) and because of the primary interest in exploring station differences.

RESULTS

Standing amounts of macroparticulate detritus

There were significant among-station, but no seasonal, differences in the sediment concentrations of detritus (Tables 2C & 3). Stn MB6 had the highest amounts of detritus, ranging from 3144 to 4980 g DW m^{-2} , and Stn MB3 had the next highest concentration of litter at 1064 to 2688 g DW m^{-2} (Table 2C). Quantities were not significantly different between Stns MB4 and MB5 and between Stns MB1 and MB2, but Stn MB1 contained the least amount of detritus (range: 3.5 to 18.4 g DW m^{-2}), more than half (68 %) of which consisted of fresh seagrass (*Halodule* spp.) blades.

This compositional difference was reflected in the mean C:N ratio of the bulk detritus with the lowest ratio at Stn MB1, the highest ratio at Stn MB2 and very similar ratios at the remaining stations (Table 2C). The ratios did not change significantly ($p > 0.05$) with season.

Litter concentrations across stations and seasons correlated positively with some other sediment characteristics: carbon ($r = +0.84$; $p < 0.001$) and clay content ($r = +0.45$; $p < 0.05$).

Interpretation of sedimentary structures

The facies at Stn MB1 (Fig. 2) consisted of a generally uniform, subsurface fabric comprised of well-compacted, medium quartz sand (Table 1) and

fragments of foraminifera, bivalve and scaphopod shell. The facies was moderately bioturbated with only a few surface amphipod and polychaete tubes and burrows. The random orientation of the shell and test

fragments indicates subsurface particle mixing from physical disturbance (e.g. storms, cyclones).

The 2 muddiest stations, MB2 and MB5, had similar sedimentary facies (see X-radiograph of

Table 2. Total (A) wet weight and (B) ash-free dry weight macroinfaunal biomass (g m^{-2}) and (C) macroparticulate ($\geq 0.5 \text{ mm}$) mangrove detritus (g DW m^{-2}) at the 6 central GBR lagoon stations. C:N ratio depicts mean of all seasons. Values are mean $\pm 1\text{SD}$

	Station					
	MB1	MB2	MB3	MB4	MB5	MB6
A. Wet weight biomass						
Feb 1987	20.1 \pm 10.6	2.5 \pm 2.4	3.4 \pm 1.3	26.5 \pm 3.0	6.3 \pm 3.8	3.9 \pm 2.0
May 1987	19.2 \pm 2.5	13.6 \pm 3.7	6.4 \pm 3.6	50.0 \pm 46.9	34.3 \pm 36.6	11.3 \pm 6.9
Aug 1987	31.2 \pm 25.8	13.7 \pm 16.8	7.3 \pm 2.2	7.8 \pm 2.9	8.5 \pm 5.4	4.7 \pm 2.9
Jan–Feb 1988	12.2 \pm 3.9	5.4 \pm 4.6	8.7 \pm 5.7	4.2 \pm 2.8	9.7 \pm 9.3	5.7 \pm 2.6
B. AFDW biomass						
Feb 1987	2.74 \pm 1.24	0.17 \pm 0.12	0.32 \pm 0.18	2.43 \pm 0.22	0.58 \pm 0.35	0.40 \pm 0.31
May 1987	1.48 \pm 0.61	1.43 \pm 0.63	0.52 \pm 0.26	6.31 \pm 6.99	5.13 \pm 6.25	1.04 \pm 0.63
Aug 1987	3.89 \pm 3.88	0.25 \pm 0.14	0.74 \pm 0.41	0.41 \pm 0.14	0.74 \pm 0.62	0.44 \pm 0.26
Jan–Feb 1988	1.22 \pm 0.43	0.46 \pm 0.53	0.90 \pm 0.67	0.53 \pm 0.35	0.90 \pm 0.85	0.55 \pm 0.22
C. Detritus						
Feb 1987	10.9 \pm 5.1	10.2 \pm 4.6	1443.7 \pm 582.9	75.2 \pm 35.8	58.7 \pm 19.1	3144.2 \pm 683.5
May 1987	18.4 \pm 11.1	9.8 \pm 2.7	1064.3 \pm 600.9	99.3 \pm 87.5	78.2 \pm 36.9	4295.7 \pm 955.6
Aug 1987	4.2 \pm 2.3	7.4 \pm 5.4	2497.9 \pm 380.3	64.2 \pm 37.1	98.5 \pm 26.8	4979.5 \pm 346.1
Jan–Feb 1988	3.5 \pm 4.1	19.4 \pm 17.7	2687.6 \pm 326.8	48.3 \pm 35.8	114.1 \pm 30.6	4592.1 \pm 432.9
C:N (molar)	31.4	66.1	57.1	57.1	50.4	57.2

Table 3. Summary of ANOVA results for macrodetritus standing stocks, total macroinfaunal biomass (AFDW) and total and major component densities of macrofauna and meiofauna. Where interaction effects were significant, trends in mean values of variates are discussed in the text. SNK test results are given below where main factors are the only significant sources of variance. F = February 1987, M = May 1987, A = August 1987, O = October 1987, J = January–February 1988. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant

Variate	Station (St)	Sources of variance Season (Se)	St \times Se
Detritus	6 > 3 > <u>5</u> 4 > <u>2</u> 1***	ns	ns
Macroinfaunal biomass (AFDW)	<u>4</u> 1 <u>5</u> <u>2</u> <u>6</u> 3**	ns	ns
Total macrofaunal densities
Polychaetes	<u>1</u> <u>4</u> <u>5</u> <u>2</u> 3 6*	ns	ns
Tanaeids	<u>4</u> 1 <u>6</u> <u>2</u> 3 5***	ns	ns
Amphipods
Decapods	4 > <u>2</u> <u>1</u> <u>6</u> <u>5</u> > 3**	MA > J > F***	ns
Total meiofaunal densities
Nematodes	ns
Copepods
Ostracods
Foraminiferans
Turbellarians	6 > <u>5</u> <u>3</u> <u>2</u> 1 > 4***	J > FOAM***	ns
Polychaetes	<u>1</u> <u>3</u> <u>2</u> <u>6</u> > 4 > 5***	JAM > OF***	ns

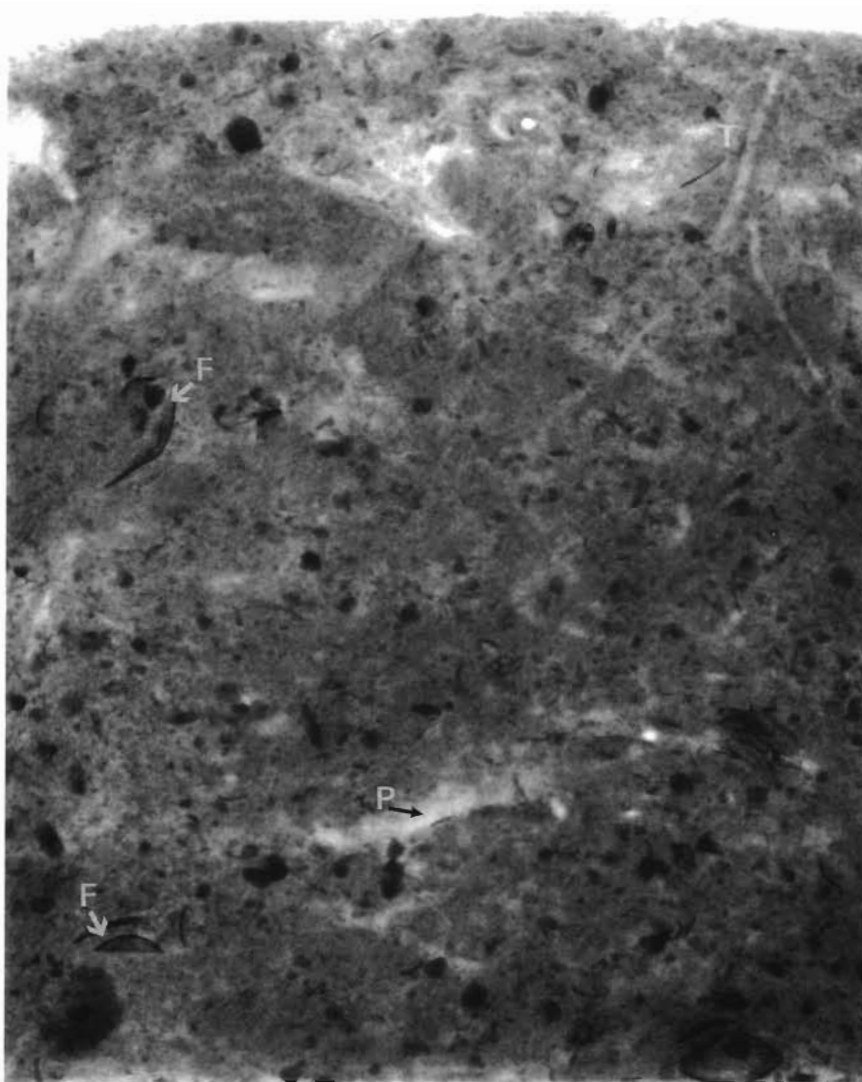


Fig. 2. X-radiograph of sediment from Stn MB1, January–February 1988 (see text for description). Length of core = 24 cm. P: Clump of seagrass detritus; T: tube; F: fragments of bivalve and scaphopod shell and foraminiferan tests

Stn MB5, Fig. 3) with dense clay clasts and an extensive network of tubes and small burrows in the upper 5 to 6 cm. A few fragments of mangrove wood and gastropod and bivalve shell had been incompletely disaggregated in the lower half of the core taken from Stn MB5 (Fig. 3). A few small, subsurface tubes or burrows appeared to be relict, separated from the upper fabric by low-angle cross-bedding (erosional bands) that were in the process of being reworked.

The facies at Stns MB3 and MB4 were similar (see Fig. 4 for X-radiograph of Stn MB3), exhibiting a well-churned, mottled fabric with irregularly oriented shells and patches of coarse sand and gravel. There was little evidence of bioturbation as most of the 'white veins' observed in the subsurface fabric were pieces of mangrove bark and twigs, as revealed by dissection. There were also a few pieces of dense mud clasts

intermixed with some coarse sand + gravel fractures. A few subsurface tubes and burrows may have been recent (Fig. 4).

The sediment fabric at Stn MB6 (Fig. 5) was dominated by tiny pieces of macerated mangrove litter irregularly interspersed with pockets of fine sand. There is no clear evidence of biogenic structures or physical laminations, but the fabric is well churned. The irregular dark patches are clay clasts.

Macroinfaunal patterns

Macroinfaunal biomass varied among stations but not seasonally (Table 3), ranging from 2.5 to 50.0 g wet weight (WW) m^{-2} and from 0.17 to 6.31 g AFDW m^{-2} , respectively (Table 2A, B). AFDW biomass was significantly greater at Stns MB4 and MB1 than at

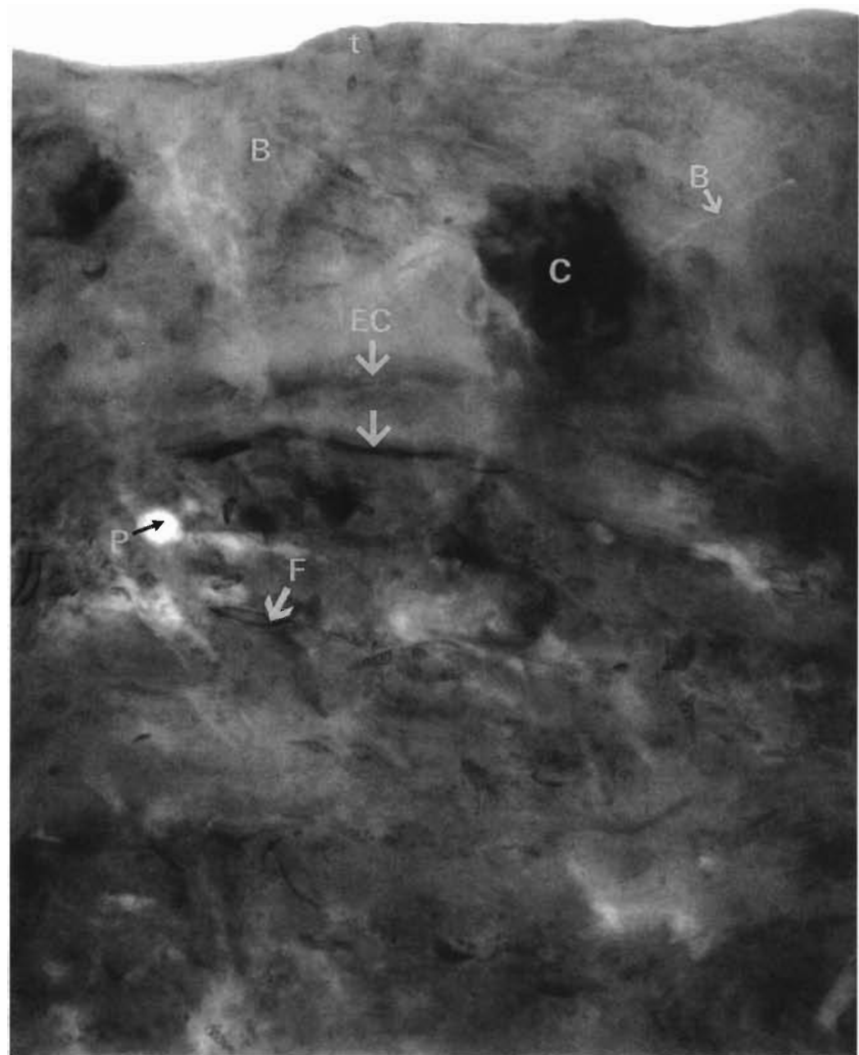


Fig. 3. X-radiograph of sediment from Stn MB5, January–February 1988 (see text for description). Length of core = 23 cm. C: Clay clast; B: burrow; t: tube; P: wood; F: fragments of prosobranch gastropod and bivalve shell; white arrows in middle of radiograph denote 2 erosional contacts (EC)

Stns MB2, MB6 and MB3 but equivalent to biomass at Stn MB5 (Table 3).

Total densities of macroinfauna ranged from 308 to 3950 ind. m^{-2} among stations (Fig. 6) with a grand mean of 1452 m^{-2} . Density variations among stations and seasons were significant, as were site \times season interactions, indicating that differences in densities among the stations changed with season. For instance, station differences in February were (SNK test): $1.4 > 2.563$; but in May were in the following order: $4.215 > 6.3$. On average (grand mean), total densities were greatest at Stns MB4 and MB1 and (summing stations) in May and August 1987 (Fig. 6).

Small, surface-dwelling polychaetes and amphipods were the dominant taxa, followed by tanaeids and decapods (mostly juvenile crabs and penaeid shrimps) and, to a much lesser extent, by bivalves, ophiuroids, cumaceans, copepods, fish, sipunculids, oligochaetes, gastropods, echinoids and asteroids

(Fig. 6). Polychaetes, tanaeids and decapods were usually most abundant at either Stn MB4 or Stn MB1 (Table 3). Amphipod abundances varied greatly with station and season, exhibiting significant interaction effects. On average, amphipods were most abundant at Stns MB4 and MB2, in May 1987 (Fig. 6). Decapods were also more abundant in the cooler months of May and August than in February 1987 and January–February 1988 (Table 3), as reflected in a significant negative correlation between decapod abundances and sediment temperature ($r = -0.49$; $p < 0.05$).

Total infaunal densities related negatively to detrital standing stocks ($r = -0.41$; $p < 0.05$), percent clay ($r = -0.50$; $p < 0.01$), carbon ($r = -0.44$) and nitrogen ($r = -0.41$) content, and positively with redox potential ($r = +0.41$). AFDW biomass correlated negatively with percent clay ($r = -0.54$; $p < 0.01$). Among individual taxa, polychaetes related positively to redox potential

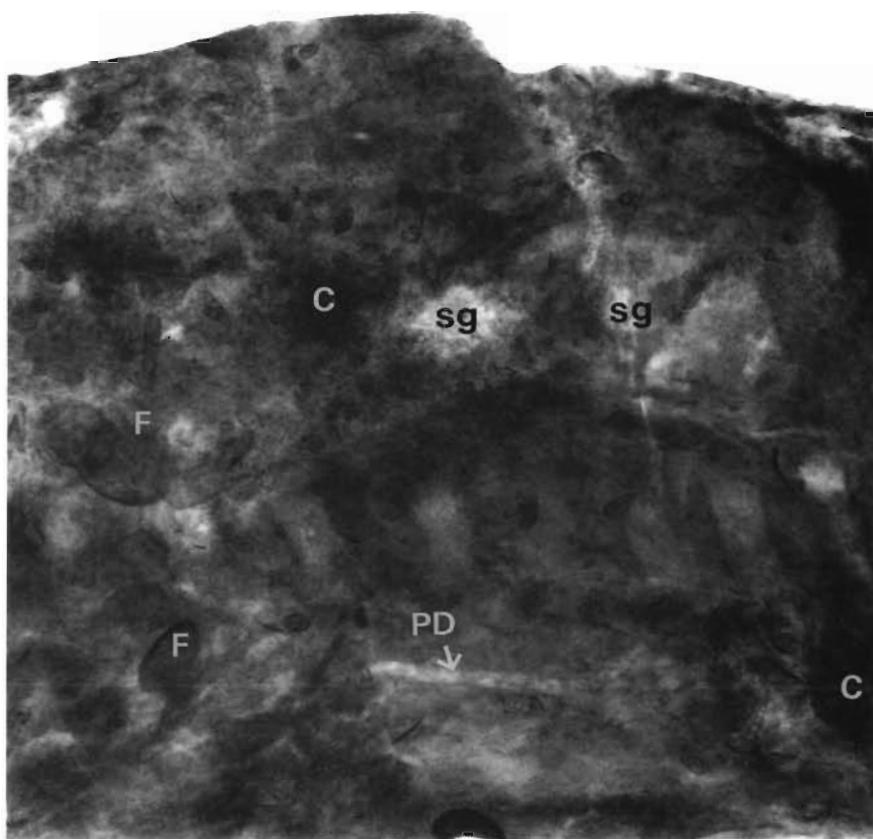


Fig. 4. X-radiograph of sediment from Stn MB3, January–February 1988 (see text for description). Length of core = 18 cm. F: Shell fragments; PD: mangrove detritus; sg: sand-gravel; C: mud clasts

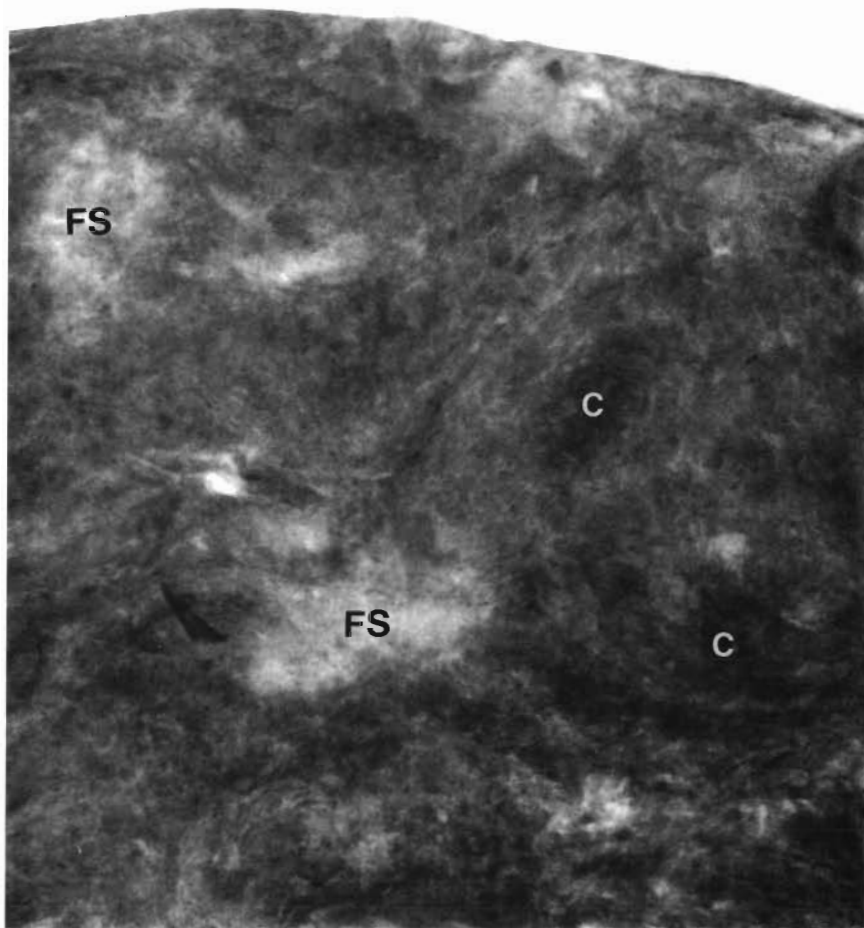


Fig. 5. X-radiograph of sediment from Stn MB6, January–February 1988 (see text for description). Length of core = 20 cm. FS: Fine sand clumps; C: mud clasts

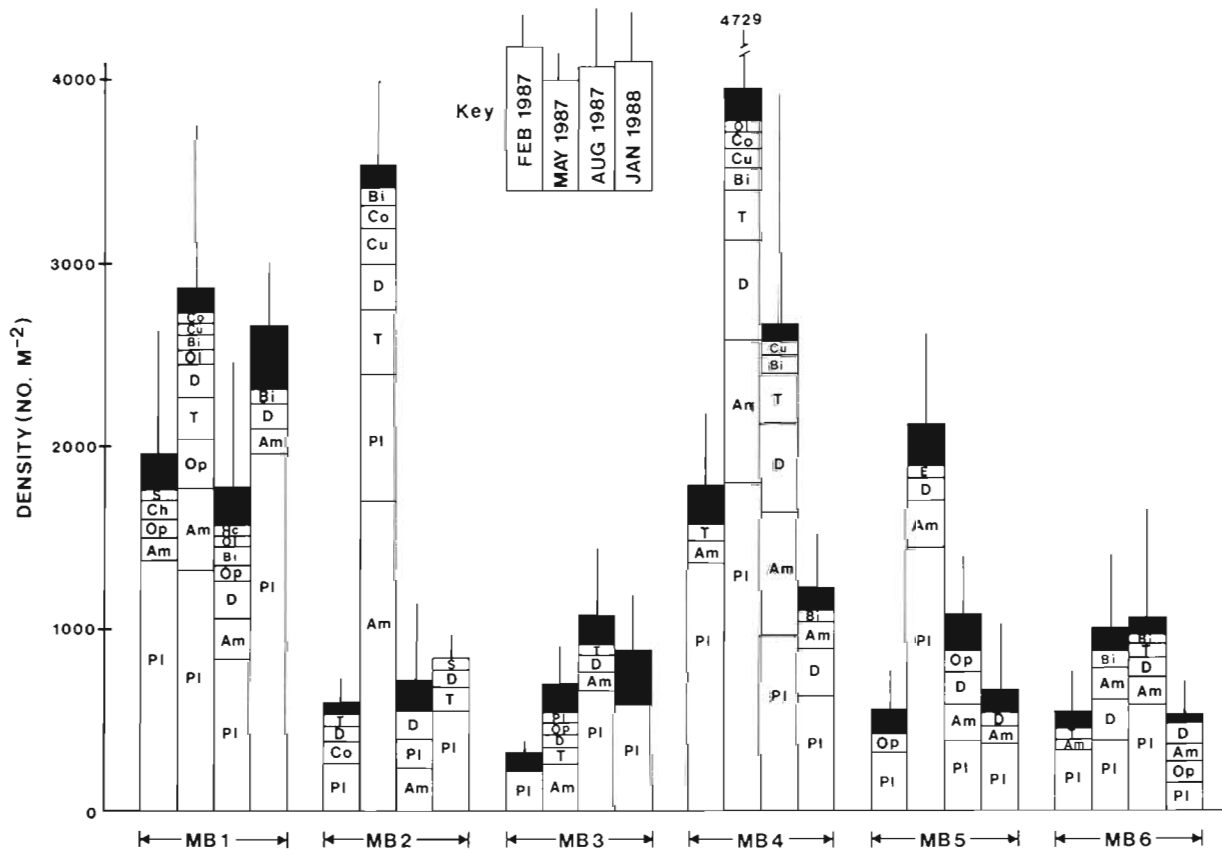


Fig. 6. Mean (+1 SD) total density (no. m^{-2}) of macroinfauna and major taxa at each station for all seasons. Am: amphipods; Bi: bivalves; Ch: chordates (teleost fishes); Co: copepods; Cu: cumaceans; D: decapods; E: echinoids; Hc: hemichordates; Ol: oligochaetes; ; Op: ophiroids; PI: polychaetes; S: sipunculids; T: tanaeids; ■: others

($r = +0.41$; $p < 0.05$) and negatively with grain size ($r = -0.47$), percent clay ($r = -0.51$) and carbon ($r = -0.45$) and nitrogen ($r = -0.50$) content. Amphipod abundances related positively with silt content ($r = +0.42$).

Meiofaunal patterns

Total meiofaunal densities were highly variable, exhibiting seasonal and station differences and interaction effects (Table 3). Among stations, total densities ranged from 295 to 1568 ind. 10cm^{-2} with an overall mean of 715 ind. 10cm^{-2} (Fig. 7). Individual taxa were abundant in the following order: nematodes (73 % of mean total) > harpacticoid copepods (10 %) > polychaetes (3 %) > turbellarians (3 %) > ostracods (2 %) > foraminiferans (1 %). Minor taxa (8 %) included amphipods, tanaeids, bivalves, isopods, kinorhynchans, oligochaetes, halacarids, cnidarians and larval or juvenile stages of macrofaunal taxa (e.g. ophiroids). Nematodes did not vary significantly with station but, as with copepods, ostracods, and foraminiferans, exhibited strong seasonal and inter-

active effects (Table 3). The very highly significant interaction terms (Table 3) indicate that density differences among stations changed with each season. For instance, in February 1987 station differences in total meiofaunal densities (SNK test) were: $3 > 4 \ 6 \ 2 \ 5 \ 1$; in August they were as follows: $1 \ 4 > 6 \ 3 \ 5 \ 2$ (Fig. 7).

Only turbellarians and meiofaunal polychaetes did not exhibit significant interaction effects (Table 3). Turbellarians were most abundant at Stn MB6 and polychaetes were least abundant at Stn MB5, although both taxa were generally most abundant in January–February 1988.

Total meiofaunal numbers related positively to redox potential ($r = +0.52$; $p < 0.05$). Among taxa, turbellarians correlated positively with sediment temperature ($r = +0.40$), tannins ($r = +0.65$; $p < 0.001$), carbon content ($r = +0.50$) and detrital standing stocks ($r = +0.50$). Copepods related positively to Eh ($r = +0.64$; $p < 0.001$), but negatively to grain size ($r = -0.59$; $p < 0.01$), percent silt ($r = -0.43$) and carbon ($r = -0.44$) and nitrogen ($r = -0.56$) content. Meiofaunal polychaetes correlated negatively with grain size ($r = -0.46$; $p < 0.05$).

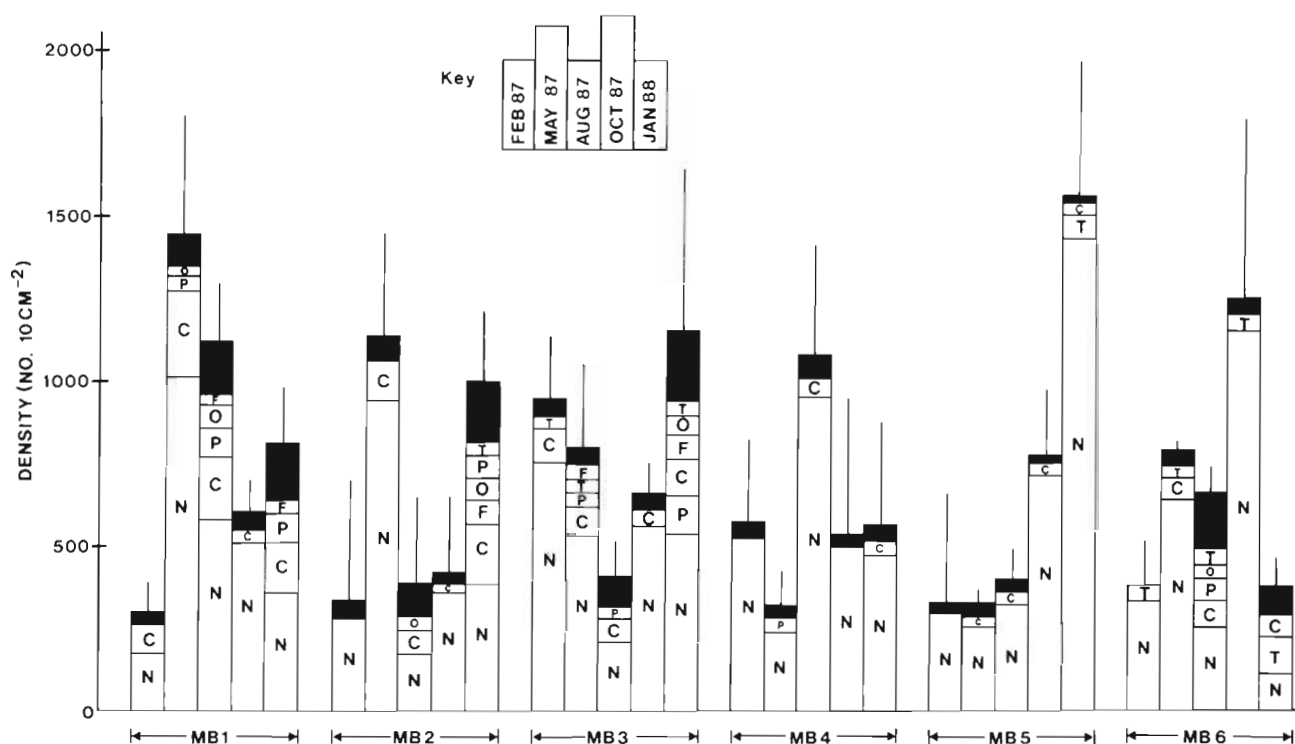


Fig. 7. Mean (± 1 SD) total density (no. 10cm^{-2}) of meiobenthic taxa at each station for all seasons. C: Harpacticoid copepods (adults + nauplii); F: foraminiferans; N: nematodes; O: ostracods; P: polychaetes; T: turbellarians; ■: others

Nematode community structure, diversity and trophic composition

The normal classification of stations (both seasons and all 159 species identified) separated Stn MB6 from both stations off the Murray River (MB4 and MB5) and from the 3 transect stations off the northern end of Hinchinbrook Island which comprised a distinct cluster of the 2 sandier stations (MB1 and MB3) agglomerated with the muddier Stn MB2 (Fig. 8A). The ordination of the collections (Fig. 8B) demonstrated a clearer distinction between Stn MB6 and the other 5 sites along Axis 2. Axis 1 divided Stns MB1 and MB2 (containing the least amounts of detritus; see Tables 2 & 3) with high scores from the other stations with greater detrital loading and lower scores. Both axes explained most of the variance with eigenvalues of 0.637 and 0.348, respectively.

Of the 159 species identified, 46 had relative abundances $\geq 0.5\%$ averaged over all 6 stations (Table 4). The epigrowth-feeders *Dorylaimopsis punctata* and *Spilophorella paradoxa* and the deposit-feeders *Terschellingia longicaudata*, *Theristus* sp. 9 and *Theristus* sp. 8 were the 5 most abundant species.

Of all the species, 27 had mean relative abundances $\geq 1.0\%$ and were agglomerated into 2 main species groups in an inverse classification (Fig. 9), then were

further analyzed using nodal analysis. The first cluster consisted of 10 species (species numbered 1, 10, 13, 3, 9, 12, 2, 5, 14 and 16) that occurred most consistently as a group at Stns MB1, MB2 and MB3. The second agglomeration (code numbers 4 to 27 at the bottom of Fig. 9) occurred most consistently as a group from Stns MB3 to MB6.

The patterns of constancy and fidelity among these dominant species (Fig. 9) explain the fair degree of separation among stations as depicted in the classification and ordination models (Fig. 8). For instance, Stn MB6 was characterized by the strong preferences of *Sabatieria* spp. 4 and 5, *Terschellingia longicaudata*, *Paramonohystera* sp. 2 and *Theristus* sp. 9, whereas the most dissimilar site, Stn MB1, was preferred by *Innocuonema* sp. 1, *Viscosia* sp. 1, *Theristus* sp. 4 and *Sabatieria* sp. 2. Some species were not faithful to a particular station, exhibiting moderate to high constancy at all or nearly all of the 6 stations. These include *Cheironchus* sp. 1, *Marilynia oculissoma*, *Ptycholaimellus* sp. 1, *Spilophorella paradoxa*, *Dorylaimopsis punctata* and *Elzalia* sp. 1.

Species diversity ranged from 2.02 (MB6) to 3.13 (MB1). Evenness was also most divergent between these 2 stations (Table 5). Species richness was highest at Station MB1; most species (65) were identified at this site (Table 5). Species diversity (H') was a function

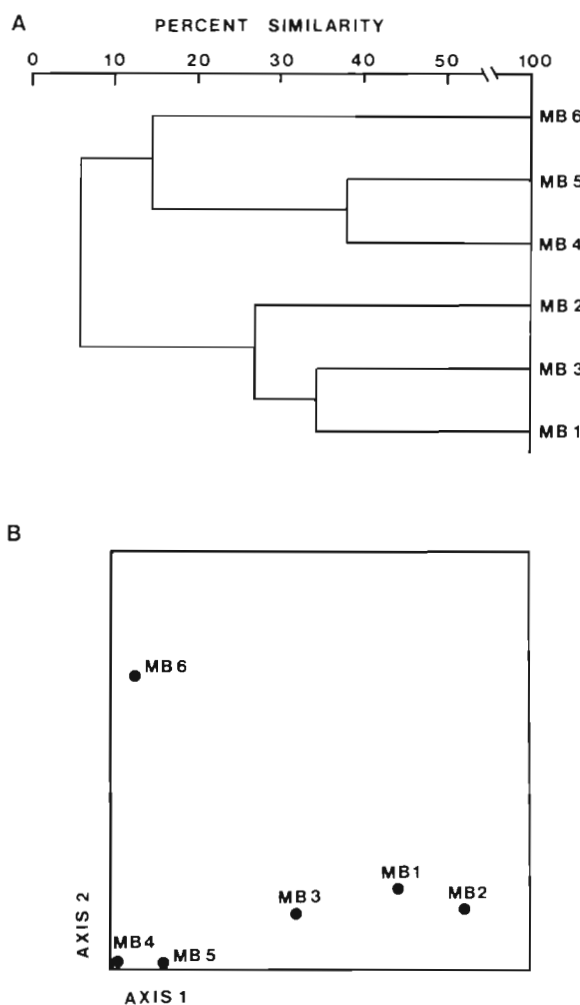


Fig. 8. (A) Normal classification of stations using all nematode species identified (August 1987, January–February 1988). (B) Detrended correspondence analysis of collections of all nematodes from all 6 stations (August 1987, January–February 1988)

of both evenness ($r = +0.95$; $p < 0.01$) and species richness ($r = +0.88$; $p < 0.05$). Diversity and evenness related negatively to detritus standing stocks ($r = -0.66$ and -0.75 respectively; $p < 0.05$) holding an intercorrelation with grain size ($r = -0.78$ and -0.79 ; $p < 0.05$) constant. SR also correlated with grain size ($r = +0.84$). H' and J' also correlated with Eh ($r = +0.90$ and $+0.88$ respectively) as well as with extractable tannins ($r = -0.77$ and -0.86). All correlations remained significant when intercorrelations were held constant.

Non-selective deposit-feeders and epigrowth-feeders were the dominant trophic types at all 6 sites (Fig. 10), ranging from 24 to 47 % and from 23 to 38 % of all species identified, respectively. The relative abundance of selective deposit-feeders varied little among stations, ranging from 11 to 19 % at Stns MB1 to MB5 and 24 % at Stn MB6. Omnivore/predators comprised

< 10 % of total relative abundance at Stns MB4 to MB6 but were relatively more abundant at Stns MB1 (23 %), MB2 (17 %) and MB3 (11 %).

On average, deposit-feeders (selective and non-selective) comprised >50 % of total relative abundances at all stations, except at Stn MB1, where epigrowth-feeders and omnivore/predators dominated (Fig. 10).

DISCUSSION

The deposition and burial of various quantities (4 to 4980 g DW m^{-2}) of mangrove detritus in this shallow inshore area does not result in the enrichment of infaunal numbers or biomass, but rather to a diminution of species richness and diversity, as shown by the free-living nematode communities. Total macroinfaunal densities related negatively to the standing amounts of mangrove detritus, with most individual taxa relating to a variety of other edaphic characteristics. With the exception of the turbellarians, meiofaunal taxa behaved similarly, showing no relationship to the deposited litter.

The analysis of nematode community structure revealed that the response of benthic infaunal assemblages may be more qualitative than quantitative. Nematode species diversity and equitability (evenness) related inversely to detritus standing stocks and extractable tannins, even after accounting for correlations with other sedimentary characteristics, such as grain size and redox potential. Highest diversity (H') was found at Stn MB1, which was farthest from the influence of mangrove outwelling, whereas lowest species diversity occurred at Stn MB6, where mangrove litter accounts for up to between 35 and 45 % of total sedimentary organic carbon (Alongi 1990b). The diversity, evenness and species richness of these inshore assemblages are less than those calculated by Tietjen (1991) for taxocenes inhabiting middle and outer shelf sands across the central GBR continental shelf, which receive little or no mangrove litter. Total densities of meiofauna and macroinfauna are also, on average, greater at these offshore sites (Alongi 1989).

The patterns of infaunal abundance observed in this inshore area of the central GBR lagoon are in contrast to most across-shelf gradients on temperate and boreal shelves where inshore (inner shelf) communities are enriched by estuarine outwelling compared to middle and outer shelf habitats that are limited by detrital availability (e.g. Hanson et al. 1981; see references in McLuskey & McIntyre 1988).

Inshore benthic communities of low biomass occur on many other tropical shelves (see review of Alongi 1990a), but usually for different reasons, including

Table 4. Percent relative abundance of dominant nematode species ($\geq 0.5\%$) found at the inner GBR lagoon stations, summer and winter samples combined. Numbers in parentheses rank the 10 most abundant species

Species	Station					
	MB1	MB2	MB3	MB4	MB5	MB6
<i>Innocuonema</i> sp. 1	8.0		1.8			
<i>Sabatieria</i> sp. 1	2.1	9.1	1.8			
<i>Viscosia</i> sp. 1	2.9	1.7		1.6		
<i>Halalaimus</i> sp. 1	2.5	2.8				
<i>Theristus</i> sp. 1	1.8	3.0				
<i>Spirinia parasitifera</i>	1.0	2.1				
<i>Spilophorella paradoxa</i> (2)	4.9		9.2	10.7	9.8	1.9
<i>Scaptrella</i> sp. 1	2.9				1.5	
<i>Paramonohystera</i> sp. 1 (8)	2.1	11.5	2.6			
<i>Pomponema</i> sp. 1	4.5					
<i>Sabatieria</i> sp. 2	4.0	1.7		5.9		
<i>Quadricoma</i> sp. 1	1.4		4.0	1.0	0.8	
<i>Terschellingia longicaudata</i> (3)	2.0	0.7	2.4	2.5	2.7	19.1
<i>Parodontophora</i> sp. 1	2.6	1.6	1.8			0.4
<i>Cheironchus</i> sp. 1	3.4	1.5	2.0	0.5		2.7
<i>Dorylaimopsis punctata</i> (1)	10.4	7.5	6.0	2.6	15.7	10.7
<i>Theristus</i> sp. 4	2.6	3.8				
<i>Marilynia oculissoma</i>	3.9	1.0	5.0	1.9		2.0
<i>Mononcholaimus</i> sp. 1	2.4	2.5				
<i>Ptycholaimellus</i> sp. 1	1.3	6.6	1.0	0.8	1.2	
<i>Mononcholaimus</i> sp. 2	2.0		0.8			
<i>Paracanthonus</i> sp. 1	0.9			2.8		
<i>Siphonolaimus</i> sp. 1	0.5	1.2	1.2	0.7		
<i>Elzalia</i> sp. 1 (6)	1.2	5.0	1.6		8.9	1.8
<i>Hopperia</i> sp. 1	1.2	1.8			2.3	
<i>Laimella</i> sp. 1	0.5	2.5				
<i>Parasphaerolaimus</i> sp. 1		3.2				
<i>Vasostoma</i> sp. 1		5.5	1.0			
<i>Choanolaimus</i> sp. 1		3.1				
<i>Viscosia</i> sp. 3		3.4				
<i>Theristus</i> sp. 8 (5)			20.5			
<i>Terschellingia</i> sp. 3			4.0	3.8	2.8	
<i>Dichromadora</i> sp. 2			5.7	1.4		
<i>Pseudopelagonema</i> sp. 1			6.1	3.5	2.6	
<i>Theristus</i> sp. 9 (4)			3.0	7.4	10.1	2.5
<i>Theristus</i> sp. 10 (10)				15.0		
<i>Halalaimus</i> sp. 6 (9)				7.2	8.8	
<i>Paramonohystera</i> sp. 2 (7)				3.0	2.2	13.2
<i>Sphaerolaimus</i> sp. 2				1.2	1.0	1.3
<i>Cervonema</i> sp. 2				0.5		2.5
<i>Theristus</i> sp. 11				1.0	4.6	
<i>Monhystera</i> sp. 4					4.1	
<i>Sabatieria</i> sp. 4					4.8	6.2
<i>Stylotheristus</i> sp. 1				4.8	1.0	
<i>Metalinhomoeus</i> sp. 2					1.8	2.3
<i>Sabatieria</i> sp. 5						14.0

periodic anoxia, sediment instability caused by thixotropic fluid muds, and 'estuarization' (in sensu Longhurst & Pauly 1987). The latter phenomenon occurs when inner regions of tropical shelves are covered by poorly oxygenated, low-salinity water derived from river runoff during monsoons. Such episodes occur regularly off large tropical rivers (e.g. the Amazon; Aller & Aller 1986) and off coasts of the wet tropics (e.g. India; Seshappa 1953, Harkantra &

Parulekar 1987). Upwelling areas are an exception, where benthic standing stocks are high beneath the highly productive surface waters (Rowe 1981).

In the central GBR lagoon, such phenomena generally do not occur, and so other factors must account for the observed patterns of low to moderate densities and low biomass of a predominantly surface- (or near-surface-) dwelling infauna. These include: (1) low food availability, (2) physical disturbances and

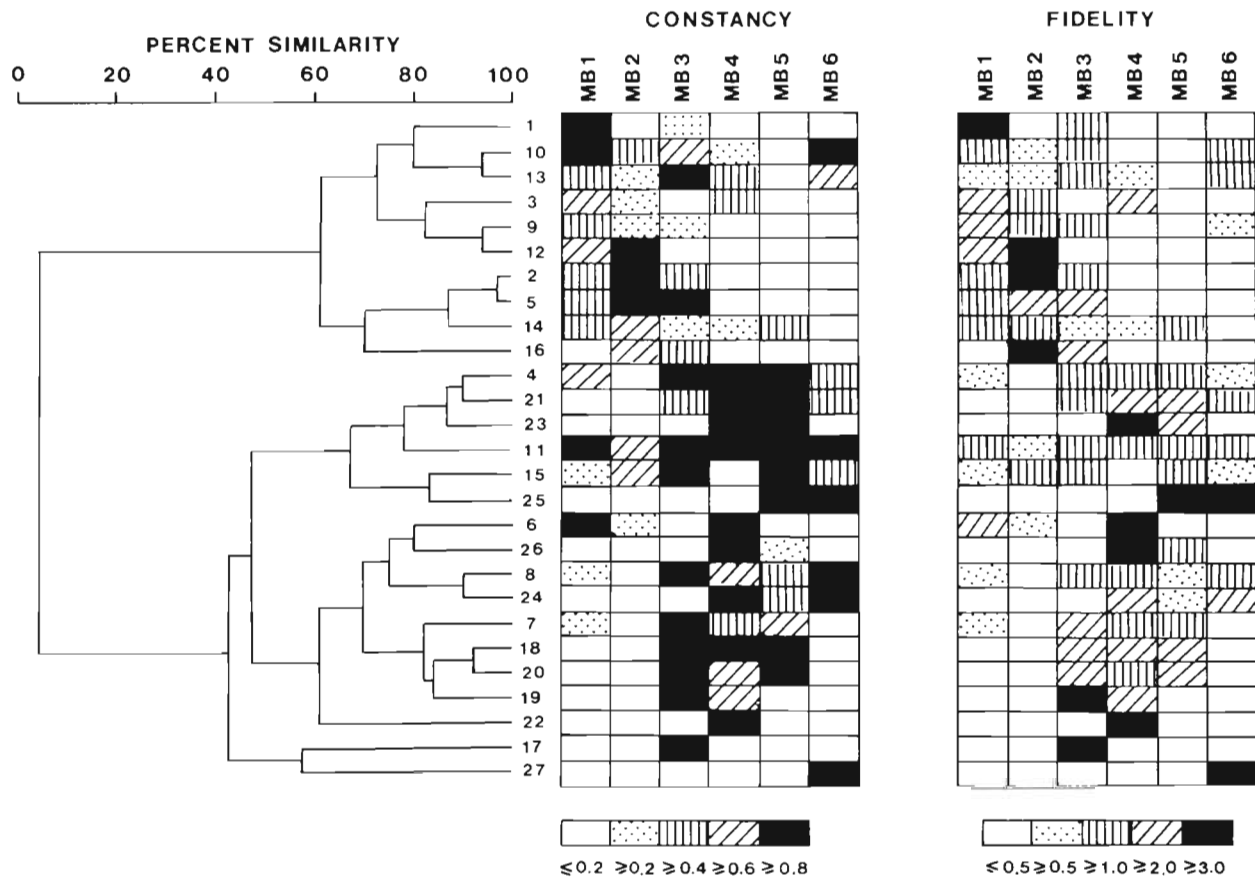


Fig. 9. Inverse classification of the dominant (mean relative abundance $\geq 1.0\%$) nematode species at all 6 stations (August 1987, January–February 1988) and their nodal statistics showing constancy and fidelity indices. Key to species: (1) *Innocuonema* sp. 1; (2) *Sabatieria* sp. 1; (3) *Viscosia* sp. 1; (4) *Spilophorella paradoxa*; (5) *Paramonohystera* sp. 1; (6) *Sabatieria* sp. 2; (7) *Quadricoma* sp. 1; (8) *Terschellingia longicaudata*; (9) *Parodontophora* sp. 1; (10) *Cheironchus* sp. 1; (11) *Dorylaimopsis punctata*; (12) *Theristus* sp. 4; (13) *Marilynia oculissoma*; (14) *Ptycholaimellus* sp. 1; (15) *Elzalia* sp. 1; (16) *Vasostoma* sp. 1; (17) *Theristus* sp. 8; (18) *Terschellingia* sp. 3; (19) *Dichromadora* sp. 2; (20) *Pseudopelagonema* sp. 1; (21) *Theristus* sp. 9; (22) *Theristus* sp. 10; (23) *Halalaimus* sp. 6; (24) *Paramonohystera* sp. 2; (25) *Sabatieria* sp. 4; (26) *Stylotheristus* sp. 1; (27) *Sabatieria* sp. 5

(3) moderate to high predation pressure by epibenthos and demersal fishes.

The former 2 explanations appear to be the most likely factors because epifaunal densities and numbers of bottom-dwelling fish are low in this area (Daniel & Robertson 1990). Seasonal variations in the amounts of mangrove detritus deposited to the seabed in this

Table 5. Species diversity (H') and evenness (J'), species richness (SR) and number of species (NS) per station in the inner GBR lagoon. Values depict summed winter and summer data

Station	H'	J'	SR	NS
MB1	3.13	0.75	10.42	65
MB2	2.42	0.68	6.03	35
MB3	2.11	0.59	5.89	36
MB4	2.65	0.66	8.08	54
MB5	2.17	0.61	5.01	35
MB6	2.02	0.56	6.81	36

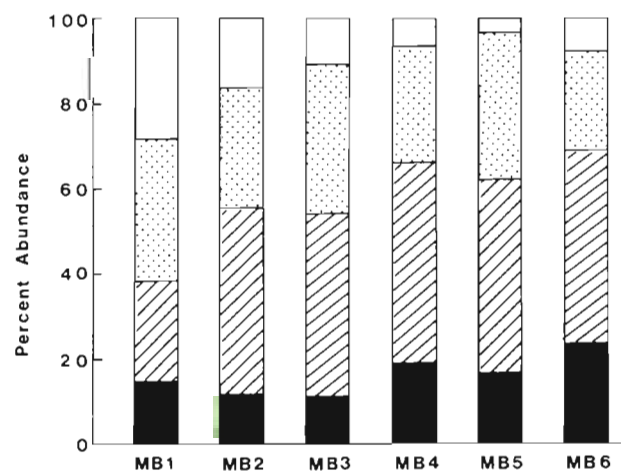


Fig. 10. Trophic structure of nematode communities (percentage of relative abundance) at all 6 stations. ■ Selective deposit-feeders; ▨ non-selective deposit-feeders; ▩ epigrowth feeders; □ omnivore/predators

region explain a significant proportion of the variance in total and component densities of epibenthos. Teleosts (mostly Gobiidae) and penaeid prawns respond positively to the litter (≥ 2 mm pieces) which may provide a refuge from predatory fish. However, these clumps of larger (≥ 2 mm) pieces of litter are generally more patchy than the finer (~ 0.5 mm) debris, occurring in highest concentration within the tidal mangrove creeks. Moreover, densities (< 2 ind. m^{-2}) and biomass (0 to 740 mg DW m^{-2}) of epibenthos were lower than those recorded in other studies. Daniel & Robertson (1990) attributed these patterns and the low abundance of epifauna to physically harsh conditions and the low food quality of mangrove litter.

It is clear that this detritus is of low nutritional quality, as reflected in its high C:N ratio (see Table 2) and as gleaned from other benthic studies on the decomposition kinetics of mangrove (*Rhizophora* spp.) detritus (Rice & Tenore 1981, Zieman et al. 1984) and its suitability as a source of food for bacteria (Alongi et al. 1989), protozoa (Alongi 1990c), meiobenthos (Alongi 1987, Tietjen & Alongi 1990) and macrofauna (Tenore 1983, Giddins et al. 1986). Nearly all of the laboratory growth studies found a similarly negative, or slightly positive, growth response (as r , intrinsic rate of natural increase) and low carrying capacity (Tenore 1983, Tietjen & Alongi 1990). Most mangrove (mainly *Rhizophora* spp.) detritus is very refractory and decomposes very slowly compared to seaweeds and even compared to other vascular plants, such as marshgrasses (Rice & Tenore 1981), which show a different mode of decomposition with respect to total nitrogen content and amino acid composition (Zieman et al. 1984).

The poor growth response of benthic organisms to mangrove detritus may be caused not only by its refractory nature, but also by polyphenolic acids (tannins) leached from the material. For example, Poo-vachiranon et al. (1986) found that feeding rate of the amphipod *Parhyale hawaiiensis* was poor on a diet of tannin-rich mangrove detritus. Similarly, the deposit-feeding nematode *Terschellingia longicaudata* did not grow on fresh, tannin-rich *Rhizophora stylosa* leaves, grew poorly on tannin-poor leaves of *Avicennia marina*, but grew best on a diet of tannin-free, mixed cereal (Alongi 1987).

Tannin content may, however, act with available nitrogen as a hierarchical feeding cue (Valiella et al. 1984, Tietjen & Alongi 1990), whereby complex relationships may exist between detrital nitrogen content, tannin content and age. For instance, the nematode *Monhystra* sp. grew poorly in the laboratory on a diet of fresh *Rhizophora stylosa* detritus but grew very well on a mixed diet of fresh *R. stylosa* detritus and cereal (Tietjen & Alongi 1990), suggesting either that the cereal absorbed (or adsorbed) the tannins or that the

high nitrogen content of the cereal more than compensated for the high tannin content of the cereal-litter mixture, as similarly observed for the marsh gastropod *Melampus bidentatus* by Valiella et al. (1984).

Total sedimentary N content in this region relates well to the standing crop of deposited litter (Alongi 1990b), suggesting that most of the total sedimentary nitrogen is mangrove-derived and nutritionally unavailable. Total N content is not always a good predictor of nutritional availability of sediments because many N-rich, organic complexes, such as fulvic and humic acids, are found in sediments but are not assimilable by organisms (Rice 1982). This may be particularly true for these sediments because other sources of nitrogen are probably minor. Bacterial numbers and production are very high in these deposits (Alongi et al. 1989, Alongi 1992), but microalgal and protozoan densities are low (Alongi 1990b, c). Benthic net primary production is usually undetectable at these stations and rates are low when detected, ranging from 12 to 77 mg C m^{-2} d^{-1} (Alongi 1990b). Plankton production is moderately high, averaging 563 mg C m^{-2} d^{-1} , but most of the production originates from the nano- and pico-size fractions (Furnas & Mitchell 1988) which is more likely to be recycled in the water column than to deposit onto the seafloor. Seagrass beds do occur in this region (e.g. near the Brook Islands), but are small in area and likely to export significant quantities of seagrass detritus only over very short distances. For example, Stn MB1 is located ~ 1 km from a fringing seagrass bed, which may account for the high infaunal densities at this site, but the quantity of seagrass detritus deposited, although of higher nutritional quality than the mangrove litter (see C:N ratios of detritus, Table 2), is small. Seagrass debris or detritus derived from other plants were not found at any of the other stations.

It is possible that higher quality food is deposited in this area as a result of river runoff during the wet season or from phytoplankton blooms resulting from cyclones (Furnas 1989). However, such inputs are episodic and difficult to monitor. Export from the GBR is also possible, but unlikely, considering water mass motion in the lagoon (Wolanski & Pickard 1985) and the high rates of detrital deposition and utilization within lagoons of individual reefs of the GBR (Hansen et al. 1992). It is therefore likely that these inshore benthic communities are food- (mainly N-) limited, deriving most of their nutrition from the bacteria, litter per se and low standing amounts of microalgae.

The other major factor likely to influence the infaunal communities in this region is physical disturbance. All of these stations are above the shoaling depth for wind waves and tidal scouring. Evidence for

infrequent physical disturbances may be found in the X-radiographs, particularly from Stns MB3 and MB5. The sedimentary fabric at these sites reveals cross-bedding and shell-gravel layers, features that are likely produced by erosional episodes (Rhoads & Boyer 1982). Summer cyclones, storms and wet-season floods are capable of scouring the seabed in this area (Gagan et al. 1988, 1990). For instance, Cyclone Winifred crossed the central GBR shelf in 1986, producing mud drapes and erosional facies out to 30 km offshore to a depth of 43 m.

More frequent disturbances may be produced by tidal scouring. With the coincidence of spring tides (up to 3.4 m) and low sea-level (sea-level may vary by up to 35 cm; Wolanski & Gardiner 1981), scouring and resuspension of the seabed is likely to occur, particularly at the shallowest, least protected sites (e.g. Stns MB3, MB4 and MB5). The frequency of such events, especially the oscillations in sea-level, is not entirely determined by astronomical tides and is likely to occur several times a year (Wolanski pers. comm.), perhaps frequent enough to maintain pioneering seres and to retard the establishment of large, equilibrium assemblages (Probert 1984).

The interpretation of the X-radiographs is in good agreement with the $\delta^{13}\text{C}$ and ^{210}Pb studies of Torgersen & Chivas (1985) in the same area. They calculated sedimentation rates ranging from 0.2 to 1.0 cm yr⁻¹, rates that would not necessarily produce clear laminated deposits (which were not observed in the X-radiographs). More importantly, based on the $\delta^{13}\text{C}$ values, most carbon in these sediments is derived from mangrove debris, which also indicates low inputs from other sources. They also calculated mixed-layer thickness, an indication of sediment remixing, and found that the shallowest sites are mixed to a depth of 5 to 30 cm, supporting the idea that these sediments are periodically disturbed. Mixing must occur mainly via physical scouring, resuspension and re-deposition, as there is little bioturbation below the top 5 to 6 cm at most of these stations (Figs. 2 to 5).

In conclusion, it appears that low food availability (poor nutritional value of mangrove litter), periodic disturbances by climatic events and tidal scouring, and, to a much lesser extent, predation by epibenthos and demersal fishes are the major factors regulating the distribution, abundance and structure of benthic infaunal assemblages in this shallow coastal region. These factors perpetuate infaunal assemblages (and their temporal-spatial heterogeneity) that are characteristic of oligotrophic and/or high disturbance regimes (sensu Rhoads & Boyer 1982) found on other shallow, tropical and subtropical continental shelves (Aller & Aller 1986, Warwick & Ruswahyuni 1987, De Wilde et al. 1989). As found in other warm-water regions (e.g.

Rodelli et al. 1984, Fleming et al. 1990), mangroves in the central GBR lagoon exert a significant, but localized, effect on coastal food chains.

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