

Meiofauna sediment relations in leeward slope turf algae of Heron Island reef

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Abstract As part of studies investigating the influence of grazers on reef meiofauna, we assessed the density, composition and richness of meiofauna (retained on a 100- μm sieve) on the leeward reef slope of Heron Reef, GBR, Australia using an airlift vacuum sampling device. Estimates of meiofauna densities ranged between 40 individuals 10 cm^{-2} and 290 individuals 10 cm^{-2} , which is considerably lower than many estimates from carbonate sediments and hard substrates from other reefs and marine habitats. The 17 taxa of meiofauna were dominated by harpacticoid copepods (40%) and nematodes (32%). Varying sediment load within algal turfs explained 37% of variation of meiofauna density. A model is proposed in which increased shelter afforded by high living coral cover reduces meiofaunal losses from grazing and increases sediment loads, balanced by

areas of low coral cover in which sedimentation rates are lower and grazing rates higher. At none of the four sites did major differences in abundance occur between November and March sampling events. Together these observations suggest that epilithic meiofaunal communities are generally spatially and temporally predictable at small scales in this reef system, indicating that their ecological services are similarly conservative.

Keywords Epilithic algal community · Grazers · Settlement · Predation · Vacuum sampling · Coral reef

Introduction

Meiofauna are important to coral reef systems. They influence primary production through micro-grazing (Jacoby & Greenwood, 1988), participate in the breakdown of particulate organic matter (Beesley et al., 2000), provide an obligate food substrate for most juvenile fishes (Choat, 1991; Coull et al., 1995), have temporary membership of motile invertebrate larvae that subsequently migrate to other habitats (Jacoby & Greenwood, 1988), and are an important component of the vertically migrating plankton that at night move up into the water column to disperse (Forward & Tankersley, 2001). Understanding the dynamics of meiofaunal communities is of considerable importance as they are fundamental to many processes that operate in reef systems (Kay, 2005).

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The meiofaunal communities of coral reefs may broadly be divided between those that occur on or within soft sediments and those that are associated with hard substrates (Netto et al., 2003), respectively termed meio-infauna and meio-epifauna (Raes & Vanreusel, 2005). The dominant cover on non-coral hard substrates in reef slope systems is composed of algal turfs (Larkum, 1983), a low-biomass, heterogeneous mat of filamentous, encrusting and unicellular algae from at least five algal divisions (Cyanophyta, Chlorophyta, Chrysophyta, Phaeophyta and Rhodophyta) (Carpenter, 1986; Scott & Russ, 1987). While these turfs provide shelter and food resources for meiofauna, they are subject to considerable grazing pressure (Townsend & Tibbetts, 2004). Hatcher (1983) reported estimates of the number of bites taken per m² of turf algae by various reef grazers per day to range from 50,000 to 150,000. However, some grazers were thought to remove algae instead comb detritus from algal turfs detritus, and presumably components of the turf meiofaunal community (Wilson, 2000).

Differences in algal turf communities between reef zones (Hatcher & Larkum, 1983; Klumpp et al., 1988) are likely to influence meiofaunal communities. Meiofaunal communities are variable both between and within reef zones (Klumpp et al., 1988), which in part may be driven by grazers. Turbulent wave action on the reef rim (Connor & Adey, 1977; Foster, 1987) restricts reef flat access by large grazers to mid to high tides. As a result of grazer exclusion, turf algae standing crop is up to 3–5 times higher on the reef crest compared to other zones (Hatcher & Larkum, 1983). By comparison constant grazing of reef slope turfs keep algal biomass low (Hay, 1981b). However, it is under these conditions of intense and continuous grazing that experiments addressing the influence of grazing on meiofaunal communities are most readily addressed due to the relatively stable conditions, constant grazing pressure and accessibility. Thus, as a prelude to manipulative experiments to determine the influence of various grazers on meiofaunal communities we assessed the natural meiofaunal density, composition and richness on Heron leeward reef slope, predicting that visually uniform turf algal mats should yield similar meiofaunal assemblages.

It is expected that tropical reef turf algae will contain both meio-epifauna, on algal surfaces, and meio-infauna in suitable habitat provided by sediment often trapped within, and at times completely

covering, turf algal mats. Sediment load was measured along with meiofaunal abundances at sample sites.

In order to obviate factors associated with distinct seasonal fluxes in meiofaunal density (Choat, 1982; Klumpp et al., 1988) such as thermal, weather (e.g., summer storms), and day length extremes, and their influence on grazing intensity, predation rates (Hay et al., 1983; Kinsey, 1983), water motion and sedimentation (Mather & Bennett, 1994) samples were taken during spring and autumn only.

Previously meiofauna have been sampled from natural hard substrates either by collecting and transporting samples of algae, sediment, loose substrate or scraping (Danovaro & Fraschetti, 2002) or removing sections of substrate and counting the animals in the laboratory (Kennelly & Underwood, 1985; Raes & Vanreusel, 2005). As an alternative, underwater microscopy has also been used to obtain in situ counts of animals, however, results may have been confounded by animals being influenced by the artificial light source (Kennelly & Underwood, 1985). Suction samplers have been used extensively in soft-bottom communities, while few studies have utilized this sampling technique to investigate hard substrate communities (Choat & Kingett, 1982). Kennelly & Underwood (1985) found that the suction sampler they used did not collect all meiofauna within a turf algal community. However, since our primary objective was to sample sediment and meiofauna from turf algae without removing the algae, we developed an enhanced suction sampler for use in this study. We hypothesized that the meiofaunal community would be depauperate, both numerically and taxonomically, due to the intense grazing pressure on algal turf communities in reef systems.

Materials and methods

Study sites

Four study sites (Fig. 1A, B) on the northern reef slope of Heron Island Reef were equidistant from the reef rim and observed to receive similar exposure to wave motion and currents with comparable temperatures between sites. Sites 1 and 2 were dominated (>50% cover) by live corals while Sites 3 and 4 were dominated by algal turf covered coral rubble. At each site a fixed 20 × 20 m quadrat was established at a depth of

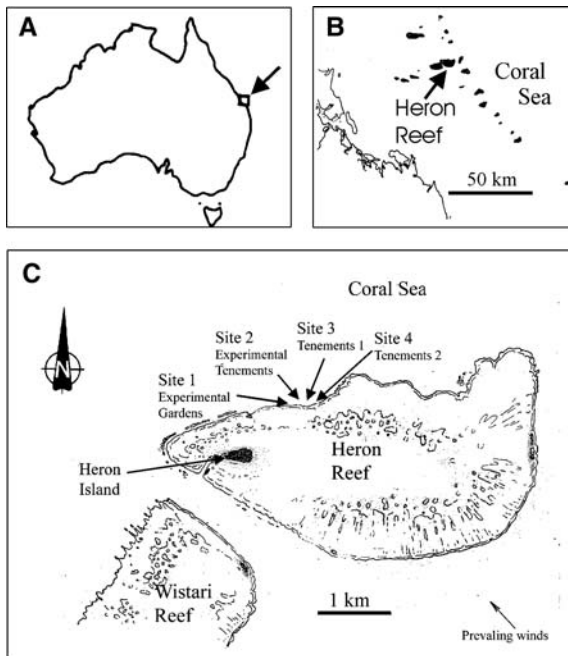


Fig. 1 (A) Map of Australia where an arrow indicates the study region. (B) The study region on which is identified Heron Reef. (C) Map of Heron Island indicating the study sites on the northern (leeward) reef slope

10–12 m (at high tide) using metal pegs and a rope. Due to dive safety and time taken to set out the rope boundaries of the fixed quadrat only a single site could be sampled in a day. Weather conditions sometimes caused up to 3 day pauses in sampling activity.

Meiofaunal sampling

Meiofauna are usually collected using 63 or 42 μm sieves, however, to meet the objectives of the wider investigation of meiofaunal grazing on epilithic algal communities, in which the focus was the larger meiofauna, and to avoid under sampling this fraction due to clogging or low vacuum pressure, we chose a 100 μm mesh. This mesh size is identical to that used by Robertson et al. (2000), similar to that used by Gunnill (1984) (90 μm), and smaller than that used in some comparable reef studies (200 μm mesh—Klumpp et al. 1988; Zeller 1988; Russo 1991).

Meiofauna and sediment were sampled from within a randomly placed 0.5 \times 0.5 m PVC quadrat placed on the upper surface of similar flat coral rubble covered by a visually uniform layer of turf algae within the permanent 20 \times 20 m sites. Four replicate

samples were collected from each of the four sites in November 1998 and March 1999 using a compressed air driven Venturi suction sampler, comprising a 1 m PVC pipe with an internal diameter of 38 mm. Meiofauna and sediment were collected in a 100 μm mesh bag at the upper end of the pipe and prevented from falling back down by a flexible one-way valve. At the mouth of the pipe was a funnel (mouth diameter 100 mm) equipped with bristles to scrape the substrate and maximize meiofauna uptake. After applying the sampler to the substrate for 10 min, the mesh bag and its contents were removed and placed in snap-lock bags for transport to the laboratory.

Rose Bengal was used to stain formalin fixed meiofauna, which were counted in a Bogorov tray and identified to the lowest possible taxonomic rank under a dissecting microscope. Collected sediment was transferred into pre-weighed aluminum trays and dried at 70°C for 72 h and then weighed using a Mettler PM1200 electronic balance (± 0.001 g).

Data analysis

A two-way analysis of variance (ANOVA) was used to test for significant differences in overall meiofaunal density, densities of separate taxonomic categories and sediment load between sites and months. Residual analysis of raw data revealed non-normal distribution of data, so meiofauna densities were log transformed ($\log_{10}(x)$) and sediment load square-rooted transformed (\sqrt{x}) to normalize the data. Tukey's Studentised range test, using data pooled from both months, was used to discern specific differences among sites.

Variation in meiofaunal richness was examined using non-parametric tests, as richness is a discrete variable. Differences in meiofauna richness between sites and seasons were tested using a Kruskal–Wallis non-parametric test. Wilcoxon–Mann–Whitney *U*-tests were used to compare specific site differences. Spearman's coefficient of rank correlations was used to examine the relationship between meiofaunal richness and both meiofaunal density and sediment load. The possible effect of sediment on meiofaunal density was examined with a two-way analysis of covariance (ANCOVA), treating site and time (month) as main factors and including sediment as the covariate. All statistical tests were performed using SAS (Statsoft Inc.).

Results

No statistically significant effect of Month on overall meiofauna density (\log_{10} transformed) was detected at any site ($F = 0.05$; $df = 1, 24$; $P > 0.05$) (Fig. 2A), allowing the pooling of November and March data in subsequent analyses. A significant site effect was evident ($F = 7.64$; $df = 3, 24$; $P < 0.0001$) with Site 2 having significantly lower densities than both Site 3 and Site 4, but similar densities to Site 1 (Fig. 2A). Meiofaunal density at Site 1 was also significantly lower than the density at Site 3 ($t > 4.12$; $df = 1, 24$, $P < 0.05$).

Meiofaunal richness at Site 1 in November (9 taxa sample^{-1}) was lower than at any other site in both months (Kruskal–Wallis: $\chi^2 = 9.6341$; $df = 3$; $P = 0.0219$) (Fig. 2B). Richness was slightly higher in November compared to March at the other three sites but was significant only at Site 4 (Wilcoxon: $\chi^2 = 4.29$; $df = 1$; $P = 0.0384$). Richness correlated poorly with both meiofaunal density and sediment load (Spearman's: $r_s = -0.21$; $P > 0.05$).

Sediment load was highly variable (Fig. 2C) and differed significantly between sites ($F = 4.63$; $df = 3, 21$; $P = 0.0123$) with Site 2 having less than either Site 3 or Site 4 comparing data pooled from both months. Sediment load at Site 2 in March was also lower than sediment load at Site 1 in the same month (sediment loads for Site 1 were not recorded in November). However, sediment loads were only statistically different between Site 2 and Site 3 ($t > 3.94$; $df = 1, 21$; $P < 0.05$). Sediment load did not differ significantly between months at any site ($F = 0.50$; $df = 1, 21$; $P = 0.486$).

Harpacticoid copepods contributed more than 40% to overall meiofaunal density at all sites (Table 1, Fig. 3A, B). Harpacticoid density differed significantly between the two sampling periods ($F = 8.77$; $df = 1, 24$; $P = 0.0063$), with densities in March being twice as high at Site 1 and Site 2 than at the same sites in November. In contrast, lower densities of harpacticoid copepods were recorded at Site 3 and Site 4 in March, compared to November. Nematodes made up more than 32% of the overall meiofaunal density. Nematode densities at Site 3 were twice those at Site 4 and between 7 and 14 times those at Sites 1 and 2, respectively. Polychaete worms, ostracods, calanoid copepods, nematodes and gastropods each contributed above 5% to overall

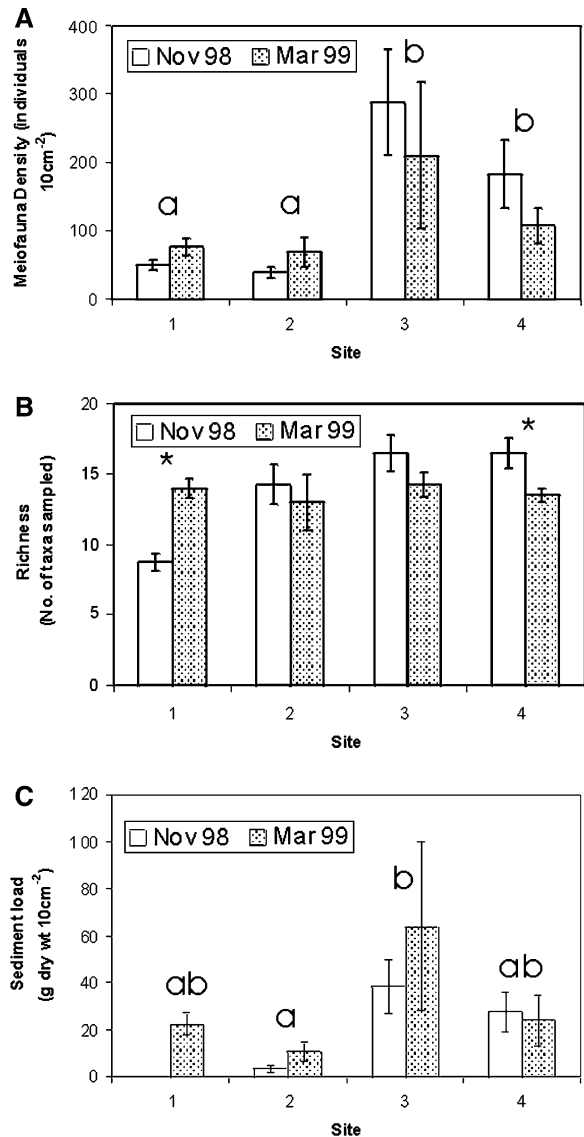


Fig. 2 (A) Meiofaunal density (individuals cm^{-2}) (B) meiofaunal richness (number of taxa), where * significant difference between months sampled; and (C) Sediment load ($\text{g dry weight cm}^{-2}$) sampled at four sites on Heron Island leeward reef slope in November 1998 and March 1999. Error bars = Standard Error. Note: Sediment load for Site 1 in November was not measured. Sites sharing the same letter are not significantly different

abundance. At Site 4 polychaetes not only comprised 22% of total meiofauna in November but only 8% in March, while the densities of ostracods, nematodes, and calanoid copepods did not vary significantly between November and March, but were influenced by site.

Table 1 Mean abundance (organisms 10 cm⁻²) of meiofauna taxa across all sites in both months of sampling at Heron Island, Great Barrier Reef, including mean sediment loads for the same sites (g. 10 cm⁻²)

Taxon	Site 1		Site 2		Site 3		Site 4		Site 1		Site 2		Site 3		Site 4	
	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999	Nov. 1998	Mar. 1999
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Amphipoda			1.04	0.31	0.64	0.26	0.80	0.55	4.48	3.06	1.84	0.66	2.88	1.90	0.80	1.18
Asciacea			0.08	0.16			0.08	0.16	0.08	0.16	0.56	0.76	0.24	0.48	1.76	1.29
Bivalvia	0.96	0.52	0.16	0.18	1.12	0.76	0.56	0.31	1.84	1.82	2.24	2.85	2.56	3.12	1.12	0.61
Calanoida	0.40	0.16	4.00	1.82	3.68	1.49	5.76	5.93	5.76	1.97	5.12	2.34	5.12	3.27	5.84	3.72
Cumacea			2.24	1.25	0.48	0.61	1.20	1.06	4.08	1.66	3.52	2.12	4.24	3.01	0.80	0.55
Cyclopoida	0.88	0.96	0.88	0.55	1.36	2.08	0.72	0.84	1.28	0.87	1.12	0.18	4.00	3.53	0.96	0.69
Decapoda	1.20	1.32			0.32	0.45			0.48	0.41	0.72	1.24	2.00	1.53		
Gastropoda	9.92	3.12	2.88	1.17	1.76	1.44	1.04	0.80	3.60	0.96	3.76	2.87	4.48	1.52	2.88	2.37
Harpacticoida	22.56	13.49	47.60	18.67	19.92	6.58	45.28	28.10	118.24	52.33	96.88	78.01	74.56	36.52	52.24	23.18
Isopoda			1.20	0.99	0.08	0.16	0.56	0.76	4.24	3.46	2.00	0.55	1.04	1.15	2.16	1.44
Nauplii			1.68	0.76	1.76	0.55	1.60	1.14	3.68	1.60	1.76	1.18	5.76	9.83	1.52	0.16
Nematoda	8.16	4.51	8.56	4.51	3.12	1.87	4.56	2.71	112.40	91.88	67.68	103.02	26.48	18.05	26.32	26.88
Ostracoda	2.96	2.73	1.36	1.02	1.84	0.48	0.88	0.96	4.64	2.92	3.28	2.22	2.00	1.89	1.28	0.52
Platyhelminthes			0.08	0.16	0.24	0.48	0.32	0.45	0.24	0.16	0.64	1.28	1.04	0.71	0.72	1.24
Polychaeta	2.16	0.84	3.36	1.82	1.60	1.73	3.52	2.14	18.16	10.32	16.56	20.86	39.84	50.62	8.64	6.79
Tanaidacea			1.04	0.71	0.16	0.18	1.12	1.39	3.04	1.06	1.76	2.30	3.28	5.92	0.32	0.45
Tardigrada			0.48	0.41	0.48	0.55	0.72	1.02	1.52	2.41	0.24	0.31	2.16	4.11	0.08	0.16
Other ^a	0.24	0.31	0.08	0.16	0.88	1.41	0.24	0.34	0.48	0.65	0.32	0.64	0.88	1.22	0.08	0.16
Total Meiofauna	49.44	15.38	76.72	25.16	39.44	15.34	68.96	44.22	288.24	154.79	210.00	213.94	182.56	99.62	107.52	51.83
Sediment Load	^b	^b	22.37	9.31	3.55	3.13	10.85	7.89	38.18	23.15	63.88	71.98	27.58	16.74	23.93	22.02

Blanks cells indicate zero values

^a 'Other' includes small numbers of Echinoida, Ophiuroidea, Stomatopoda, Arachnida, Pycnogonida, Oligochaeta & Hydrozoa

^b Sediment loads for Site 1 were not recorded in November 1998

Examination of sums of squares in the two-way ANCOVA, testing for site and season effects and including sediment load as the covariate, showed that 37% of variation in overall meiofaunal density can be explained by sediment load. The effect of site becomes insignificant once sediment load is considered. Sediment load significantly affected the densities of all taxa of meiofauna examined separately.

Discussion

Meiofaunal abundances in Heron turf algae were in the lower range of values published for many coral reef benthic habitats (Table 2). They are similar but still lower than densities reported by Danovaro & Fraschetti (2002), who sampled meio-epifauna from

hard substrates in the Mediterranean. They found that the nature and structure of substrate is the primary determinant of meiofaunal assemblages, reporting a sevenfold fewer meiofauna on hard substrates of submerged rock cliffs, covered in macroalgae and mussels, compared with sediment samples at the cliff-base. While meiofaunal densities in the present study are probably partly influenced by mesh size, because the 100 µm mesh is likely to have permitted escape of the smaller meiofauna, the results agree with Danovaro & Fraschetti's (2002) prediction.

Meiofauna density did not differ significantly between November and March, at any site. Similarly, Klumpp et al. (1988) recorded slight or no seasonal variation of meiofaunal density on open grazed areas of turf algae on Davies Reef. However, significant differences between summer and winter have been observed (Choat & Kingett, 1982; Gibbons &

Fig. 3 Relative abundance of significant meiofauna taxa sampled at 4 sites on Heron Island leeward reef slope in (A) November 1998 and (B) March 1999. Significant taxa are considered those comprising an average equal to or greater than 5% of total meiofauna abundance at one or more sites

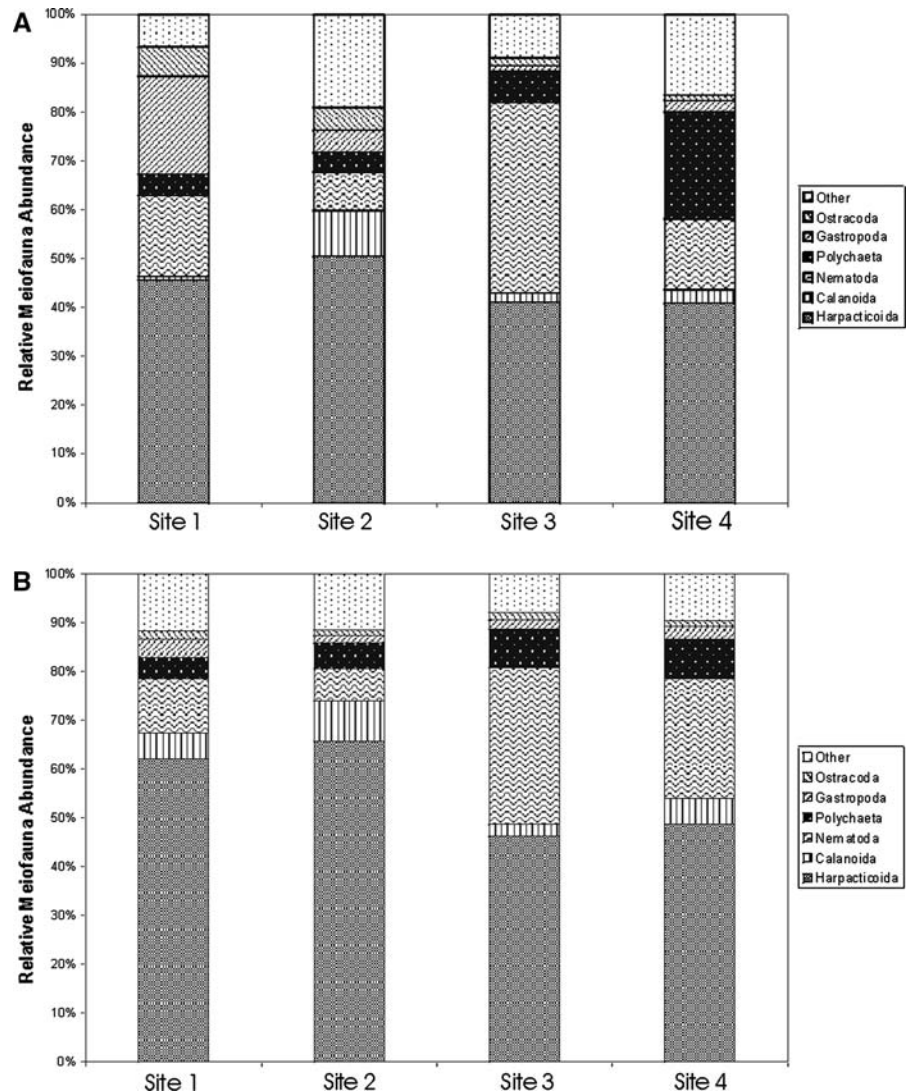


Table 2 Published mean meiofaunal densities (ind. 10 cm⁻²) from a range of tropical and temperate substrates

Mean meiofaunal density	Substrate	Location	Source
38.7	Reef lagoon sediments	French Polynesia	Thomassin et al. (1982)
54–250 ^a	Reef turf algae	GBR	Present study
99–575	Subtidal carbonate sand	Costa Rica	Guzman et al. (1987)
130–940 ^a	Hard substrates	Mediterranean	Danovaro & Fraschetti (2002)
278–4,165	Reef edge pool sediments	Brazil	Netto et al. (2003)
9,989	Reef lagoon sediments	French West Indies	Boucher & Gourbault (1990)
3,150–6,095	Carbonate sediments	Madagascar	Thomassin et al. (1976)

^a Meio-epifauna

Griffiths, 1986), correlating with seasonal fluxes in turf algae biomass in areas of reduced grazing pressure (Klumpp et al., 1988). Danovaro &

Fraschetti (2002) report a similar positive correlation of copepod and amphipod density with macroalgae biomass and substrate complexity on a submerged

cliff in the Mediterranean Sea. Klumpp et al. (1988) also found that while densities of amphipods and copepods were significantly lower in most locations in winter, densities of other crustaceans did not differ significantly between seasons. Thus, it seems likely that meiofauna densities in the turf algae of GBR reefs are relatively stable over time.

Slightly higher values of richness, in November 1998, result from transient or temporary meiofauna, such as larval decapods, which comprised less than 2% of total meiofaunal numerical composition. A similar increase in richness was reported by Gibbons & Griffiths (1986) as a result of addition of “temporary meiofauna” to a rocky shore community.

Sediment and meiofaunal density and richness

Sediment load accounted for 37% of variation within meiofaunal density between sites, and had a comparable effect on densities of each major taxon investigated. Total meiofaunal densities were lower at live coral dominated sites (1 and 2) than at rubble dominated sites (3 and 4). This might be a function of increased substrate complexity at live coral dominated sites providing refuges for a higher density of grazers (Hay et al., 1983) and meiofaunal predators. A higher density of grazers could reduce the biomass of turf algae (Hay, 1981a, b) and sediment load, and thus, reduce meiofaunal densities compared with other sites.

Reports of positive correlations between meiofaunal densities and sediment load are common (Hicks, 1980; Hulberg & Oliver, 1980; Gibbons & Griffiths, 1986; Danovaro & Fraschetti, 2002). Increased sediment load in algal turf enhances the heterogeneity of the substrate (Gibbons & Griffiths, 1986) and provides more suitable habitat for species such as nematodes and cumaceans, resulting in a direct increase in meiofauna density. Low nematode densities at Sites 1 and 2 corresponded with low sediment loads while the highest nematode density in the present study was seen at Site 3 along with the highest sediment load. Hulberg & Oliver (1980) used this relationship to explain why an increase in the abundance of polychaete worms correlated with enhanced sand deposition within cages in a sandy bottom system. Similarly, nutrients associated with sediment may enhance algal growth, thus, providing further habitat and food (Hicks, 1980). Algae can act to baffle water flow, increasing the deposition of sediment (Gibbons

& Griffiths, 1986). Low grazing rates could similarly cause an elevation of sediment, retention of nutrients, and thus, a larger meiofaunal community.

Sediment load is also likely to reflect deposition rates, which may be influenced by the topographic complexity of surrounding substrata (i.e., dominance of branching coral). A large number of the taxa found within turf algae have been classed as demersal zooplankton, which rise into the water column at night (Jacoby & Greenwood, 1988). Settlement of planktonic larvae and demersal zooplankton might be enhanced by factors that increase rates of sediment deposition, resulting in increased meiofauna density. While cause and effect cannot be separated without manipulative experiments the direct positive relationship between meiofaunal abundance and sediment suggests that factors affecting sediment load are likely to influence meiofaunal communities. In our model, intense grazing may lower both sediment load and meiofaunal density, and/or increased shelter (among living coral communities) by slowing water velocity may reduce grazing (removal of sediment and meiofauna) and precipitate sediment. These factors may be central to the patterns of abundance of meiofauna on reef substrates, and therefore, influence their capacity to contribute to reef grazing services.

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