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# THE MICRODISTRIBUTION OF CORAL SAND MEIOFAUNA AFFECTED BY WATER CURRENTS

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CORAL SAND  
FLUME EXPERIMENT  
HYDRODYNAMICS  
MEIOFAUNA  
INTERSTITIAL FAUNA

**ABSTRACT** – The influence of different flow regimes, caused by coral heads, on the meiofauna distribution has been studied in sublittoral sediments of a Jamaican coral reef. Quantitative sediment cores were sampled and *in situ* flow rates measured by SCUBA diving. Laboratory experiments simulating different flow regimes were conducted in a circulating flume tank. The sediment was coarse grained and well oxygenated. Both field studies and laboratory experiments showed a significantly increased abundance of interstitial meiofauna where flow rates were increased but sediment was not eroded. Where the flow regime caused sediment destabilization and erosion, the abundance of meiofauna decreased significantly. The results indicate that in a coral reef system the distribution pattern of interstitial meiofauna is substantially influenced by the complex and temporally changing water flow regime.

SABLE CORALLIEN  
CANAL HYDRODYNAMIQUE  
HYDRODYNAMIQUE  
MÉIOFAUNE  
FAUNE INTERSTITIELLE

**RÉSUMÉ** – L'effet de régimes de courants différents causés par des bancs de coraux sur la distribution de la méiofaune a été étudié dans les sédiments sublittoraux d'un récif corallien de la Jamaïque. Les prélèvements quantitatifs ont été effectués et la vitesse du courant mesurée *in situ* en plongée. Les expériences ont été réalisées dans un canal hydrodynamique dans lequel l'eau circule à des vitesses différentes. Le sédiment était grossier et bien oxygéné. Les recherches *in situ* ainsi que les expériences au Laboratoire montrent une abondance élevée de la méiofaune interstitielle lorsque la vitesse du courant croît sans perturber le sédiment. Si les courants déstabilisent ou érodent le sédiment, l'abondance de la méiofaune diminue de façon significative. Les résultats indiquent que, dans les systèmes de récifs coralliens, le régime hydrodynamique complexe et variable exerce une grande influence sur la distribution de la méiofaune interstitielle.

## INTRODUCTION

In many coral reef sediments, large singular blocks termed 'coral heads' are found. They are mostly covered with stony corals, soft corals, sponges and different filamentous algae. Hydrodynamically, these coral heads represent isolated roughness elements. When encountered by a steady flow, these structures produce a secondary flow pattern with enhanced currents in their wakes due to the formation of eddies (Eckman *et al.*, 1981). Hence, they create a complicated hydrodynamic pattern of possible relevance for meiofauna distribution.

It is known, that the horizontal and vertical distribution of meiofauna depends on numerous abiotic and biotic factors among which the water regime and grain size composition play a key role (Gray, 1966; Boaden, 1968; Coull, 1970; Rieger

& Ott, 1971; Riedl & Machan, 1972; Fegley, 1987). But only few studies considered the impact of hydrodynamics on the meiofauna from calcareous sands with their granulometric regime differing from that of siliceous sands (Giere, 1993).

During a short stay in a Jamaican coral reef, the senior author had the occasion to investigate the influence of water currents on the abundance and vertical distribution of interstitial meiofauna in subtidal calcareous sediments. An area outside a coral head wake, influenced only by the main stream flow, was investigated for its meiofauna abundance and distribution and compared with an area inside the wake where the flow pattern was modified by the protruding boulder structure. Field studies were supplemented by laboratory experiments using a seawater flow tank with original sediment in order to prove the effect of various water flows on the vertical distribution of meiofauna.

## METHODS

### Study area

The study was carried out by SCUBA diving in the coral reef of Discovery Bay, off the north coast of Jamaica, West Indies, from February to March 1990. The study site was a sand channel on the fore reef area ("Mooring One") with several isolated coral heads in a water depth of 13 m. The coral head chosen (1.5 m diameter) was located in a wide channel, through which passed the main stream flow. The sample location outside the coral head wake, serving as a reference, was always 2 m away from the coral head sampled. Local flow speeds inside and outside the wake were measured one centimeter above the sediment surface with a thermistor flowmeter (LaBarbera & Vogel, 1976). Mean flow speed was determined 0.5 m above the sediment with a conventional electromagnetic flow recorder (S4-meter).

### Granulometry

Core samples were collected at nine dives with a perspex corer (internal diameter 4.2 cm = 13.6 cm<sup>2</sup> area) to 6 cm depth. Due to restricted diving time, at each dive one sediment core inside and one core outside the wake of the coral head were taken for granulometric analysis. After determining the wet weight, the core (80 cm<sup>3</sup>) was dried at 85° for 12 h, weighed again and the water content calculated. By dry sieving the median grain size (Md) was assessed and the sorting coefficient calculated as the "inclusive graphic standard deviation" (Gray, 1981; Giere *et al.*, 1988).

### Meiofauna

At each dive two cores for meiofauna evaluation were taken adjacent to the cores for granulometric analysis, i.e. one core inside and one core outside the wake of the coral head. Each core was subdivided in two 3 cm-sections (volume 40 cm<sup>3</sup> each) for separation of a "surface layer" from a "deeper layer". The living fauna was then extracted by triple decantation through a 63 µm sieve after anaesthesia (7.5 % MgCl<sub>2</sub>). This method is appropriate in coarse sediments where the large sediment particles have a higher sinking rate than meiofauna (Ankar & Elmgren, 1976, Pfannkuche & Thiel, 1988). Sorting and enumeration of the specimens was done in a "Bogorov sorting tray" (Giere, 1993) at 20 × magnification using a dissecting microscope. In this study the meiofauna was classified to higher taxonomic levels only. Interstitial protozoans were not considered.

### Flume experiments

The laboratory experiments were conducted in a circulating flume of natural seawater (LaBarbera & Vogel, 1976; Vogel, 1983) flowing over a bottom compartment which contained natural sediment (Fig. 1). For each experimental series (see below), one stratigraphically undisturbed sediment boxcore (15 × 25 × 7 cm) was carefully collected by SCUBA-diving from the sand channel and brought in the laboratory. Here, the sediment core was positioned in the flume tank so that the sediment surface was flush with the edges of the bottom compartment in the flow tank. After at least 1 h of equilibration time, each experimental series started by exposing the sediment to flow regimes causing no visible sediment movement (flow speed between 2.0 and 30.0 cm·sec<sup>-1</sup>). After an exposure time of 1.5 h, one meiofauna core was taken from the sediment.

Finally, a flow regime causing sediment erosion, was induced by removing the flow straighteners out of the flow tank (flow velocity: 30.0 cm·sec<sup>-1</sup>). The water was checked for suspended animals after installation of a 63 µm-sieve at the end of the flow channel. After an exposure time of 0.5 h, one meiofauna core was taken from the sediment.

In order to keep disturbance and dislocation through the sampling procedure reasonably low, the core samples (4.2 cm<sup>2</sup>) were only pushed down to a depth of 4 cm, but not to the total depth available in the flume system (7 cm, Fig. 1B). The

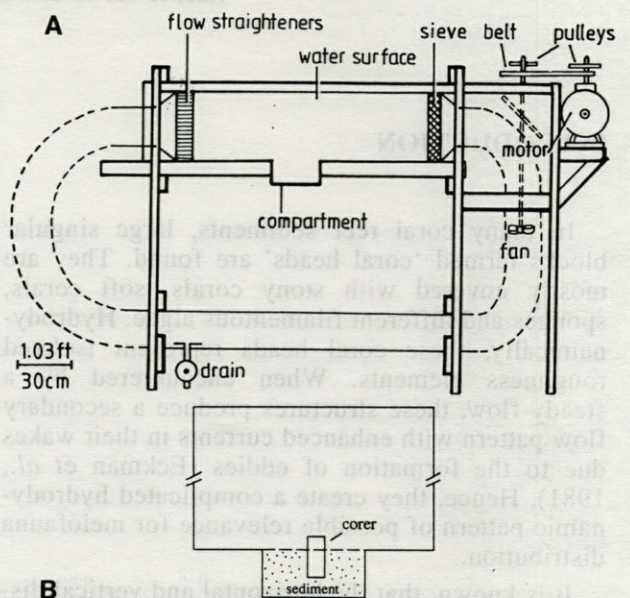


Fig. 1. - Flow tank (after Vogel, 1983; modified): A, side view of the circulating system and B, cross section of the flow tank with corer in sampling position.

cores taken were subdivided into two 2 cm-sections and treated as described above for quantitative fauna analysis. For independent replicates, each flume experiment was repeated four times with newly collected sediment.

### Statistics

Statistical comparisons among the various meiofauna groups were made using a paired t-test (Sokal & Rohlf, 1981): (a) in the field, conditions were compared inside and outside the coral head wake, (b) in the flume, those under non-erosive and erosive currents.

## RESULTS

### Abiotic parameters

#### Flow rates in the field (Table I)

The water flow downstream a coral head was recorded to be often twice as fast as the main general flow in the channel. Seven dives in calm weather had fairly uniform conditions without any visible sediment movement or erosion: While the averaged flow speed in the main channel ( $6 \pm 2 \text{ cm}\cdot\text{sec}^{-1}$ ) and outside the wake of the coral head ( $7 \pm 2 \text{ cm}\cdot\text{sec}^{-1}$ ) were relatively low and similar, it increased to  $14 \pm 3 \text{ cm}\cdot\text{sec}^{-1}$  inside the wake of the coral head. Clearly different flow speeds were recorded from two dives in rough weather. Here, sediment erosion was observed inside the coral head wake and flow speed increased up to  $39.5 \text{ cm}\cdot\text{sec}^{-1}$ .

Table I. – Flow rates ( $\text{cm}\cdot\text{sec}^{-1}$ ) at investigation sites from each sampling. n.d. = not determined, + = visible sediment movement.

WEATHER CONDITION	DATE	MAIN STREAM	INSIDE WAKE	OUTSIDE WAKE
CALM	18.2.90	8,1	16,1	7,8
	21.2.90	5,1	n.d.	n.d.
	24.2.90	4,8	n.d.	n.d.
	06.3.90	3,2	n.d.	n.d.
	19.3.90	6,1	10,4	4,2
	20.3.90	4,6	n.d.	n.d.
	21.3.90	8,2	15,9	7,7
ROUGH	08.3.90	15,6	+ 39,5	12,1
	17.3.90	9,8	+ 28,1	9,3

### Granulometric analysis

At "calm" flow regimes the median particle diameter (MD) both inside and outside the wake was fairly uniform. Its median grain size ( $600 \mu\text{m} \pm 100 \mu\text{m}$  SD) corresponded to "medium" sand, its sorting coefficient (QDI = 0.81-0.85) indicated the sediment to be "moderately sorted". At rough flow conditions causing sediment movement, the sediment inside the coral head wake had changed composition: "coarse" sand (Md =  $1300 \mu\text{m}$ ), "moderately well sorted" (QDI = 0.64). Outside the wake, the sediment remained essentially the same as under "calm" conditions: "medium" sand and moderately sorted (QDI = 0.9). It is interesting to note that after the period of erosive agitation due to rough weather, the sediment structure fairly quickly re-established to values typical for the previous calm weather. This indicates a dynamic but fairly resilient system.

Average water content at all flow regimes was 30 % ( $\pm 1.7$  % SD). Judging from the coloration, the sediment in the sampling cores was fully oxidized throughout.

### Fauna composition

98 % of the meiofauna found in the field sites belonged to 6 main groups: copepods (39.3 %), nematodes (20.4 %), polychaetes (17.2 %), turbellarians (12.6 %), ostracods (7.4 %) and oligochaetes (1.5 %). Other meiofaunal groups that occurred with less than 1 % were halacarids (0.8 %), tardigrades (0.5 %), the hydrozoan *Halammohydra* sp. (0.5 %) and several gastrotrichs (0.2 %). Interstitial protozoans were not considered in this study. These six dominant groups were evaluated for meiofauna abundances inside and outside the wake of the coral head.

### Field samples

The total meiofauna density at each sampling date is shown in Fig. 2. Each column represents one core, therefore no standard deviations are indicated. The somewhat higher overall numbers of meiofauna in mid-March may be referred to a seasonal increase, but this does not alter the general notion that (with one exception on March 19) usually the sediment inside the wake under relatively high, but yet non-erosive flow conditions harboured more meiofauna than that outside the wake. The situation was clearly changed when inside the wake erosive flow conditions prevailed (March 8 and 17): meiofauna numbers became reduced below the level of those outside the wake.

In a more differentiated analysis (Fig. 3) of various meiofauna taxa comparing flow conditions without sediment erosion only, it became visible

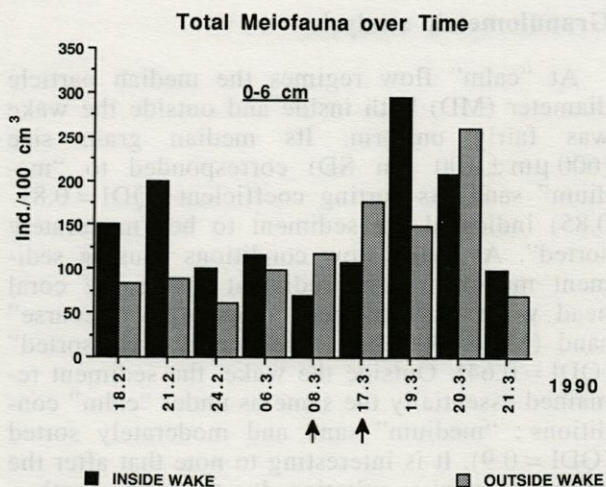


Fig. 2. – Meiofauna density ( $100\text{ cm}^3$ ) per core and sampling date inside and outside the coral head wake in 0-6 cm sediment depth.  $\uparrow$  = visible sediment movement inside the wake.

that the numerical dominance of meiofauna groups under the higher flow rates inside the wake was restricted to the surficial sediments (0-3 cm, Fig. 3 a), but did not refer to the deeper layer (3-6 cm, Fig. 3b). Especially the harpacticoid copepods ( $P < 0.01$ ) and polychaetes ( $P < 0.05$ ) showed a highly significant differentiated pattern, but the overall trend was apparent in all groups.

This distributional pattern is in clear contrast to conditions where turbulent eddies caused a visible sediment movement inside, but not outside the wake (Fig. 4). Now, the surface layer inside the wake contained generally lower meiofauna numbers than under the calmer conditions outside. Especially the abundance of harpacticoid copepods ( $P < 0.1$ ) and nematodes ( $P < 0.05$ ) in the surficial stratum became significantly reduced. Again, at 3-6 cm depth no significant differences between 'inside and outside the wake' were found.

### Flume samples

Fig. 5 summarizes the results of the four flume experiments at different flow conditions comparing the situation at the surface (Fig. 5a) with that in a slightly deeper stratum (Fig. 5b). After flow conditions had increased within 30 min from non-erosive to visible, erosive sediment movement (= no flow straighteners, velocity  $30.0\text{ cm}\cdot\text{sec}^{-1}$ ), in the surface layer nearly all meiofauna groups had lower numbers than before under calmer conditions. This difference was especially marked in harpacticoid copepods ( $P < 0.05$ ) and polychaetes ( $P < 0.1$ , Fisher PLSD = 0.352;  $P < 0.05$ ). In the immediate deeper layer (2-4 cm), no significant changes in abundance could be detected. Here, copepods had

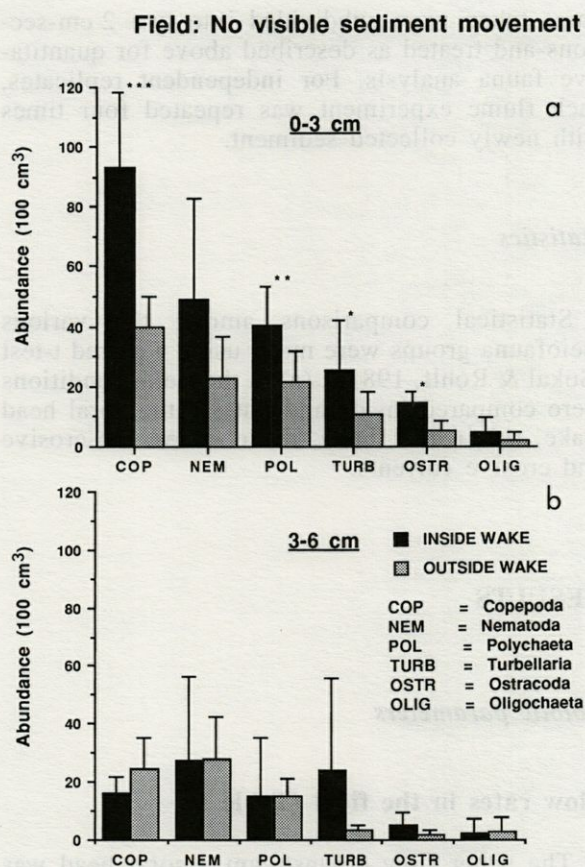


Fig. 3. – Average ( $n = 7$ ) abundance of meiofauna groups ( $100\text{ cm}^3$ ) inside and outside a coral head wake at flow conditions with no sediment movement: (a) 0-3 cm sediment depth and (b) 3-6 cm sediment depth. \* = significant ( $P < 0.1$ ), \*\* = significant ( $P < 0.05$ ), \*\*\* = significant ( $P < 0.01$ ).

even higher numbers under conditions which caused sediment movement at the surface.

Under erosive flow conditions, the sieve installed for retention of suspended animals contained numerous meiofauna with harpacticoids prevailing and nematodes only in a minor portion.

### DISCUSSION

The water flow inside the coral head wake was always considerably higher than the main water current of the "reference" location in the sand channel. In coarse carbonate sediments with their mainly irregular, splintery grains of biogenic origin, a high porosity and permeability is typical, at least for the surface layers (Guzmán *et al.*, 1987). This means that enhanced currents above the sediment will also increase the flow of pore water through the interstitial system. It can be assumed that the interstitial meiofauna inhabiting

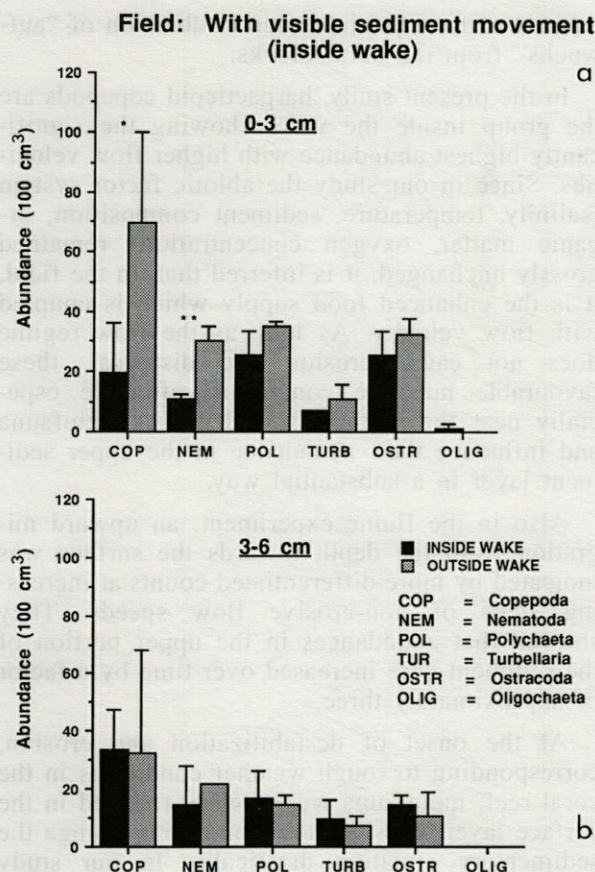


Fig. 4. - Average (n=2) abundance of meiofauna groups (100 cm<sup>3</sup>) inside and outside a coral head wake at flow conditions with visible sediment movement inside the wake : (a) 0-3 cm sediment depth and (b) 3-6 cm sediment depth. \* = significant (P < 0.1), \*\* = significant (P < 0.05).

the sediment around a coral head is exposed to a strong flow in the upper pore water system. This study indicates that interstitial meiofauna preferred these sediments with enhanced flow as long as the current was sub-erosive.

Under non-turbulent field conditions, factors known to be associated with an increased water flow and of possible impact to abundance and distribution of interstitial fauna are :

- enhanced supply with oxygen
- changes in sediment structure
- increased nutrient supply (particulate and dissolved matter)

Below, the relevance of these factors for the results presented here, has to be discussed.

**Oxygen:** Grelet *et al.* (1987), who also recorded highest meiofauna densities in areas of increased water currents in coralline sand, attributed these results to a better oxygenation of the sediments as a consequence of the increased interstitial water flow. In our study, the distribution

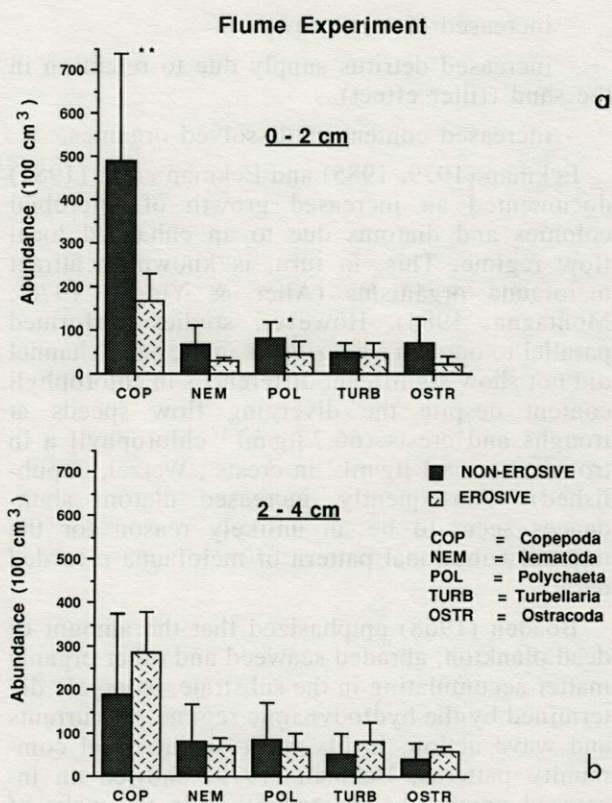


Fig. 5. - Flow tank experiment ; mean (n = 4) abundance of meiofauna groups (100 cm<sup>3</sup>) at flow conditions causing no sediment movement and under flow conditions causing visible sediment movement : (a) 0-2 cm sediment depth and (b) 2-4 cm sediment depth. \* = significant (P < 0.1), \*\* = significant (P < 0.05).

pattern of meiofauna cannot be related to a pattern of varying oxygen supply. Even in areas with a slow flow regime, all the horizons considered were well oxygenated, a visible RPD layer was never encountered.

**Sediment structure:** The structure of the sediment, indicated by grain size and sorting coefficient, is often the key factor for distribution and abundance of infaunal organisms. This refers also to calcareous sands (Renaud-Mornant *et al.*, 1971 ; St. John *et al.*, 1989). However, in the present study this factor seems to be of moderate importance only. Under calm weather conditions (non-erosive flows) the granulometric analysis of the various samples showed no significant differences in sediment composition between the area inside and outside the coral head wake. Nevertheless, the meiofauna abundance in the two areas differed significantly. It was not before the sediment became agitated that differences in the sediment composition became established.

**Food enrichment:** A richer supply of food through enhanced local flow conditions may result from an

- increased bacterial growth

- increased diatom growth
- increased detritus supply due to retention in the sand (filter effect)
- increased content of dissolved organics.

Eckman (1979, 1985) and Eckman *et al.* (1981) documented an increased growth of microbial colonies and diatoms due to an enhanced local flow regime. This, in turn, is known to attract meiofauna organisms (Aller & Yingst, 1978; Montagna, 1984). However, studies performed parallel to ours on sand ripples in the sand channel did not show significant differences in chlorophyll content despite the diverging flow speeds at troughs and crests (66.7  $\mu\text{g}\cdot\text{ml}^{-1}$  chlorophyll a in troughs vs. 68.1  $\mu\text{g}\cdot\text{ml}^{-1}$  in crests; Wetzel, unpublished). Consequently, increased diatom abundances seem to be an unlikely reason for the microdistributional pattern of meiofauna recorded here.

Boaden (1968) emphasized that the amount of dead plankton, abraded seaweed and other organic matter accumulating in the substrate, is largely determined by the hydrodynamic regime, by currents and wave action. In his work on intertidal community patterns, Eckman (1979) showed an increased number of macrobenthos in the wake of structures protruding from the sediment surface. He attributed this to an enhanced particle transport supplying the animals with food particles. The capacity of meiobenthos to sense and accumulate at detrital aggregations has been often underlined (e.g. Gerlach, 1977; Lee *et al.*, 1977; Hogue & Miller, 1991). From deep-sea sediments, harpacticoid copepods were reported to increase in number around biogenic mudballs. This pattern was attributed to the enhanced transport of solutes in these areas of high shear stress (Eckman & Thistle, 1991).

Exposed calcareous sediments can have a low content of particulate organic matter (Salvat & Renaud-Mornant, 1969; Renaud-Mornant *et al.*, 1971; Guzmán *et al.*, 1987). Under these conditions, in coral reefs transport and retention of allochthonous organic matter by an increased flow regime would gain considerable importance for the nutrition of interstitial meiofauna. This would refer not only to particulate, but also to dissolved organic matter. Calcareous sand grains have a microscopical surface structure of a high adsorptive capacity explaining the rich concentrations of dissolved organic substances which are known to be of relevance for many meiofauna (Tempel & Westheide, 1980).

In coral reef areas, harpacticoid copepods are regularly the dominant or sub-dominant meiofauna group (Coull, 1970; Thomassin *et al.*, 1982; Guzman *et al.*, 1987; Arlt, in press). Preferring microphytobenthos and phytal detritus many of them seem to benefit from the higher

amount of food particles due to abrasion of "aufwuchs" from the coral blocks.

In the present study, harpacticoid copepods are the group inside the wake showing the significantly highest abundance with higher flow velocities. Since in our study the abiotic factor system (salinity, temperature, sediment composition, organic matter, oxygen concentration) remained grossly unchanged, it is inferred that, in the field, it is the enhanced food supply which is coupled with flow velocity. As long as the flow regime does not cause erosion and dispersal, these favourable nutritive conditions, effective especially near the surface, would attract meiofauna and influence their abundance in the upper sediment layer in a substantial way.

Also in the flume experiment, an upward migration from the depth towards the surface was indicated by more differentiated counts at increasing steps of non-erosive flow speeds. They showed that abundances in the upper portion of the sediment core increased over time by a factor of approximately three.

At the onset of destabilization and erosion, corresponding to rough weather conditions in the coral reef, meiofauna were clearly reduced in the surface layer. Erosive flow conditions change the sedimentary situation drastically. In our study area, the turbulent water flow eroded the sediment in the wake of the coral head while outside no sediment movement was observed. In the affected areas, a significantly lower meiofauna density, especially for the harpacticoids and nematodes was recorded in the upper sediment layer.

The reduced population density at erosive conditions is usually referred either to an avoidance reaction by vertical migration (Boaden & Platt, 1971; Rieger & Ott, 1971; Nixon, 1976; Meineke & Westheide, 1979; Joint *et al.*, 1982; Fegley, 1987) or to suspension in the water column (Palmer, 1984; Palmer & Gust, 1985; Armonies 1988, 1989). Particularly for harpacticoids, both reactions have often been observed in the field and experimentally confirmed in flume experiments (Palmer & Molloy, 1986; Foy & Thistle, 1991). In the present study, there was no evidence for a downward migration of the organisms: an expected increase in meiofauna abundance in the deeper layer was not recorded in the field. Also the results of the flume experiment do not indicate a downward migratory reaction of meiofauna: after the onset of erosive currents, the 2-4 cm layer adjacent to the surface stratum showed no significant increase in meiofauna density, compared to the situation at non-erosive currents (Fig. 5).

There remains suspension as the other cause for the reduced animal abundance in the surface layer at erosive flow velocities. It has been suggested

that meiofauna organisms can be considered as passive particles subject to erosion by tidal currents (Bell & Sherman, 1980; Palmer, 1986). Palmer & Gust (1985) showed that the number of meiofauna, again particularly that of harpacticoid copepods, in the water column increased as currents and friction increased.

Particularly the investigations by Armonies (1989) demonstrated that suspension of meiofauna is a widespread and common phenomenon. As in the present study, suspension referred mainly to harpacticoids and nematodes. Aggregation near the surface with subsequent emergence may even be beneficial to some meiofauna as an effective means of distribution (Armonies, 1988; Palmer, 1984).

Since, at erosive flow speed, we could not find a significant increase of animals in the deeper sediment layer, we refer the surficial reduction of meiofauna abundance under these flow regimes mainly to suspension of animals. This interpretation is corroborated by the enhanced number of harpacticoid copepods and nematodes retained in the sieve filtering the water above the sediment.

A reaction of meiofauna to a changed predatory pressure seems improbable to explain the quantitative results presented here considering the (experimental) time-scale of the fluctuations and their good correlation with the flow speed.

The results of this study allow for three conclusions:

(1) Meiofauna organisms in the coral sand detect higher flow velocities and respond positively to this factor as long as the flow regime stays sub-erosive. Enhanced flow velocities may improve the trophic situation by an increased input of organic matter.

(2) At erosive water currents, suspension and dispersal of animals lead to reduced surficial meiofauna populations.

(3) Occurring within a short time, the changes in meiofauna abundance can be well separated in time-scale from abundance fluctuations due to reproductive cycles (e.g., changes in recruitment rates at higher flow velocities, Eckman, 1983) or predatory effects.

In the subtidal of a coral reef, the hydrodynamic heterogeneity is an important physical factor structuring the abundance and vertical distribution of meiofauna. Similar results have been previously reported from intertidal communities. The rapid reaction of interstitial meiofauna to changes in the flow regime adapts the animals to the often irregularly fluctuating and strong current regime occurring particularly in the fairly exposed coral reef sands.

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