# Effects of burrowing macrofauna on meiofauna community structure.

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ABSTRACT: Effects of burrowing macrofauna on meiofauna community structure. **A laboratory experiment was carried out aiming to verify meiofauna community's responses to disturbance caused by the macroinfaunal polychaete *Laeonereis acuta* Treadwell 1923 regarding both vertical distribution patterns in sediments, collected from an estuarine region of Patos Lagoon, and predation. Samples were sliced in 6 vertical layers: 0-1, 1-2, 2-4, 4-6, 6-8 and 8-10 cm deep. From the analysis of variance and analysis of similarity and clusters it could be seen that *L. acuta* changed the sedimentary environment, probably irrigating deeper layers and increasing oxygen availability, and hence increasing the abundance of meiofauna organisms in this microhabitat. Predation was not registered for any meiofauna taxa.**
Key-words: **vertical distribution, *Laeonereis acuta*, meiofauna, predation, polychaete,**

RESUMO: Efeito de estruturas construídas pela macrofauna bentônica escavadora nas associações de meiofauna. **Os padrões de distribuição dos organismos bentônicos podem ser alterados por perturbações naturais ou antrópicas no ambiente sedimentar. Através de um experimento de laboratório foi investigado o efeito da presença do poliqueta *Laeonereis acuta* Treadwell 1923 sobre a distribuição vertical da meiofauna no interior dos sedimentos, coletados na região estuarina da Lagoa dos Patos. As amostras foram seccionadas em 6 estratos verticais: 0-1, 1-2, 2-4, 4-6, 6-8 e 8-10 cm. Através de análises de variância do tipo ANOVA e análises de similaridade e agrupamento do tipo ANOSIM e CLUSTER foi possível verificar que a presença de *L. acuta* alterou os gradientes verticais do sedimento, induzindo a migração dos organismos da meiofauna para as camadas mais profundas do sedimento. As condições do experimento em laboratório permitiram ainda, separar o efeito de bioperturbação da predação, verificando que não houve predação de nenhum grupo da meiofauna pelo poliqueta.**
Palavras-chave: **distribuição vertical, *Laeonereis acuta*, meiofauna, predação, poliqueta.**

## Introduction

**The abundance and distribution patterns of benthic invertebrates are both related to the heterogeneity of the sediment environment which they inhabit (Woddin, 1981). The heterogeneity is generated mainly by both natural and antrophic physical and/or biological processes (Hicks, 1984). The biological processes, i.e. bioturbation (Widdicombe & Austen, 1999), are, in general, small scale processes caused by organism activities, *eg.*, when one species changes its surrounding environment, leading to negative or positive responses on the part of another species.**

**Benthic activities in sediments play an important role in changing habitat's physical and chemical characteristics, and hence the meiofauna community structure, in many ways (Reise & Ax, 1979; Creed & Coull, 1984; Ólafsson et al., 1990). This usually occurs over a short time scale (Wilson, 1991). Macrofauna activities tend to favor water circulation, thus increasing the oxygen content in the deeper layers (Mortimer et al., 1999) through burrowing and gallery and tube building (Jones & Jago, 1993). An increase in oxygen content may also be caused by their movement inside these**

structures, while their excretion improves nutrient concentration (Reise, 1985; Warwick et al., 1986) and therefore feeding conditions.

Other trophic-related activities, such as predation and competition may be a potential source of meiofauna disturbance (Austen et al., 1998). Predators can alter meiofauna abundance and distribution by feeding (Coull, 1999) and the bioturbation caused by damaging sediments to catch prey (Sherman et al., 1983).

It is well known that meiofauna animals may occupy different depths in sediment (Joint et al., 1982), although the ecological factors responsible for this behavior remain unclear (Foy & Thistle, 1991), often being related to variations in sediment's physical factors (Fenchel & Riedl, 1970; Smol et al., 1994; Kapusta et al., 2002). Several authors have pointed to interference competition as a factor leading animals to inhabit different vertical layers (Schroener, 1974). However, laboratory experiments with copepod species showed that vertical distribution patterns are more probably related to physical factors than interference competition (Fleeger & Gee, 1986). A macrofauna, which alters the physical characteristics of its habitat, may also alter the vertical distribution patterns of meiofauna community.

In Brazil, few authors focus on bioturbation effects, such as Guilherme (1999) for the polychaete *Diopatra cuprea*.

The choice of macrofauna species when studying effects on meiofauna is in general associated to its ecological importance in terms of abundance and occurrence in the environment to be studied. In the Patos Lagoon estuarine region, southern Brazil, the deposit feeder polychaete *Laeonereis acuta* Treadwell 1923 is of great importance in local trophic food structure, acting as one of the main links between debris and higher trophic levels (Bemvenuti, 1997a). It also achieves significant values of both abundance and biomass (Bemvenuti, 1997b). It is a burrower species, which builds vertical tubes reaching a depth of 20 cm in sediment. This species may therefore affect meiofauna community through both bioturbation and predation.

According to Austen & Trust (2001), meiofauna seems to be relatively insensitive to disturbance caused by the physical handling of sediment, making it suitable for 'cause and effect' laboratory experiments specifically aimed at the study of biological disturbance.

In this study, a laboratory experiment was carried out aiming to test the following hypotheses: 1. The macrofauna activity - with macrofauna represented here by *L. acuta* - changes vertical distribution patterns in sediment and 2. The polychaete *L. acuta* uses meiofauna as a food resource.

## Material and methods

Before setting up the experiment in the laboratory, a sampling of macrofauna was done at two sampling stations placed at opposite ends (Northeastern and Southwestern) of Pólvora Island. This island is located in the Saco do Arraial, a shallow water bay in the central part of the Patos Lagoon estuarine region, RS (32° 01′ 201″ S and 052° 05′ 477″ W) (Fig. 1). Animals were sampled with a 10 cm inner diameter PVC corer pushed 20 cm into the sediment. Samples were sieved through 300 mm mesh, fixed with 4% formaldehyde and stained with Bengal Rose. At the laboratory, they were sorted and quantified under a stereoscopic microscope and any *L. acuta* over 5 cm in length were excluded.

This size class was chosen in order to minimize the effects of variability caused by specimens of different size classes, which may exert distinct ecological functions in the natural environment. A mean density of 470 ind.10 cm$^{-2}$ was registered in the southwest end. The experiment was carried out in the following manner: sediment from the island's northeast end, where no *L. acuta* longer than 5 cm length had been found, was sampled with a 15 cm inner diameter PVC corer pushed about 15 cm into the sediment. The sampled sediment was transported to another PVC corer, which differed from the former only by a lid on the bottom. The PVC inner volume was 0.0026 m$^3$ classifying it as a microcosm (Cowie et al., 2000). The above procedure was repeated 12 times taking great

care with the structure of the sediment environment and hence the meiofauna habitat. Natural water was added to the microcosms, resulting in a water column of 5 cm still in the field. This material was placed in a room with a constant temperature of 27° C, 12:12 light/dark photoperiod, salinity 15, pH 6.8 and permanent aeration. The sediment granulometry ranged from fine to very fine sand (0.125 to 0.145 mm), poorly sorted, with silt and clay mean percentages of 8.15 and 4.49% respectively.
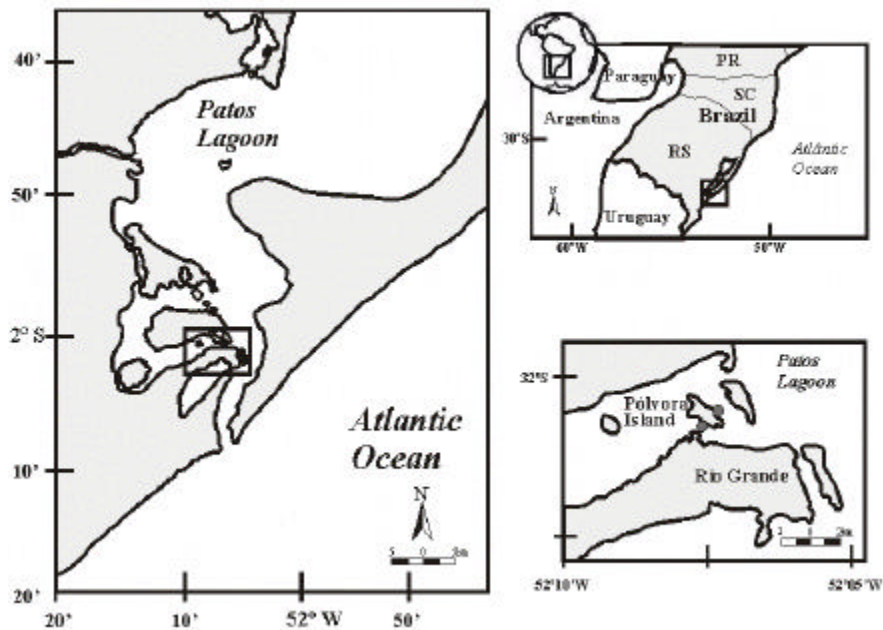


**Figure 1**: Sampling area of sediment and organisms used to set up the experiment  ( ).

Sixty (60) specimens of *L. acuta* over 5 cm in length were sampled one day after the microcosms were set up. The animals were caught by hand, placed in a container with water, carried to the laboratory and randomly introduced into microcosms defining treatments as follows:

Treatment A: **4 microcosms where 10 polychaetes were added, resulting in 588 ind.10 cm$^{-2}$ in each, considered high density.**
Treatment M: **4 microcosms where 5 polychaetes were added, resulting in 294 ind.10 cm$^{-2}$ in each, considered mean density.**
Treatment C: **4 microcosms where no polychaete was added, considered as the experiment control.**
The experiment started 24 hours after the animals had been added, which was considered enough time for microcosm stabilization, and lasted 5 days. During that period, the experiment was monitored in order to maintain the initial abiotic conditions and no food was offered to the animals.
On the fifth day, the meiofauna was sampled in all microcosms being one sample on each, resulting in 4 replicates per treatment. Samples were done with a 0.78 inner diameter PVC corer pushed 10 cm into the sediment and sliced in six vertical layers: 0-1, 1-2, 2-4, 4-6, 6-8 and 8-10 cm. Samples were fixed with 4% formaldehyde, stained with Bengal Rose and the meiofauna organisms quantified and identified at high taxonomic level under a stereoscopic microscope.
The remaining sediment was sieved through 300 **mm** mesh and the macrofauna species fixed, identified and quantified. Feeding content was observed in 10 *L. acuta* specimens through a longitudinal cut in their bodies.

## Statistical treatment

In order to verify whether the only parameter that differed in the treatments was the density of *L. acuta* under 5 cm in length, an analysis of variance was done for macrofauna - except *L. acuta* - density in every treatment. StatisticaÒ v. 5.0 software was used.

To investigate whether mortality had occurred due to both predation and/or bioturbation, the 0-10 cm layer meiofauna in each treatment replicate was analyzed through ANOVAs, comparing the treatments and the control.

It was not possible to attain ANOVA requirements for the differences in meiofauna group density in the vertical layers, so multivariate analysis such as CLUSTER and similarity analysis such as ANOSIM were done using PRIMER (Plymouth Routine in Marine Ecological Research) v. 5.2.4 package. The data was transformed by fourth root as recommended by Clarke & Warwick (1994).

# Results

The analysis of variance done for macrofauna density showed that there was no significant difference ($p < 0.05$) between treatments, which means that the polychaete effects were isolated.

The meiofauna was made up of 7 groups, taking into account all the treatments: Nematoda, Ostracoda, Copepoda, Nauplius, Acari, Rotifera, Turbellaria and two species considered temporary meiofauna: the mollusk *Erodona mactroides* and the polychaete *Laeonereis acuta.*

The total mean density of the meiofauna was 6,756, 6,685 and 6,250 ind.10 cm$^{-2}$ in treatment A (high density), M (mean density) and C (the control) respectively (Tab. I). When a

**Table I:** Mean and standard deviation of the meiofauna groups (ind.10cm$^{-2}$) in each layer (0=0-1cm, 1=1-2 cm, 2=2-4 cm, 4=4-6 cm, 6=6-8 cm, 8=8-10 cm and 10= sum of layers) for each treatment.

| HIGH | | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| **0** | **1** | **2** | **4** | **6** | **8** | **10** |
| **Groups** | | | | | | |
| **Nematoda** 964±736 | 1,133±369 | 1,968±1,224 | 840±452 | 366±216 | 248±180 | 5,522±1,566 |
| **Ostracoda** 477±200 | 101±66 | 44±39 | 31±30 | 9±6.3 | 3.1±6.3 | 668±264 |
| **Copepoda** 242±128 | 19±16 | 35±12 | 15±19 | 12±10 | 6.3±12 | 331±141 |
| **Nauplius** 105±92 | 3.1±6.3 | 3.1±6.3 | 6.3±12 | 0 | 0 | 117±109 |
| **Acari** 0 | 0 | 0 | 3.1±6.3 | 0 | 0 | 3.1±6.3 |
| **Rotifera** 19±12 | 0 | 3.1±6.3 | 0 | 6.3±12 | 0 | 28±21 |
| **Turbellaria** 31±22 | 0 | 0 | 0 | 0 | 0 | 31±22 |
| **Bivalve** 3.1±6.3 | 0 | 0 | 0 | 0 | 0 | 3.1±6.3 |
| *Laeonereis acuta* 3.1±6.3 | 3.1±6.3 | 0 | 0 | 0 | 0 | 6.3±7.3 |

| MEDIUM | | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| **0** | **1** | **2** | **4** | **6** | **8** | **10** |
| **Groups** | | | | | | |
| **Nematoda** 1,589±1,041 | 716±730 | 955±1,229 | 515±363 | 248±191 | 76±77 | 4,101±3,322 |
| **Ostracoda** 697±310 | 592±902 | 178±196 | 44±7.3 | 9.5±6.3 | 15±24 | 1,538±1,249 |
| **Copepoda** 222±157 | 98±146 | 38±44 | 9.5±6.3 | 6.3±12 | 6.3±7.3 | 382±284 |
| **Nauplius** 299±96 | 229±433 | 19±22 | 3.1±6.3 | 0 | 0 | 550±545 |
| **Acari** 28±19 | 6.3±12 | 3.1±6.3 | 0 | 0 | 3.1±6.3 | 41±28 |
| **Rotifera** 0 | 3.1±6.3 | 0 | 0 | 0 | 0 | 3.1±6.3 |
| **Turbellaria** 6.3±7.3 | 0 | 0 | 0 | 0 | 0 | 6.3±7.3 |
| **Bivalve** 0 | 3.1±6.3 | 0 | 0 | 0 | 0 | 3.1±6.3 |
| *Laeonereis acuta* 12±18 | 0 | 3.1±6.3 | 0 | 0 | 0 | 15±16 |

| CONTROL | | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| **0** | **1** | **2** | **4** | **6** | **8** | **10** |
| **Groups** | | | | | | |
| **Nematoda** 1,662±723 | 872±956 | 1,006±1,588 | 407±526 | 289±353 | 76±40 | 4,315±4,037 |
| **Ostracoda** 786±659 | 159±47 | 82±39 | 130±195 | 15±24 | 25±14 | 1,200±673 |
| **Copepoda** 277±149 | 9±12 | 3.1±6.3 | 6.3±12 | 3.1±6.3 | 0 | 299±161 |
| **Nauplius** 315±138 | 9±19 | 0 | 0 | 0 | 0 | 324±152 |
| **Acari** 15±6.3 | 15±12 | 0 | 6.3±7.3 | 0 | 0 | 38±18 |
| **Rotifera** 15±24 | 0 | 3.1±6.3 | 0 | 0 | 0 | 19±22 |
| **Turbellaria** 9±12 | 0 | 0 | 0 | 0 | 0 | 9±12 |
| **Bivalve** 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Laeonereis acuta* 3.1±6.3 | 0 | 0 | 0 | 0 | 0 | 3.1±6.3 |

comparison was done between the total meiofauna at 10 cm through analysis of variance, no statistically significant difference was observed. Similar results were found for each meiofauna group at both 10 cm and each one of the vertical layers.

For vertical distribution, the mean density of total meiofauna in the superficial layer (0-1 cm) was higher in the control than in the other two treatments, reaching 3,105 ind.10 cm$^{-2}$. In treatments M and A the mean density in this layer was 2,875 and 1,859 ind.10 cm$^{-2}$ respectively. There was an evident decrease in the group's density in the 0-1 cm layer in the high density polychaete treatment (Fig. 2).
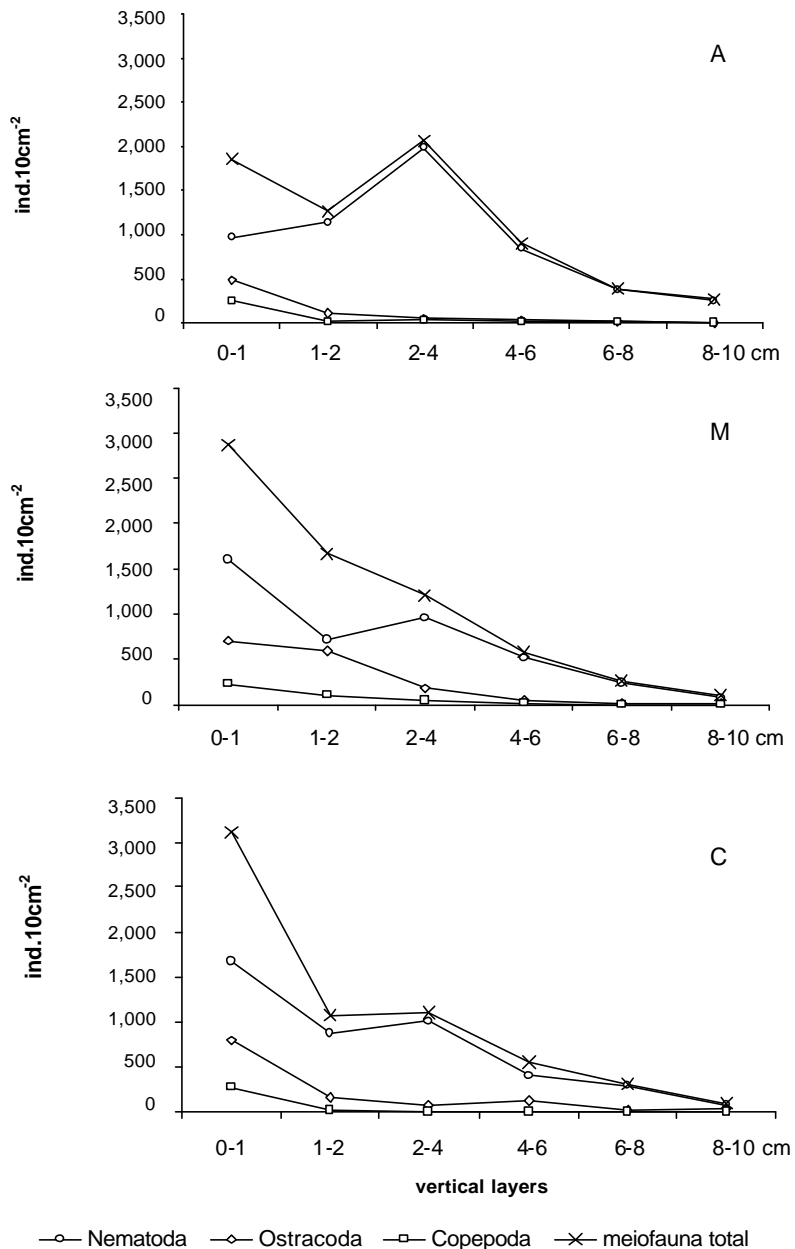


Figure 2: Density of meiofauna groups and of total meiofauna in the high density (A), medium density (M) and control (C) treatments.

Nematode density in treatment A reached a maximum (1,980 ind.10 cm$^{-2}$) at 2-4 cm deep, where it started to decrease until 8-10 cm where it reached 250 ind.10 cm$^{-2}$. The nematode density values in the vertical layers were always higher in treatment A than in the control, except at 0-1 cm.

Ostracoda density reach highest values at 2-4 cm vertical layer in all treatments. No Acari specimen was recorded in treatment A's superficial layer while in the control it reaches 16.02 ind.10 cm$^{-2}$. The other meiofauna groups recorded were more frequent in superficial layers (Tab. I).

Analyzing the organisms density from each vertical layer treatment using CLUSTER analysis, the formation of two groups with 80% similarity at 0-1 cm deep could be seen - the first formed only by treatment A replicates, and the second grouping M and C treatment replicates (Fig. 3, Tab. II). ANOSIM analysis confirmed these significant differences and showed the similarity that could be seen in M and C for all the vertical layers studied. Significant differences were only found between the high density treatment and the control (Tab. II).

**Table II:** Significant Anosim results for the groups of meiofauna in the different layers of treatments A (high density), M (medium density) and C (control).

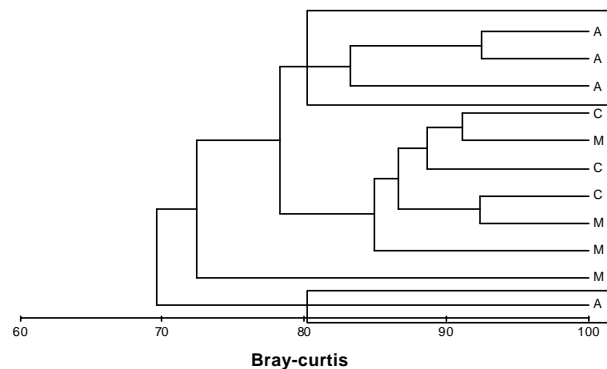| Layer | Treatment | $R$ | $p(<0,05)$ |
|---|---|---|---|
| 0-1 cm | A-C | 0.521 | 0.029 |
| 2-4 cm | A-C | 0.944 | 0.050 |
| 8-10 cm | A-C | 0.870 | 0.029 |



**Figure 3:** Cluster for the 0-1 cm deep layer, comparing the three treatments (A=high density, M=medium density and C=control).
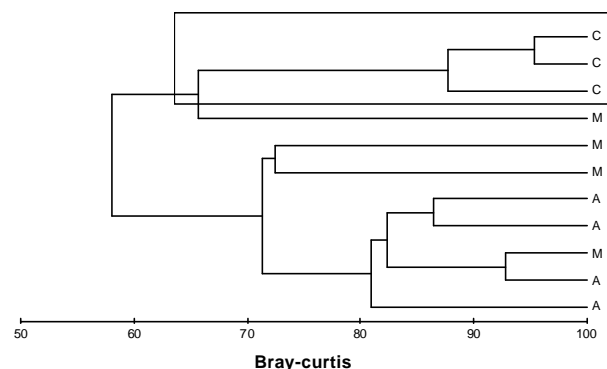


**Figure 4:** Cluster for the 2-4 cm deep layer, comparing the three treatments (A=high density, M=medium density and C=control).
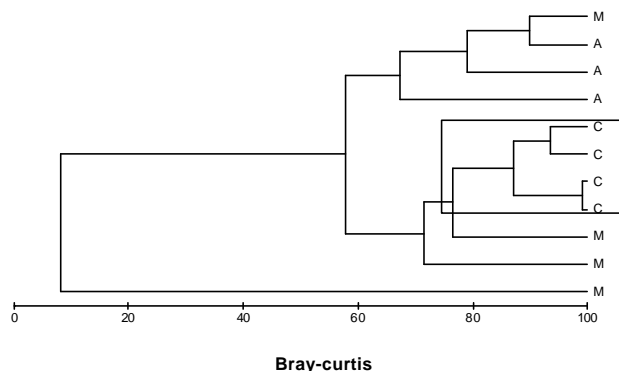
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                                                          M
                                                          A
                                                          A
                                                          A
                                                          C
                                                          C
                                                          C
                                                          C
                                                          M
                                                          M
                                                          M
      0        20        40        60        80       100
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**Bray-curtis**

**Figure 5:** Cluster for the 8-10 cm deep layer, comparing the three treatments (A=high density, M=medium density and C=control).

Significant differences were also found when analyzing 2-4 and 8-10 cm. Differences regarding increasing Copepoda and decreasing Ostracoda density for the 2-4 cm depth, and increasing Nematoda density for the 8-10 cm depth were both found in treatment A. For both situations, CLUSTER analysis (Fig. 4 and 5) highlighted two clusters: one formed by treatment A replicates and the other by M and C treatments with 70% (2-4 cm) and 65% (8-10 cm).

Analysis of the polychaete feeding content recorded the presence of several diatom species and diverse sized sediment grains.

# Discussion

## Vertical distribution

The results lead us to conclude that disturbance caused by *Laeonereis acuta* probably changed the vertical gradients and hence meiofauna distribution, allowing them to penetrate deeper in the sediments.

The ANOSIM analysis, which highlighted significant differences in the 0-1 and 8-10 cm depth layers, supports this statement, since these differences are the result of a decrease in the nematode density of the superficial layer and an increase in that of the deeper layer, where polychaetes are present. The same effects may also have influenced the high nematode values recorded in the high density treatment 2-4 cm layer. A high occurrence of the meiofauna in the sub-superficial sediment in the presence of *L. acuta* may indicate that the polychaete caused the Nematoda to migrate in order to avoid bioturbation. This migration may be due to activities inside the tubes as well as the feeding strategy and the depth where *L. acuta* feeding occurs.

The fact that diatoms, micro algae found in first sediment millimeters (Joint et al., 1982), prevailed in the feeding content of *L. acuta* indicates that this species is a sub-surface or surface deposit feeder. This kind of feeding strategy was also observed for *L. acuta* by Palomo & Iribarne (2000). Tita et al. (2000), consider that *Nereis virens*' feeding strategy plays an important role in both superficial and deeper dweller meiofauna.

Another explanation for the Nematoda migration may be the probable improvement of the oxygen availability of the deeper interstitial habitat, which agrees with the results found by Wilson (1991) and Deckere et al. (2001). These authors conclude, also through experiments, that fauna activities lead to both higher porosity and water content in the sediment, especially in the case of a deposit-feeder animal as this behavior changes sediment's granulometry.

There are a number of deposit feeders, which have an unknown feeding strategy (Retraubum et al., 1996). Another Nereididae polychaete, *Nereis diversicolor*, however,

was considered by Esselink & Zwarts (1989) as the one of the best studied estuarine zoobenthic species to date. *N. diversicolor* and *L. acuta* are similar in habits, both being deposit feeders which build vertical tubes (Omena, 1998).

In order to investigate sedimentary environmental variation caused by *N. diversicolor*, Mortimer et al. (1999) suggest that the organisms tubes are strongly irrigated when submersed and their tube walls improve the water-sediment interface where, according to Reise (1985), both the vast majority of chemical reactions and higher meiofauna density can be found. Mortimer et al. (1999) also suggest that *N. diversicolor* had an impact on the redox layer, leading to oxic conditions in the sub-surface due to sediment irrigation by the polychaete.

For the groups which show significant differences compared to the control, it was expected that Copepoda, because of its epibenthic habit (Giere, 1993), would show no response in the superficial layer, since a species' abundance normally increases or diminishes in this layer due to bioturbation, as has been registered by other authors in the field (Hicks, 1984; Alongi & Tenore, 1985). However, in the present study, significant differences found were attributed to Copepoda only for the 2-4 cm layer. The most probable explanation for this may lie in the hydrodynamics conditions produced by the experiment, which are different to those in the natural environment. This led to greater stability in the superficial layer and thus influenced Copepoda to remain in the surface layer. Palmer (1988) and Foy & Thistle (1991) showed Copepoda migration to inner sediments in high hydrodynamic conditions through "flume" experiments.

The associated effects of macrofauna predation (meiofauna ingestion) at the surface are sometimes mistaken for the capability of Nematoda and other meiofauna groups to migrate/escape to deeper sediment layers (Rönn et al., 1988; Gregg & Fleeger, 1998). In the present study, *L. acuta* feeding at the surface provoked disturbance leading to a negative effect for Nematoda. On the other hand, the absence of high hydrodynamics may actually have favored the permanence of Copepoda through the occupancy of the new spaces or niches generated. It seems that these different meiofauna groups, Nematoda and Copepoda, had an inverse response to polychaete disturbance. Sutherland et al. (2000) observed that the response to the same disturbance is usually different for these two groups. Aller & Yingst (1978) found that only Nematoda was affected by the presence of a polychaete. Cross & Curran (2000), when studying bioturbation by a ray, recorded that only Nematode and the total meiofauna were negatively affected at the surface, while Copepoda was not.

In spite of these clues, it is not possible to affirm that the presence of *L. acuta* affected the vertical distribution patterns of the Copepoda due to both the low abundance and occurrence found in the experiment, added to the fact that Copepoda were not identified to species level. The same seems to happen to other groups such as Acari and Ostracoda, thus hindering discussion of the results.

Comparing *N. diversicolor*'s known behavior and the results found here, it is possible to conclude that *L. acuta* contributes to the creation of a more favorable meiofauna deeper interstitial habitat due to an increment of microorganisms activities, leading to a higher food availability, along with habitat irrigation and oxygenation.

## Meiofauna predation by Laeonereis acuta

As a confined experiment where no significant differences were found in the treatments and control when analyzing meiofauna at 10 centimeters, it can be concluded that the absence of mortality was due to polychaete activities. This means that *L. acuta* did not prey on meiofauna during the experiment period. Density variations in the organism's vertical distribution are caused by polychaete sediment disturbance. *L. acuta*'s feeding content - composed of diatoms and sand grains, which agrees with Mantovanelli's (1995) findings, corroborates the above result since no evidence of meiofauna ingestion was observed.

Other observations were found by Warwick et al. (1986) for *Streblosoma bairdi*, Ólafsson et al. (1990) for *Mellina palmata*, Retraubum et al. (1996) for *Arenicola marina*,

Tita et al. (2000) for *Nereis virens* and Rönn et al. (1998) for *N. diversicolor*. These authors suggest that meiofauna predation by diverse macroinfauna polychaete species occurred. Tita et al. (2000), despite registering macroinfauna predation upon meiofauna, affirm that the effect of bioturbation is more evident and significant, and that meiofauna predation is probably passive.

Higher trophic levels and meiofauna interactions have been studied since the 1980's and meiofauna has been shown to be a food resource for both small and juveniles fishes, and several macrofauna organisms (Gee, 1989). However, most studies, particularly those in the field, did not discuss meiofauna feeding, due to both the small sized meiofauna and lack of records on feeding content. According to Coull (1999), macrofauna preys on meiofauna, although given that these predators have a low impact on prey in natural environment, densities did not decrease markedly. Mantovanelli (1995) highlighted that the quantities of material ingested by *L. acuta* populations represent a small fraction of its different food resource biomass, never exceeding environment support capacity.

When decreasing meiofauna density is registered, it is often related to predation and/or the associated bioturbation effects (Aarnio et al., 1998). It is very difficult to separate both processes and attribute the meiofauna response to interaction between them (Brenchley, 1981).

The relatively short period of 5 days of the laboratory experiment used in this study should be taken into consideration. Tita et al. (2000) carried out a fifteen-day experiment and conclude that an experiment of short duration has some advantages over longer ones, mainly that of eliminating meiofauna recruitment, since meiofauna characteristics, such as short life and high reproductive rates, may mask predation effects (Aarnio, 2000).

This paper agrees with Kennedy (1993) who, in a six-day experiment, found similar results for *N. diversicolor,* suggesting minimal predation by this polychaete. Tita et al. (2000) disagree with Kennedy (1993), considering six days a very short time period. A factor to be taken into account here is the species focused on by Tita et al. (2000), *N. virens*, since although it belongs to the same family of deposit feeders (Kennedy, 1993) as *L. acuta* and *N. diversicolor*, it is a predatory species (Commito, 1982).

## Aknowledgments

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