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RESEARCH ARTICLE

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Colonization and early succession on artificial hard substrata by meiofauna

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Abstract An experiment was undertaken at Farol Island, Brazil, to examine colonization of bare aluminium surfaces by microbes and meiofauna. It was hypothesized that a primary source of meiofaunal colonists was sediment resuspended during upwelling events, two of which occurred during the experiment. Microbial biofilms formed on the experimental substrata within 1 day, and continued to develop throughout the experimental period. Among meiofaunal groups copepods also appeared on the first day, and nematodes on the second. Meiofaunal community structure developed in three main phases: an initial phase of 2 days, characterized by low abundances of copepods; a second phase during the first upwelling period characterized by higher abundances of copepods and also by turbellarians; and a third phase from day 13 onwards characterized by relatively stable abundances of a range of taxa including copepods, cirripedes, nematodes and ostracods. Nematode assemblages also developed in three phases, but with different timings coinciding with upwelling events: an initial phase, from the beginning of the experiment to day 9, characterized by few species and low (or no) abundances; a second phase following the first upwelling characterized by moderate abundances of *Chromadorina*, *Chromadorella*, *Daptonema* and *Euchromadora* sp. 3; a third phase following the second upwelling period (from day 26 onwards) in which *Daptonema* disappeared and the assemblage was characterized by moderate to high abundances of *Euchromadora* (species 1 and 2) and *Chromadorella*. Although shifts in nematode assemblage structure coincided with upwelling events no evidence was found for sediments being the primary source of colonizers on the aluminium substrata, in contrast to our hypothesis.

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Introduction

Fouling of surfaces by abiotic substances and living organisms has three levels of organization (Rittschof 1999). Molecular fouling is the accretion of organic and/or inorganic molecules from solution onto submerged surfaces. Microfouling is the colonization of surfaces by micro-organisms, followed by the secretion of polymers that anchor and often embed the micro-organisms and other particles. Macrofouling is the colonization of surfaces by macroscopic fauna and flora, usually by means of micro- or meiosized propagules. In the classic model on colonization and succession of surfaces in aquatic environments, molecular films attract microbes and these in turn facilitate the settlement of macrofoulers (Wahl 1989). Larvae of some invertebrates settle preferentially on microbial films (Scheltema 1974; Kirchman et al. 1982), however, several studies in both field and laboratory settings have shown microfouling not to be a prerequisite for macrofouling (Roberts et al. 1991; Maki et al. 1992; Mary et al. 1993).

The position and role of meiofauna in fouling processes has hitherto received little attention. Meiofauna communities on hard substrata tend to differ radically from those in neighbouring sediments (Atilla and Fleeger 2000; Danovaro and Fraschetti 2002; Atilla et al. 2003), but the dynamics of colonization and succession

of these organisms and their role, if any, in fouling processes, remain unknown. Nematodes are usually by far the dominant meiofauna in soft sediments (Heip et al. 1985), and are known to occur in a wide range of—sometimes extreme—habitats including microbial biofilms on hard substrata (Atilla et al. 2003). Like other meiofauna they have, however, very limited active dispersal capacities. They have no pelagic stages, but can temporarily survive when suspended in water. Resuspension and passive transport by water currents may be important mechanisms by which they recruit (permanently or temporarily) onto submerged substrata (Palmer and Gust 1985), but it is unclear whether and how nematodes maintain populations on such substrata.

Here we analyse colonization and succession patterns of meiofauna (at the level of higher taxa) and nematodes (at the level of genus/species) onto artificial hard substrata suspended in the water column at a shallow coastal site in Brazil. In addition to analysing meiofaunal community development we also quantified micro- and macrofouler assemblages on the substrata. The distance (approximately 3 m) between the experimental units and the nearest source of natural meiofauna (sediment) was assumed to be too large for significant active migration of meiofauna, and especially of nematodes, to occur. However, since our experiment was conducted in an area characterized by upwelling, we expected passive dispersal from underlaying sediment. We hypothesized that early-colonizing meiofauna and nematode communities would reflect roughly the taxonomic composition of the sediment communities, but that only few taxa and species would be capable of maintaining themselves. We also investigated whether increasing biological complexity (assessed from micro- and macrofouler development) affected meiofaunal colonization and population development and/or influenced succession patterns and community composition.

Materials and methods

Study site

We performed our experiment at Farol Island, Arraial do Cabo (23° 44′S and 42°00′W), in the north of the state of Rio de Janeiro (Fig. 1). This is the sole area on the Brazilian coast where upwelling occurs as a result of incoming water from the South Atlantic Central Water current (ACAS). These incoming waters are very nutrient-rich and characterized by high phytoplankton densities, and have relatively low temperature (generally $< 15°C$) compared to inshore waters (Valentin 1984;

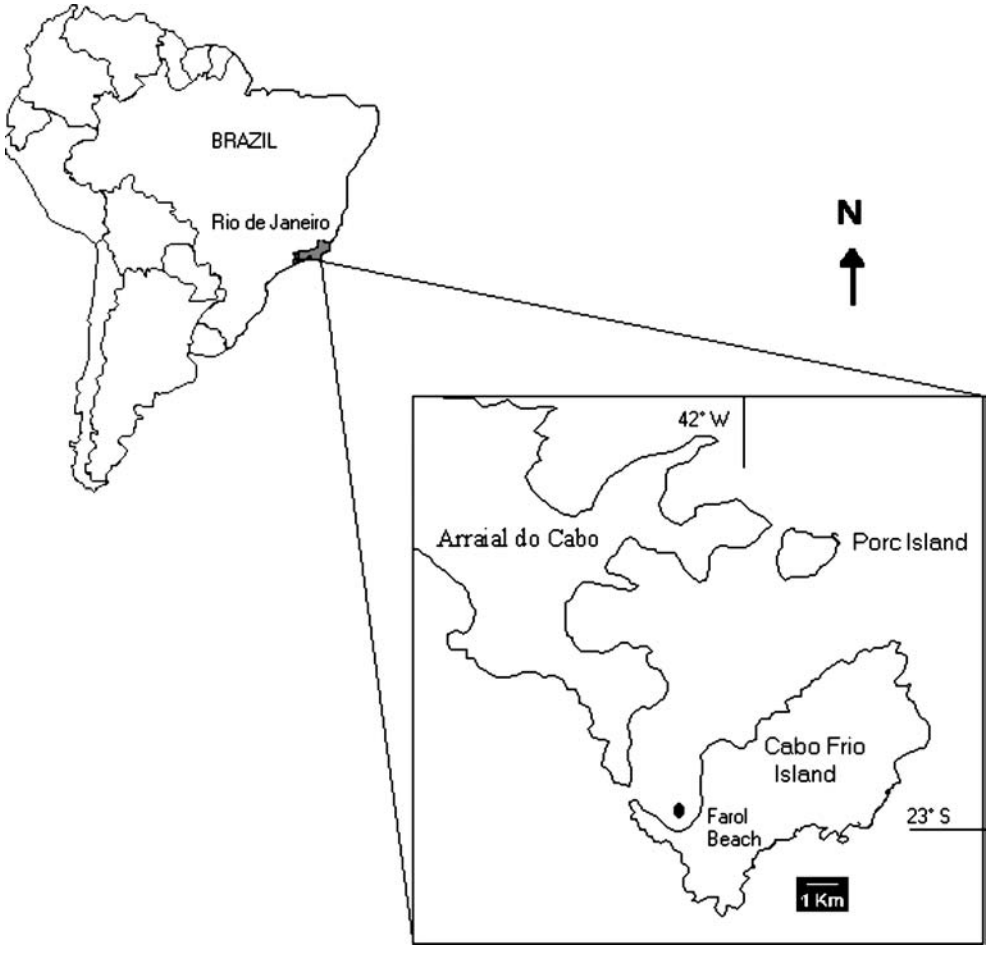

Fig. 1 Location of the study site near Farol Beach

Valentin et al. 1987). This area is protected by the Brazilian navy and is open to experimental research.

Experimental design

Four iron structures (1.2 m diameter) were suspended at least 3 m above the seafloor at a site where water depth varies between, on average, 4.5 and 6 m, at low and high tide, respectively. Hence, the structures were continuously submerged. They were anchored to buoys and to the sediment. Distance between the different structures averaged 25 m. The sediment underneath one of the structures was covered with *Sargassum furcatum*, while bare sediment underlaid the others. Thirty aluminium plates (10×10 cm^2) were attached to each of these structures using nylon strips at both ends (Fig. 2). Aluminium behaves passively in seawater and the fouling sequence on aluminium substrata is generally similar to that on non-toxic inorganic substrata such as slate (Efird 1976; Chandler 1979). The experiment started on 27 August and lasted until 30 September 2001. We did not observe any significant corrosion or pit formation during this time. Samples were taken daily for 3-day periods, each sampling period followed by 3 days without sampling. On each sampling day, one plate was collected at random from each of the four experimental structures: three replicate plates for the analysis of meiofauna and macrofauna, and one for the characterization of microbial communities. Plates were immediately put in plastic containers and transferred to the laboratory.

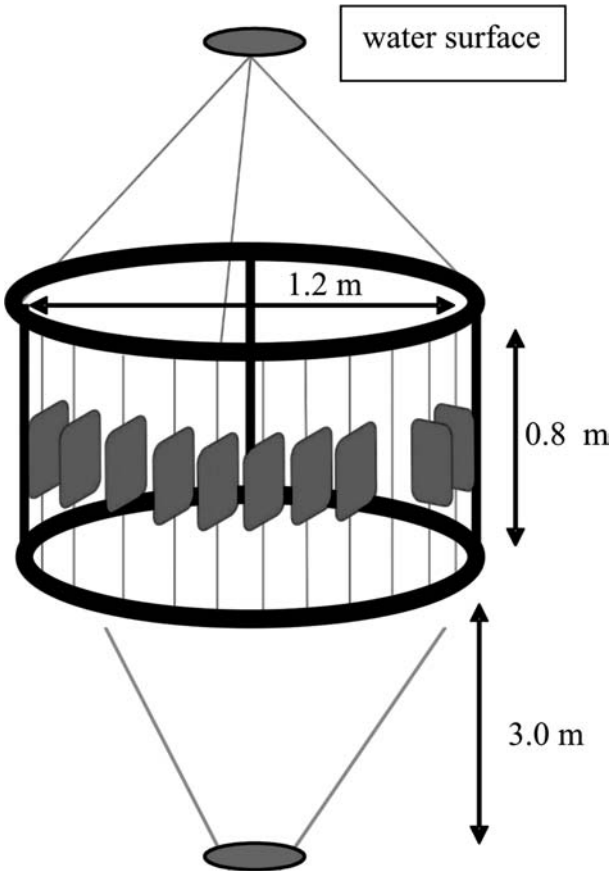

Fig. 2 Schematic of an experimental unit, consisting of an iron frame with aluminium plates attached by nylon strings. Frames were anchored to buoys and to the sediment

Sample processing and analysis

Cirripedes were quantified using a binocular dissecting microscope and then each plate was washed gently with filtered seawater over 500 and 44 μm meshes to remove macro- and meiofauna. Both size-fractions were then thinly spread on 200-square Dolffus plates and individuals belonging to major taxa were counted, again using a binocular dissecting microscope. Meiofauna were preserved in a 4% neutral formaldehyde solution. Densities of all metazoan taxa are reported as numbers per experimental unit and hence encompass all individuals retrieved from both sides of the aluminium plates. For nematode identifications all individuals were picked out by hand and then transferred to glycerol using a modification of the evaporation technique described by Warwick et al. (1998). Specimens were first transferred to a glycerol/4% formalin (1/99 v/v) solution and placed in a desiccator for 24 h. A solution of glycerol/95% ethanol (5/95 v/v) was then added and the ethanol allowed to evaporate for 2 h. This procedure was repeated four times, before a final transfer of the nematodes to a glycerol/ethanol solution (50/50 v/v). Ten specimens at a time were transferred to a drop of anhydrous glycerol placed within a pre-prepared paraffin-wax ring on a microscope slide (Somerfield and Warwick 1996), covered with a coverslip, and the whole preparation carefully placed on a hotplate to melt the wax and seal the slide. Under a compound microscope specimens were identified to genus using the pictorial key in Warwick et al. (1998), and within genera to putative species on the basis of recognizable morphological features. Data on the generic composition of nematodes in the sediment underlying the experimental structures at the time of the experiment have been published elsewhere (Fonsêca-Genevois et al. 2004). At weekly intervals during the experiment the nematodes in four 1 l water samples from around the experimental structures were also quantified and identified.

Microbial biofilms were scraped off 3 1 cm^2 areas on the aluminium plates with a blade. The samples were placed on a microscope slide with 4% formalin and a coverslip and observed under a stereoscopic microscope. Five fields per slide were chosen at random using an ocular micrometre, and (morpho)type and numbers of micro-organisms were counted. Densities are reported per cm^2. Because of inherent methodological constraints, these densities provide only a relative measure and should be interpreted as such. Bergey's manual (Buchanan and Gibbons 1974) was used as the main taxonomic reference.

Statistical treatment of data

Non-parametric multivariate methods (Clarke 1993; Clarke et al. 2005) in Primer v.6.0 (http://www.primer-e.com) were used. Species that were non-randomly clustered across times were downweighted (Clarke et al. 2005a), and the resulting dispersion-weighted abundance data were used to calculate inter-sample similarities. An adjusted form of the Bray–Curtis similarity measure (Clarke et al. 2005b) was chosen for this study as samples with few or no individuals (such as those from the early stages of colonization of bare surfaces) might be considered to be similar even if they contain no species in common. The resulting similarity matrices were ordinated by non-metric multidimensional scaling (MDS) and clustered using hierarchical agglomerative clustering with group-average linkage. The ANOSIM randomization test (Clarke and Green 1988) was used to test for differences in community structure between predefined groups of samples. The taxa contributing most to similarities within and dissimilarities between groups were identified using (dis)similarity percentages analysis (SIMPER; Clarke 1993). Non-parametric Mantel tests (RELATE) were used to test for linear seriation patterns with (for meiofauna and nematodes) and without (for microbes) replication.

Results

Conditions with warm (19–22°C) clear (secchi depth >6 m) water predominated during the experiment. Two upwelling events occurred during the experimental period: one between 3 and 9 September when water temperature dropped to 15°C and turbidity was high; the other, less pronounced, between 11 and 21 September (Fig. 3).

Densities of organisms in both biofilms and fauna showed increasing trends throughout the experimental period, although rates of increase tended to be highest between, and densities decreased during, upwelling periods (Fig. 4). Microbial biofilms covered the artificial substrata from the first day of sampling and were most prominent between upwelling periods. They were mainly composed of bacteria but also included phytoflagellates, Cyanophyceae and diatoms. Coccoid bacteria dominated the microbial community, although a succession was observed with *Myxoccocus* and *Chlorobium* dominating during the first week and *Rhodopseudomonas* and *Pseudomonas* reaching peak values during the second and third weeks. *Chromatium*, *Diplococcus*, *Thiocapsa* and *Rhodospirillum* occurred irregularly, usually at low densities. The fauna on the aluminium plates comprised Turbellaria, Nematoda, Gastrotricha, Harpacticoidea (adults and nauplii), Ostracoda, Oligochaeta, Polychaeta (adults and larvae), Bivalvia, Gastropoda (Prosobranchia and Nudibranchia), Amphipoda, Cirripedia (settled juveniles and cyprid stages) and several other (including planktonic) taxa (Euphausiids, calanoid and cyclopoid copepods, the appendicularian *Oikopleura* sp. and the hydrozoan *Obelia* sp.).

Calanoid and cyclopoid copepods occurred on the artificial substrata from the beginning of the experiment but were most abundant after the second upwelling event (Fig. 5a). Cirripede nauplii, *Obelia* sp. and *Oikopleura* sp. appeared after the first upwelling event (Fig. 5a, b). Among the benthic macrofauna, polychaetes were the first colonizers (from 7 days onwards), with *Armandia* sp. as the dominant species. Ostracods and Amphipods (Caprellidae and Gammaridae only) appeared later (Fig. 5c). The only macro-fouler reaching very high abundances was, however, the cirriped *Balanus trigonus*. Cirripedes appeared as nauplii after the first upwelling event and cyprid stages started to develop when water temperature exceeded 20°C. Most thoracican barnacles have a planktotrophic development and show little variation among species in the general organization of the nauplius. Stage V–VI nauplii, cyprids and juveniles were

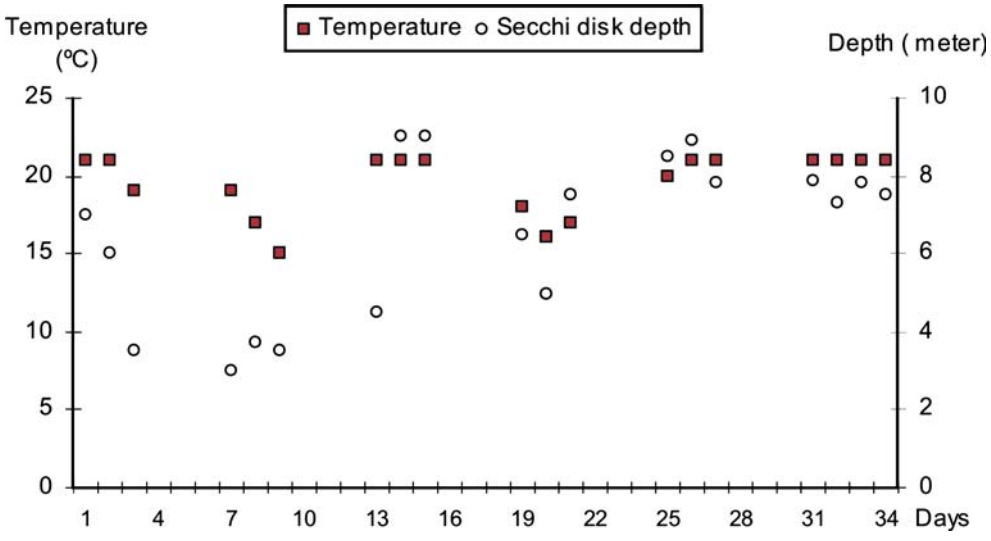

Fig. 3 Water temperature (°C) and turbidity (Secchi disc depth, m) during the experiment at Cabo Frio Island

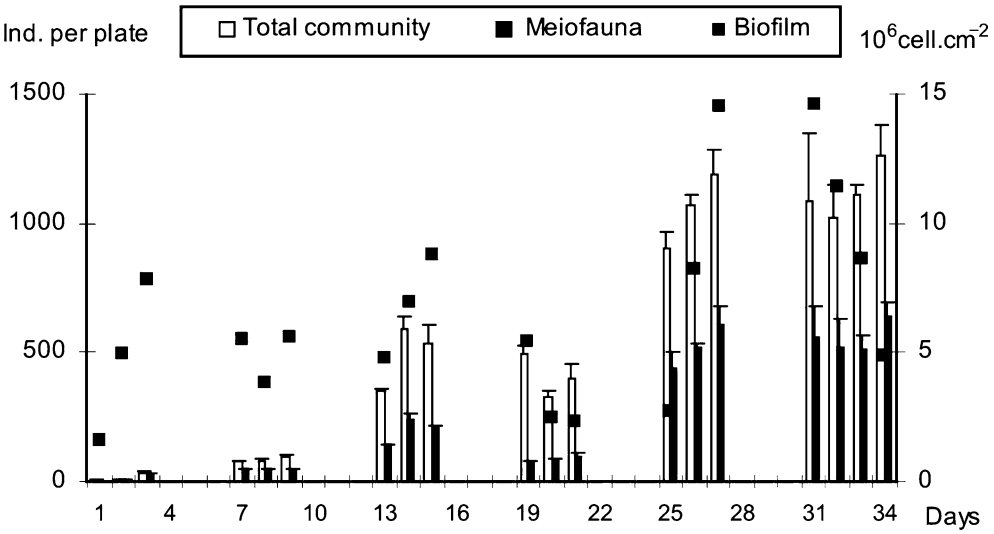

Fig. 4 'Total community' (meio- and macrofoulers combined), meiofauna and biofilm density variations over the experimental time

observed in our study, but only juveniles were possible to key to species. Since *B. trigonus* was by far the dominant barnacle species on our plates, we assume that the nauplii and cyprids were also this species. It peaked between upwelling periods and, by the end of the experiment, completely covered the artificial substrata with densities of up to 349 ind. per plate (Fig. 5b).

Meiofauna densities peaked concomitantly with *B. trigonus* (cyprids and metamorphosed juveniles) (Fig. 5d). Among higher taxa, harpacticoid copepods were the fastest colonizers, appearing (albeit in very low numbers) after 1 day. Copepod nauplii, largely dominated by harpacticoids, were abundant between upwelling periods but absent during both upwelling events, suggesting in situ reproduction. Harpacticoid copepods were also the most abundant meiofaunal taxon (comprising 27–79% of total meiofauna), with peak densities of >400 individuals per plate, except during the second upwelling event and during the last 3 days of the experiment. Nematodes appeared after 2 days and turbellarians after 1 week. Nematodes attained their highest densities (308 individuals per plate) at the end of the experiment when the microbial biofilm collapsed but macro-fouling was most pronounced. They comprised 9–60% of the total meiofauna community. Turbellarians comprised $\leq 10\%$ of meiofaunal numbers except during the first upwelling event, when their relative abundance increased to 26–51%. In general, while nematode densities increased steadily throughout the experiment, densities of other meiofaunal taxa (except turbellarians during the first upwelling event) decreased during upwelling periods and—to a lesser extent—also towards the end of the experiment.

In all three biotic components sampled (microbial biofilms, meiofaunal major taxa, and putative species of nematodes) there were highly significant temporal patterns. ANOSIM tests for differences between days (biofim, $R=0.511$; meiofaunal groups, $R=0.965$; nematode putative species, $R=0.832$) were all highly significant ($P<0.0001$). RELATE tests for linear structure (linear changes through time) without replication (for biofilm data) and with replication (for meiofaunal taxa and nematodes) were also all highly significant (biofilm, $\rho=0.302$, $P<0.005$; meiofaunal taxa, $\rho=0.961$, $P<0.001$; nematodes, $\rho=0.874$, $P<0.0001$). MDS ordination of data from microbial biofilms (Fig. 6) illustrates the linear trend in community development. Day-to-day changes tend to decrease in magnitude over the experimental period, except during upwelling periods when daily changes tend to be large. For meiofaunal major groups (Fig. 6) there are three main phases of community development; an initial phase of 2 days, characterized by low abundances of (primarily) calanoid and harpacticoid copepods; a second phase during the first upwelling period characterized by higher abundances of calanoids, cyclopoids and harpacticoids and also by turbellarians; and a third phase from day 13 onwards characterized by relatively stable abundances of a range of taxa including copepods, cirripedes, nematodes and ostracods.

A total of 19 nematode genera were recovered from the plates, with a maximum occurring simultaneously of 11 after the first upwelling event (Fig. 7). In general, there were very similar and constant proportions of adult males, adult females and juveniles throughout the experiment. *Euchromadora* was the dominant nematode genus both in terms of density (46.35% of the total time-integrated nematode density) and diversity (four putative species, all hitherto undescribed). Other abundant species/genera were *Chromadora macrolaimoides*, *Chromadorella filiformis*, *Chromadorina* sp.n., *Oncholaimus aff. dujardini*, *Atrochromadora denticulata*, *Daptonema* sp., *Ptycholaimellus* sp., *Acantonchus* sp. and *Viscosia* sp.. *Cricolaimus* sp.n., *Symplocostoma* sp., *Thoracostoma* sp., *Catanema* sp., *Graphonema* sp. and *Terschellingia* sp. appeared irregularly and at low densities. All genera other than *Euchromadora* were represented by single morphospecies.

Chromadora macrolaimoides colonized the plates from day 2 of the experiment (Fig. 8). Its population dynamics

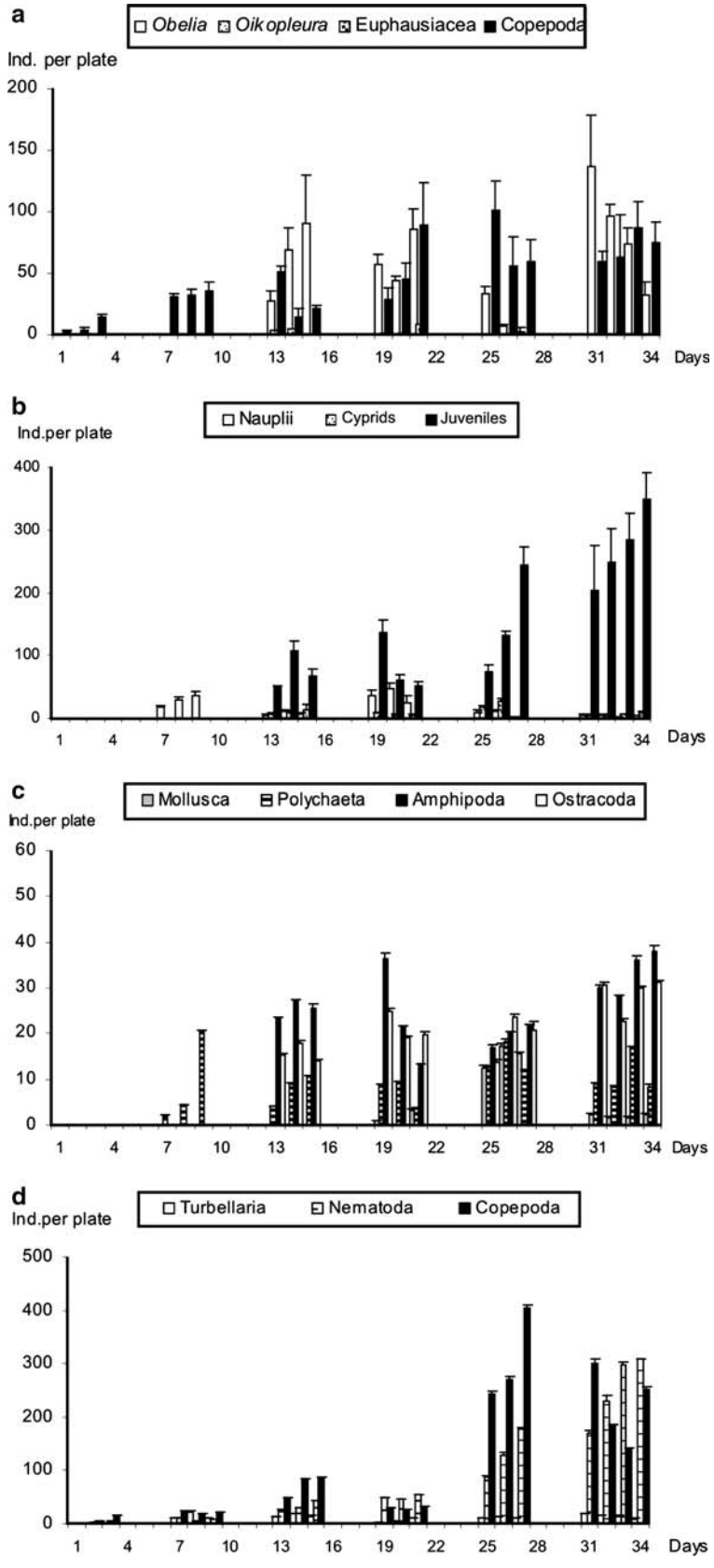

Fig. 5 Densities of planktonic macrofauna (**a**), *Balanus trigonus* (**b**), other macrofoulers, and major meiofauna taxa (**d**) on aluminium plates. Data are means ± 1 STD of three replicate units

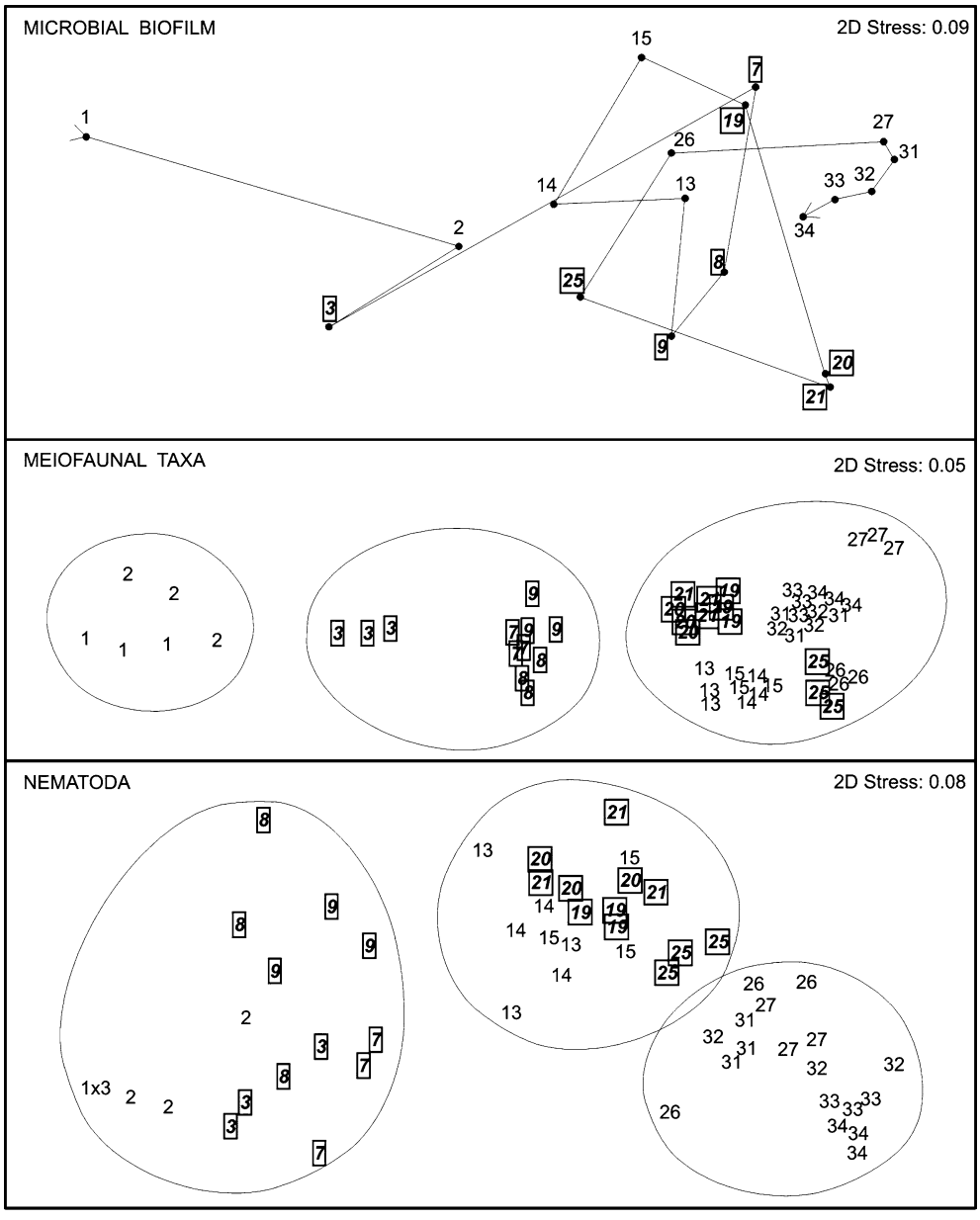

Fig. 6 Multidimensional Scaling ordinations of adjusted Bray–Curtis similarities calculated from dispersion-weighted abundances of microbes, meiofaunal major taxa, and nematode putative species. For microbes in biofilms there is only one sample from each date, being the average of several counts (see text for details), and the line is added to aid interpretation of the development of the assemblage through time. For meiofauna and nematodes contours indicate samples grouped together at the 40% similarity level. In all three plots sample locations are indicated by numbers indicating the number of days from the beginning of the experiment when samples were collected, and numbers enclosed by *boxes* indicate samples from upwelling periods

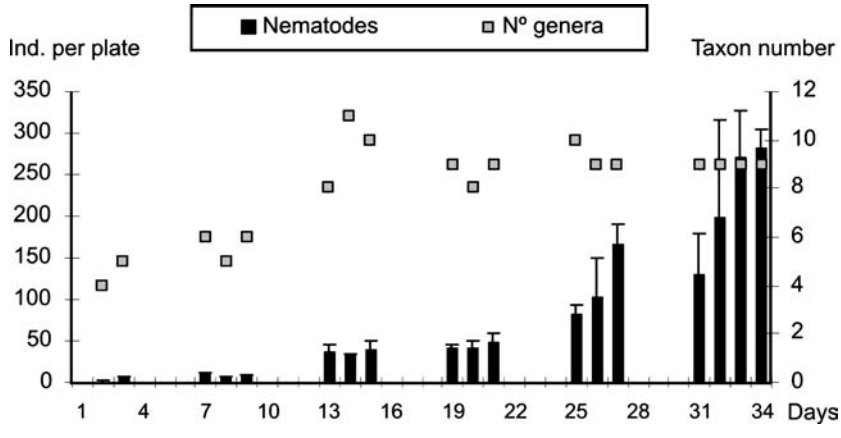

Fig. 7 Nematode density and genus diversity (expressed as number of genera) throughout the experiment

followed the dynamics of biofilm development, albeit with an initial time lag, its numbers showing a tendency to decrease during upwelling events and towards the end of the experiment. Similar population dynamics were observed for *C. filiformis* and *Chromadorina* sp.n.. *Daptonema, Atrochromadora*, and *Euchromadora* sp. 3 even disappeared completely from the plates after the second upwelling period (Fig. 8). By contrast, the densities of the other *Euchromadora* species increased throughout the experiment. *Viscosia, Acantonchus, Ptycholaimellus* and *Oncholaimus* colonized the plates only after the second upwelling event, and increased in numbers until the end of the experiment (Fig. 8).

Multivariate analysis of nematode communities also shows three phases (Fig. 6), although the details of the changes are slightly different to those shown by meiofaunal major taxa, with the main shifts in assemblage structure following upwelling events. The initial phase, from the beginning of the experiment to day 9, is characterized by few species and low (or no) abundances. Following the first upwelling the nematode assemblage is characterized by moderate abundances of *Chromadorina*, *Chromadorella*, *Daptonema* and *Euchromadora* sp. 3. Following the second upwelling period (from day 26 onwards) *Daptonema* disappears and the nematode community is characterized by moderate to high abundances of *Euchromadora* (species 1 and 2) and *Chromadorella*.

Discussion

In spite of their smooth surfaces, the aluminium structures were readily fouled by micro-organisms. The microbial biofilm was dominated by bacteria throughout the experiment, while diatoms, phytoflagellates and cyanobacteria were present only in low densities. Similar microbial succession patterns to that observed in the present study have been found in other experiments in the same area (Baeta Neves et al; unpublished): coccoid bacteria colonize first and are followed by filamentous forms. That rapid colonizers such as *Pseudomonas* and *Rhodopseudomonas* only peaked during the second and third week of the experiment is probably linked to nutrient availability: *Pseudomonas* and *Rodopseudomonas* are copiotrophic and thus require high nutrient concentrations, as provided by the inflow of turbid, nutrient-rich water during upwelling (Jackson 2003). On the other hand, total bacterial densities were lower during upwelling, probably as a result of lower water temperatures, stronger currents, or both. However, upwelling currents at our study site were typically almost

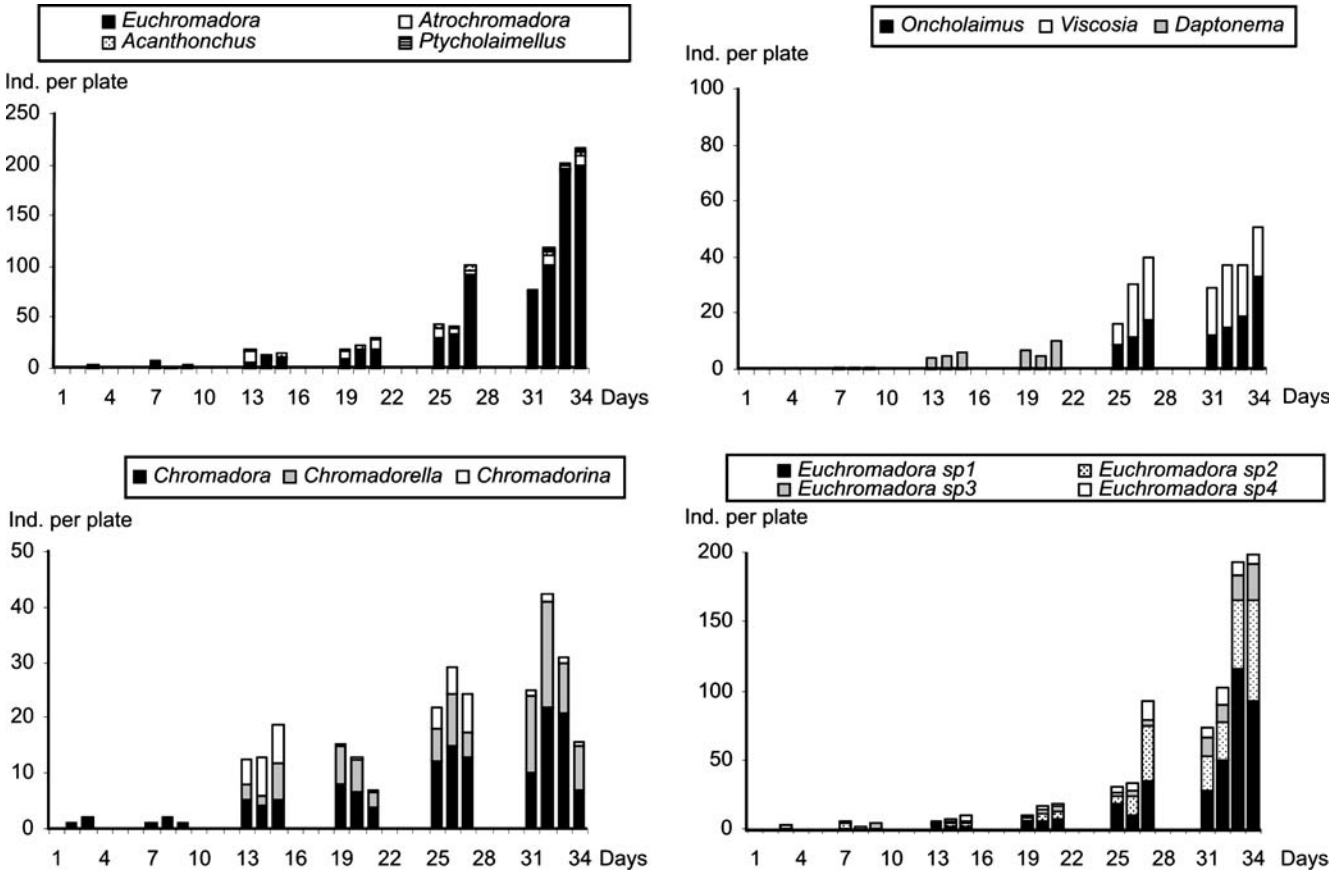

Fig. 8 Cumulative abundances of the main nematode species colonizing aluminium plates. Data are means of three replicates

an order of magnitude weaker (ca. 3 m s^{-1}) than horizontal currents (20–30 m s^{-1} under normal weather conditions) and were therefore probably of lesser importance (R. Candela, Personal communication).

Bacterial (a.o. *Pseudomonas*-derived) exopolysaccharide secretions have been shown to facilitate (Szewyk et al. 1991) or inhibit (Gatenholm et al. 1995) attachment of larvae of some macrofauna to surfaces. In turn, however, microbial biofilms in our study collapsed as macro-fouler densities reached peak values, probably as a result of competition for space. *B. trigonus* was the dominant macrofouler on our plates. It is the most common cirripede species that recruits in the subtidal zone at Cabo Frio during winter and spring (Costa and R. Coutinho, unpublished). In this region, naupliar stages of cirripedes typically peak during upwelling events, whereas the cyprid stage tends to be most abundant when water temperatures are higher (Skinner and Coutinho 2002).

Interestingly, although a large proportion of the meiofaunal community is expected to feed on the microbial biofilm (Montagna 1995), the decrease in microbial abundances towards the end of this experiment generally did not negatively affect meiofaunal numbers—rather the contrary (see below).

Harpacticoid copepods were the fastest meiofaunal colonizers, consistent with their comparatively high propensity to emerge from sediments (Bell and Sherman 1980; Palmer 1984, 1988) and colonize a variety of artificial substrata (Atilla and Fleeger 2000; Commito and Tita 2002). Although the first nematodes appeared on the plates after 2 days they reached maximum densities later than did copepod populations. In contrast to harpacticoids and other abundant meiofaunal taxa (mainly turbellarians), which showed a tendency to decrease in density near the end of the experiment, nematodes continued to increase in numbers. However, these taxon-level trends mask genus- or species-specific succession patterns, as exemplified by the nematode putative-species data.

Nematode diversity in terms of putative species encountered reached a maximum after the first upwelling event and remained virtually unchanged thereafter, in spite of increasing total density. A succession from early-colonizing *Chromadora, Chromadorella* and *Chromadorina* to *Euchromadora* and *Ptycholaimellus* was visible among the epistrate-feeders, and from *Viscosia* to *Oncholaimus* among the facultative predators. Interestingly, with the exception of the deposit-feeding *Daptonema*, epistrate-feeders and facultative predators were the only two feeding types recovered in significant numbers on the artificial structures, in line with their comparatively high dispersal capacities (see below). Epistrate-feeders are generally regarded as microalgal grazers, but their food range may also include bacteria and yet other small organisms (Moens and Vincx 1997, 1998). From the population dynamics observed here it is clear that at least *Euchromadora* and *Ptycholaimellus* reproduced on the artificial structures, and in view of the low densities of microalgal epigrowth, they probably largely benefited from other than microalgal food. Whether the co-occurrence of several genera of the same feeding type with roughly similar mouth structures (and indeed of no less than four species within the genus *Euchromadora*) indicates highly specialized feeding habits or can be explained otherwise, for instance by differential colonization dynamics, remains unclear.

Facultative predators are capable of predation on nematodes and perhaps other meiofaunal organisms (Moens et al. 1999c), hence the increase in their population may have contributed to the decline and even disappearance of several other nematode species towards the end of the experiment (Moens et al. 2000). In addition, however, they probably also feed on detrital particles and/or their associated micro-organisms (Moens and Vincx 1997, and references therein), and may take up dissolved organic matter (Chia and Warwick 1969; Lopez et al. 1979). It may be that this ability allows oncholaimids to thrive on surfaces colonized by microbial biofilms. In temperate intertidal and subtidal sediments, *Viscosia viscosa* is often found concentrated in the surface layers of sediments, especially when these are covered with microalgal mats (Moens et al. 1999a). Oncholaimidae often show a surprising capacity to colonize suitable spots rapidly (Riemann 1986; Lorenzen et al. 1987; Prein 1988), even to such an extent that passive dispersal alone, or passive dispersal in combination with the presumed limited active dispersal capacities of nematodes, may no longer explain these colonization events.

In fact, whereas we started from the hypothesis that initial colonization of our artificial structures by nematodes would be through upwelled bottom-sediments, and thus involve the same species which dominate the benthos at this site, this was largely contradicted by our data. The genera colonizing, and establishing a population on, our aluminium plates were often rare or even absent from bottom sediments. Out of 19 genera found on our plate structures, only seven occur in the sediment below. Among these are the abundant oncholaimids *Oncholaimus* and *Viscosia*, but not, for instance, the most abundant nematode genus on our plates, *Euchromadora*. Nevertheless, nematodes found in water samples encompassed all abundant sediment-dwelling plate colonizers (*Chromadora, Daptonema, Viscosia, Oncholaimus* and *Theristus*), showing that benthic nematodes indeed emerged into the water column, either through passive resuspension or through active migration (see below). *Euchromadora*, and virtually all other genera found on aluminium plates, however, were dominant members of nematode assemblages on a nearby *Sargassum furcatum* bank and/or in calcareous algal vegetation on a rocky shore situated ca. 500 m further (Table 1). Remarkably, of the typical epiphytic nematodes, only *Euchromadora* was recovered in the water samples from around our experimental structures. Two rather occasional genera on our plates, *Catanema* and *Rhabdodemania*, were found neither in nearby

sediment nor on algal vegetation although they are typically found in sediments.

The question thus remains whether passive dispersal alone can be at the basis of the colonization of the suspended aluminium structures. Nematodes are frequently observed in planktonic samples although they have no specific pelagic dispersal stages (Palmer 1984, 1988). Ullberg and Olafsson (2003), however, challenged the conception of nematodes as passive particles in the water column by showing that they are capable of actively choosing sedimentary habitats when settling from the water column. Harpacticoid copepods, and by extension perhaps other meiofauna like nematodes, may associate with marine snow, thus affecting their capacity for transport through the water column (Walters and Shanks 1996). In addition to the above-mentioned (active) dispersal of oncholaimid nematodes and to the remarkable floating capacity of *V. viscosa* (T. Moens, unpublished), *Chromadorina germanica* was found to emerge from sediment and swim to algal substrata, probably in response to chemical cues emanating from the algae or their epigrowth (Jensen 1981). Chemotaxis over short (in the order of centimetres) distances is probably a general feature in aquatic nematodes (Riemann and Schrage 1988; Moens et al. 1999b; Höckelmann et al. 2004). However, in general nematodes are considered to be poor swimmers (Palmer 1984), and in view of the small size of most species in this study it is doubtful whether active swimming alone could explain the colonization of substrata more than 3 m above the sediment and tens to hundreds of meters away from the nearest algal stands. We rather suggest that nematodes colonized our experimental structures through a combination of passive dispersal through (upwelling) water and active movement over short distances. Passive dispersal capacities differ among nematodes based on morphological as well as behavioural characteristics (Ullberg and Olafsson 2003), and the behaviour and position of nematodes in sediments may affect their chances of being resuspended (Commito and Tita 2002). Thus, the predominance of epistrate-feeding nematodes on our experimental structures is in line with the observation that they often dwell at or near the surface of sediments (Eskin and Palmer 1985; Commito and Tita 2002) and dominate epiphytic nematode assemblages (Heip et al. 1985).

Depending on their size, density and spatial distribution, barnacles may have important effects on water flow over, and drag on, surfaces (Thomason et al. 1998). Size differences within barnacle colonies may also create troughs that enhance 'recruitment' of small organisms such as nematodes (Snelgrove 1994), while at the same time distributing potential food particles for these organisms non-uniformly across the substrate (Abelson et al. 1993). Hence, a dense macro-fouler cover will alter hydrodynamic impacts on the meiofauna that colonizes hard substrates, and thus also the conditions for their feeding and reproduction. Indeed, while other meiofaunal taxa and several nematode species decreased or even disappeared as barnacle densities peaked, total nematode densities, in particular those of the relatively large-bodied facultative predators *Oncholaimus* and *Viscosia*, increased with increasing macro-fouler density and hence substrate complexity. Our observations show that *Oncholaimus* anchored themselves to the substrate by the tail, a behaviour probably involving mucus secretions from the caudal glands. This suggests that some nematodes may utilize mucus secretions to actively counteract physical disturbance on exposed substrates. Further research is, however, needed to unravel the

Table 1 Presence (+) of nematode genera found on aluminium plates, in underlying sediments, and nearby on algal vegetation

	Aluminium plates suspended in the water column (present work)	Sediment underneath the experimental units[b]	Nearby (at 5–75 m) *Sargassum furcatum* vegetation[a, d]	Calcareous algal vegetation on nearby (at ca. 500 m) rocky shores[c]
Acanthonchus	+		+	+
Atrochromadora	+		+	
Calyptronema	+			+
Catanema	+			
Chromadora	+	+	+	+
Chromadorella	+		+	+
Chromadorina	+		+	+
Cricolaimus	+	+		
Daptonema	+	+	+	+
Euchromadora	+		+	+
Graphonema	+			+
Oncholaimus	+	+	+	
Ptycholaimellus	+	+		+
Rhabdodemania	+			
Sigmophoranema	+			+
Symplocostoma	+		+	+
Theristus	+	+	+	+
Thoracostoma	+			+
Viscosia	+	+	+	+

Data sources are [a]Da Rocha (2003), [b]Fonsêca-Genevois et al. (2004), [c]Lages (unpublished), [d]Nunes (unpublished)

effects of macro-foulers on meiofauna and vice versa (see, e.g., Dahms et al. 2004, for a study of how meiofauna can effect macrofaunal recruitment).

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