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PRIMARY RESEARCH PAPER

Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low- and high-energy environments

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Abstract How do small, benthic meiofaunal organisms become cosmopolitan over large geographic ranges? Abiotic forces including oceanic currents are believed to be of key importance in aiding marine meiofaunal dispersal. We investigated the effect of distance from substrate and site exposure on meiofaunal colonization and transport in the water column. First, we tested how distance from substrate and sediment grain size affected colonization of azoic sediments by meiofauna in a sheltered inlet. Nematodes, crustacean nauplii and small amphipods colonized distant sediment cages (3 m above bottom) as quickly and abundantly as cages closer to the ocean floor. Some of the 30 recorded genera of nematodes predominated in one height treatment whereas abundance of others was not related to distance from the substrate. Polychaetes and harpacticoid copepods colonized near-benthic cages more rapidly and abundantly than those farther away suggesting active dispersal. Nematodes, harpacticoids and polychaetes were more abundant in fine than in coarse sediments, while nauplii and amphipods did not differ in abundance between sediment types. In part two of this study, we surveyed occurrence of meiofauna in the water column at several sheltered and exposed sites using plankton nets towed at fixed distances from 0.5 to 6.5 m above the ocean floor. Because oceanic currents increase sediment suspension and transport, we expected to see more meiofauna in samples collected from exposed than from sheltered sites. However, with the exception of polychaetes, which were more abundant in the water column of sheltered sites, there was no difference in meiofaunal abundances between the two exposure classes. Meiofauna, including the 14 identified nematode genera, were collected in greatest numbers nearer to the ocean floor and dwindled further up in the water column. The presence of meiofauna high in the water column of even the most sheltered sites combined with the quick and abundant colonization of distant, sheltered sediment cages suggests that even very weak currents are sufficient to suspend and transport these animals or that many meiofaunal taxa are capable of active dispersal into the water column.

Keywords Meiofauna · Nematodes · Copepods · Colonization · Paradox · Dispersal

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Introduction

The marine benthic environment is home to an enormous diversity and abundance of meiofaunal organisms (metazoans passing through a sieve with a mesh of 1 mm and retained on a mesh of ca. 40 µm; Heip et al., 1985; Snelgrove, 1999). Meiofauna are often the numerically dominant metazoans in marine environments ranging from abyssal plains and trenches (Tselepides & Lampadariou, 2004) to the muddy intertidal (Heip et al., 1985) and are often the first metazoans to colonize newly available sediments (Ullberg and Ólafsson, 2003a, b). Many species are widespread or cosmopolitan (Coomans, 2000; Bhadury et al., 2008; Derycke et al., 2008) which is surprising given that benthic meiofaunal organisms typically do not have planktonic larval stages (Giere, 1993; Fenchel & Finlay, 2004; Bhadury et al., 2008). Instead they have direct development or brooding of the early stages of young that, when ready, are released into nearby sediment as smaller versions of the adult. Considering these dispersal limitations, the global ubiquity of meiofauna has been called a paradox (Giere, 1993). How have these small, benthic organisms with little mobility become cosmopolitan over such large geographic ranges?

Nematodes and harpacticoid copepods are generally the most abundant marine meiofaunal animals (Platt & Warwick, 1980; Heip et al., 1985). These two taxa reach their greatest abundances in fine-grained or muddy sediments. Heip et al. (1985) found that although marine nematode density was usually greater in finer sediments, diversity was generally greater in coarser sediments. A shift in dominance from nematodes to harpacticoid copepods with larger grain size was observed by Coull (1970). Large numbers of harpacticoid nauplii are also encountered typically in sites with adult harpacticoids. Meiofaunal polychaetes, of which there are approximately 250 species, generally rank in the top four most abundant meiofauna (Giere, 1993). Unlike many larger macrofaunal polychaetes that release larvae into the water column (Qian, 1999), the meiofaunal polychaetes do not have planktonic trochophore larvae (Giere, 1993). Small amphipods, although often exceeding the upper meiofaunal size limits, can also be abundant and exhibit adaptations for a meiobenthic existence including small size and vermiform body (Giere, 1993).

Meiofaunal capacity for active dispersal by crawling or swimming is generally low but varies between taxa (Sterrer, 1973; Gerlach, 1977; Savidge & Taghon, 1988; Ólafsson, 2003). Although nematodes have been collected from plankton samples (Hagerman & Rieger, 1981; Sibert, 1981) and marine snow (Shanks & Walters, 1997), they are poor swimmers (Fegley, 1985) and likely become suspended in the water column via external forces (water currents or bioturbation), as is assumed for most meiofaunal taxa (Hagerman & Rieger, 1981; Mott & Harrison, 1983; Fleeger et al., 1984; Fegley, 1985; Armonies, 1988; Palmer, 1988; Bertelsen, 1998; Powers, 1998; Fonseca-Genevois et al., 2006). Many harpacticoid copepods, however, are much better active dispersers than nematodes (Widbom, 1983; Ólafsson & Moore, 1990, 1992) and occasionally enter the water column under their own power (Alldredge & King, 1980, 1985; Bell et al., 1988; Kurdziel & Bell, 1992; Walters and Bell, 1994; Teasdale et al., 2004). Fonseca-Genevois et al. (2006) found that the colonization of azoic plates suspended above the ocean floor was faster for harpacticoids than for nematodes, which relied more heavily on periodic upwelling events for dispersal. Remarkably, Kurdziel & Bell (1992) found that sea grasses positioned as high as 20 m away from potential harpacticoid colonists reached background densities only after 2 days. However, with the exception of some harpacticoids, most meiofauna appear capable of only limited active dispersal into the water column and their presence there is rare compared to their high densities in sediment (Sibert, 1981; Ullberg and Ólafsson 2003a, b).

Once in the water column, meiofaunal organisms may be carried long distances by oceanic currents, which are believed to be of crucial importance to long-range dispersal of benthic meiofauna including juvenile polychaetes (Gerlach, 1977; Hagerman & Rieger, 1981; Palmer & Gust, 1985; Butman, 1987; Derycke et al., 2007). Epibenthic harpacticoids and nematodes are more easily dispersed by currents given their typical position on the surface of sediments (Fleeger et al., 1984), while species residing deeper in the sediment are less likely to become suspended and transported passively. In habitats where currents are not strong enough to suspend meiofaunal animals into the water column, colonization of azoic sediments is much slower and may be limited to the active dispersal capacities of the meiofauna (Alldredge & King, 1980, 1985; Thistle, 1980; Alongi et al., 1983; Chandler & Fleeger, 1983; Sherman et al., 1983; Widbom, 1983; Walters & Bell, 1986; DePatra and Levin, 1989; Ólafsson & Moore, 1990, 1992; Aarnio & Bonsdorff, 1992; Bonsdorff, 1992; Vriser, 1998) or by the bioturbation of larger animals (Ullberg and Ólafsson 2003a, b).

Although sediment grain size, water currents and distance to the new habitat have all been found to affect dispersal and colonization of new substrates by meiofauna, these factors have rarely been studied simultaneously to determine which most limits meiofaunal colonization. Our first aim for this study was to examine meiofaunal colonization rates of coarse and fine azoic sediment suspended at increasing distances above the ocean floor in a low-energy environment. Given relative rates of active dispersal, we predicted that harpacticoid copepods would colonize nearby habitats faster and more abundantly than the slower dispersing nematodes and that colonization of the most distant sediment will be slowest for all meiofaunal taxa. Our second aim was to survey the occurrences of meiofaunal organisms in the water column by simultaneously sampling plankton at 1 m intervals above the ocean floor (from 0.5 to 6.5 m) in several low and high-energy environments.

Materials and methods

The study site

Field studies were conducted at the Bamfield Marine Sciences Centre on Vancouver Island, British Columbia, Canada (48°49′50″ N; 125°07′56″ W; Fig. 1). The sediment colonization study was run from 18 October to 28 November 2005 inside a protected inlet at a maximum depth of 12 m. The plankton surveys were conducted from 18 to 20 July 2006 inside and outside three sheltered inlets at a maximum depth of 8 m.

Part one: colonization rates of coarse and fine azoic sediment suspended at different heights above the ocean floor in a low-energy environment

A PVC grid was constructed and suspended 4 m above the ocean floor (12 m depth, Fig. 2B). Eighteen ropes of three different lengths were hung from the grid: six each of 3, 2 and 1 m lengths. Two rectangular cages (8 × 6 × 4 cm) containing either fine gravel (grain size 1–5 mm retained by a 1-mm plastic mesh) or coarse gravel (grain size 6–10 mm retained by a 5-mm plastic mesh) were attached to the ends of each rope hanging from the suspended grid (Fig. 2A). Sediment was made azoic by rinsing thoroughly with hot fresh water (80°C) and then freezing for 48 h at −20°C. Samples of each sediment type were subsequently investigated and confirmed to be free of any residual animal. The sediment cages were suspended from above rather than being tied to the ocean floor to eliminate the possibility of meiofauna creeping up the ropes (Gerlach, 1977). Half of the sediment cages were carefully collected in sealed containers by SCUBA divers (three cages from each rope length) after 21 days and the second half after 42 days. The sediment below the study apparatus was primarily mud littered with shell and woody debris and was haphazardly core sampled three times at the end of the

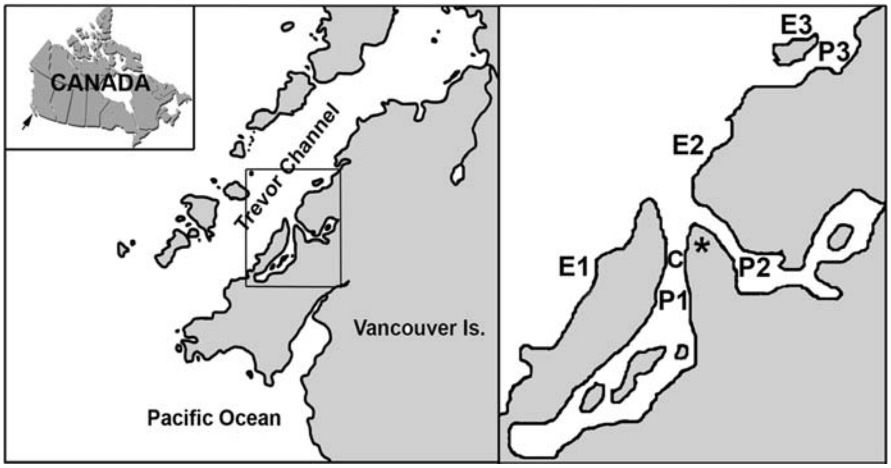


Fig. 1 Map showing location of study sites on Vancouver Island, British Columbia, Canada. Exposed plankton collection sites are denoted by "E" and protected sites by "P". Sediment colonization study location denoted by "C". Bamfield Marine Sciences Centre represented by the asterisk (*). Site names: *E1* Scott's Bay, *E2* Goby Town, *E3* Dixon Out, *P1 Bamfield Inlet*, *P2* Grappler Inlet, *P3* Dixon In

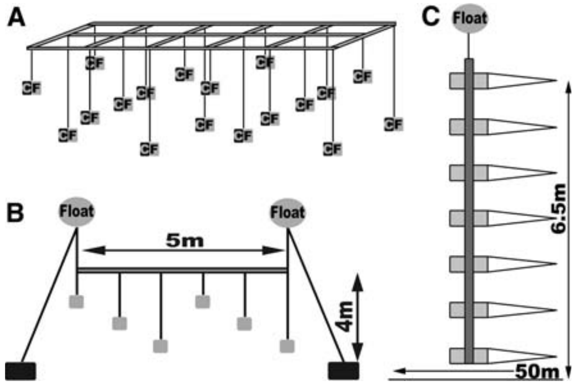


Fig. 2 Sediment colonization grid showing **A** arrangement of height/grain size treatments (*C* coarse grain, *F* fine grain) and **B** method of suspending the grid above the ocean floor. **C** Plankton collection device with seven plankton nets

study. The cores consisted of 5 cc of sediment and were taken using a 10 cc plastic syringe cylinder (1.5 cm diameter, 8 cm height). Nematodes from these cores were identified and compared to those that colonized the baskets above.

Part two: surveying vertical distribution of meiofauna in the water column

Six sites were chosen based on exposure level and associated intensity of water movement: three protected sites situated inside sheltered inlets and three exposed sites in the unprotected channel (Fig. 1). The ocean floor at each of the six sites was typified by fine and silty sediment littered with shell and woody debris. We fabricated a plankton-collecting device (PCD) to simultaneously collect plankton samples from 0.5, 1.5, 2.5, 3.5, 4.5, 5.5 and 6.5 m heights above the seafloor (Fig. 2C). At each of the six sites, the PCD was held vertically in the water column by two divers, one at the bottom and one at the top. Each of the seven plankton samplers attached to the device consisted of a 10-cm diameter PVC cylinder with a 53-μm Nitex® net secured with elastic bands over one end. The other end of each cylinder was kept sealed with a PVC cap during deployment to prevent plankton entering until the PCD was in the correct position in the water column. Once in position at a depth of 10 m, the caps were removed from each of the seven plankton samplers, and the PCD was pushed through the water column along a pre-laid transect-line for 50 m (maintaining a maximum depth of 10 m). It took approximately 10 min at each of the sites for the PCD to travel the entire 50 m. At the end of the transect, the two divers re-capped all of the plankton samplers and the entire device was carefully hauled out of the water and into the boat where the Nitex nets were removed, bagged and fixed in 8% formalin.

Processing and analysis of meiofauna

Samples from the sediment colonization study were preserved in 8% formalin. Meiofauna were isolated from sediments first by sieving through a 1-mm mesh and then via LUDOX flotation (see Warwick et al., 1998 for description). Animals were sorted into broad taxonomic/life-history groups under a stereo microscope (25×). Nematodes were slowly processed to glycerin (Seinhorst, 1959), slide mounted and identified to genus under DIC lighting using several taxonomic guides (Wieser, 1954; Warwick et al., 1998).

For the colonization study, differences in numbers of the numerically dominant groups of meiofauna (nematodes, post-larval harpacticoid copepods, crustacean nauplii and polychaetes) between sediment and height treatments and over time were investigated using 2 two-way ANOVAs (one for each sediment type, abundance data was log + 1 transformed to improve normality) and Tukey's post hoc tests (SPSS 13.0 for Windows). A series of paired *t*-tests were also conducted to investigate differences in abundances of animals colonizing the coarse- and fine-grained sediment baskets at the end of each line (SPSS 13.0 for Windows). For the plankton study, abundances of meiofauna between the various water column heights and exposure classes were also analysed for the plankton collection experiment using ANOVA (SPSS 13.0 for Windows).

Results

Part one: colonization rates of coarse and fine azoic sediment suspended at varying heights above the ocean floor in a low-energy environment

Nearly 10,000 animals colonized the sediment cages over the duration of the study (Table 1). Harpacticoid

Table 1 Abundances of fauna that colonized the sediment baskets in fall 2005 (summed across all height and grain treatments)

Taxon	Week 3	Week 6	Total
Harpacticoid copepods	4,816	3,633	8,449
Nauplius larvae	367	192	559
Nematodes	135	291	426
Amphipods	146	114	260
Polychaetes	69	58	127
Turbellarian flatworms	44	59	103
Euphausids	4	7	11
Juvenile bivalves	0	6	6
Halacarid mites	0	3	3

copepods accounted for 85% of all individuals sorted. Nauplius larvae and nematodes were the second and third most abundant taxa, respectively, followed by polychaetes and turbellarian flatworms. Euphausids, juvenile bivalves and halacarid mites were slowest to colonize and were the least abundant taxa. Although nauplii and some polychaete larvae are typically planktonic and are often found in the water column, they are included here as meiofauna given that they colonized the sediment within the cages. Six nematode genera were identified from the background sediment collected below the baskets (Table 2).

Harpacticoid copepod abundance declined between weeks 3 and 6 in the fine sediment treatments (DF:1, $F = 20.12$, $P = 0.001$) but increased from weeks 3 to 6 in the coarse sediment treatments (DF:1, $F = 13.46$, $P = 0.003$, Fig. 3a, b). However, copepod abundance was lower in the coarse grain treatments throughout the study (3 weeks: DF:8, $t = 9.219$, $P < 0.0001$; 6 weeks: DF:8, $t = 3.94$, $P = 0.004$; Fig. 4), and it took more time for copepods to become abundant compared to the fine grain sediment. There was no difference in numbers of copepods colonizing substrate cages at different heights in the water column for the fine sediment treatments (DF:2, $F = 2.295$, $P = 0.143$). However, in the coarse sediment treatments copepods were faster to colonize sediment cages lower in the water column than those farther from the ocean floor (DF:2, $F = 4.528$, $P = 0.034$).

Nauplii showed the opposite trend to adult harpacticoid copepods with regard to colonization time and sediment size (Fig. 3c, d). Nauplii abundance in fine sediment was greatest after 6 weeks (DF:1, $F = 4.773$, $P = 0.049$), but was greatest after 3 weeks in the coarse sediment (DF:1, $F = 34.897$, $P < 0.001$). Overall nauplii abundance was initially greater in the coarse-grained sediment, but by the end of the study nauplii were most abundant in fine sediment treatments (3 weeks: DF:8, $t = -5.688$, $P = 0.0005$; 6 weeks: DF:8, $t = 2.684$, $P = 0.028$; Fig. 4). There were no significant differences in nauplii abundance between the different height treatments for both the fine and coarse sediment treatments (DF:2, $F = 3.459$, $P = 0.065$ and DF:2, $F = 1.721$, $P = 0.220$, respectively).

Nematode abundance across height treatments tended to increase over time for both the fine and coarse sediments but was significant only for the fine sediment (DF:1, $F = 8.607$, $P = 0.013$ for fine, DF:1, $F = 4.224$, $P = 0.062$ for coarse; Fig. 3e, f). Overall nematode abundance was greater in the fine sediment treatments versus the coarse sediment treatments, although this relationship was only significant after 6 weeks (3 weeks: DF:8, $t = 1.695$, $P = 0.13$; 6 weeks: DF:8, $t = 3.957$, $P = 0.004$; Fig. 4). Like the nauplii, there were no significant differences in nematode abundances among the three different height treatments for both the fine and coarse sediment treatments (DF:2, $F = 0.181$, $P = 0.837$ and DF:2, $F = 1.5$, $P = 0.262$, respectively). Nematodes were as quick after 3 weeks to colonize treatments farther from the ocean floor as they were to colonize those hanging lower in the water column.

Thirty nematode genera colonized the sediment baskets over the 6-week study (only 262 of the 426 specimens could be identified due to either poor condition or loss of specimens during processing, Table 2). After 3 weeks, the genera represented by 10 or more individuals were *Neochromadora* ($N = 19$), *Oncholaimus* ($N = 17$) and *Paracanthonchus* ($N = 13$); after 6 weeks, the genera with most individuals were *Prochromadorella* ($N = 33$), *Oncholaimus* ($N = 28$), *Paracanthonchus* ($N = 23$), *Hypodontolaimus* ($N = 18$), *Draconema* ($N = 15$), *Anticoma* ($N = 11$) and *Theristus* ($N = 10$). Members of the chromadorids are epigrowth feeders and comprised 56% and 32% of the nematode fauna after 3 and 6 weeks, respectively (Table 2). *Neochromadora* had the greatest abundance after 3 weeks (primarily in fine-grained treatments) but was not

Table 2 Abundances of nematode genera that colonized the sediment baskets in fall 2005

	3 Weeks																		6 Weeks																
	Low (1 m)						Middle (2 m)						High (3 m)						Low (1 m)					Middle (2 m)						High (3 m)					
	Fine			Coarse			Fine			Coarse			Fine			Coarse			Fine		Coarse			Fine			Coarse			Fine			Coarse		
Enoplea																																			
Phanodermatidae																																			
Phanoderma												1																							
Anticomidae																																			
Anticooma	1																		1	1		1		2		2	1	3							
Leptosomatidae																																			
Deontostoma																																1			
Thoracostoma																			1				1								1				
Oncholaimidae																																			
Oncholaimus (1)	2			2			1		3	2	1	1	2	1	1	1				1		2		1	2	5		3	2	8	2		1		1
Viscosia (1)						1											2		1			1		1		1	2				1		1		1
Enchelidiidae																																			
Eurystomina																			3					1	1	1					1				2
Symplocostoma						1						1																							
Rhabdomemaniidae																																			
Rhabdodemania																								1											
Chromadorida																																			
Siphonolaimidae																																			
Siphonolaimus (1)																																			
Axonolaimidae																																			
Ascolaimus						1	1	2			1							3																	
Axonolaimus																																			1
Desmoscolecidae																																			
Desmoscolex																																	1		
Diplopeltidae																																			
Araeolaimus																			1		1				1										
Draconamatodae																																			
Draconema														1					1		1		2	2		2		1	1	2	1	1	1		
Epsilonematidea																																			
Epsilonema																						1		1								1		1	
Chromadoridae																																			
Acanthonchus	1						2				1																								
Actinonema											1																								
Chromadora (3)																																			
Chromadorina	1												2				2																		
Chromadorita													1	3																					
Dichromadora (1)																																			
Hypodontolaimus																										1			11	6					
Neochromadora	2	1	2				4	2	2			1	3	1				1																	
Parapinnanema											1																								
Prochromadorella																			3	6			1	1	4	3		2		4	1	2	1	2	3
Ptycholaimellus													2																						

Table 2 continued

	3 Weeks																		6 Weeks																
	Low (1 m)						Middle (2 m)						High (3 m)						Low (1 m)					Middle (2 m)						High (3 m)					
	Fine			Coarse			Fine			Coarse			Fine			Coarse			Fine		Coarse			Fine			Coarse			Fine			Coarse		
Cyantholaimidae																																			
Paracanthonchus					1	1	2			2	1		3			1	2		2	1	1			1	1	2			4	8		1			2
Desmodoridae																																			
Metachromadora																										1									
Monhysterida																																			
Xyalidae																																			
Diplolaimella																														1					
Theristus														3				1	2	1						2			2		2	1			
Areolaimida																																			
Axonolaimidae																																			
Axonolaimus (1)																																			
Comesomatidae																																			
Sabatieria hilarula	1																																		
Aegialoalaimidae																																			
Aegiolaimus																				2														1	

A large number of specimens were damaged, lost during processing for slide-mounting, or were otherwise unidentifiable and are not listed here. The abundance of each nematode genus represented in samples of background sediment is given in parentheses following the genus name

found again in any of the sediment baskets after 6 weeks. Conversely, *Prochromadorella* had the greatest abundances of all nematode genera after 6 weeks but was not found in any of the baskets at 3 weeks. *Oncholaimus* and *Paracanthonchus* were found in relatively large numbers after both 3 and 6 weeks. Only two of the six nematode genera identified from the background sediment samples were also found colonizing the suspended baskets (Table 2).

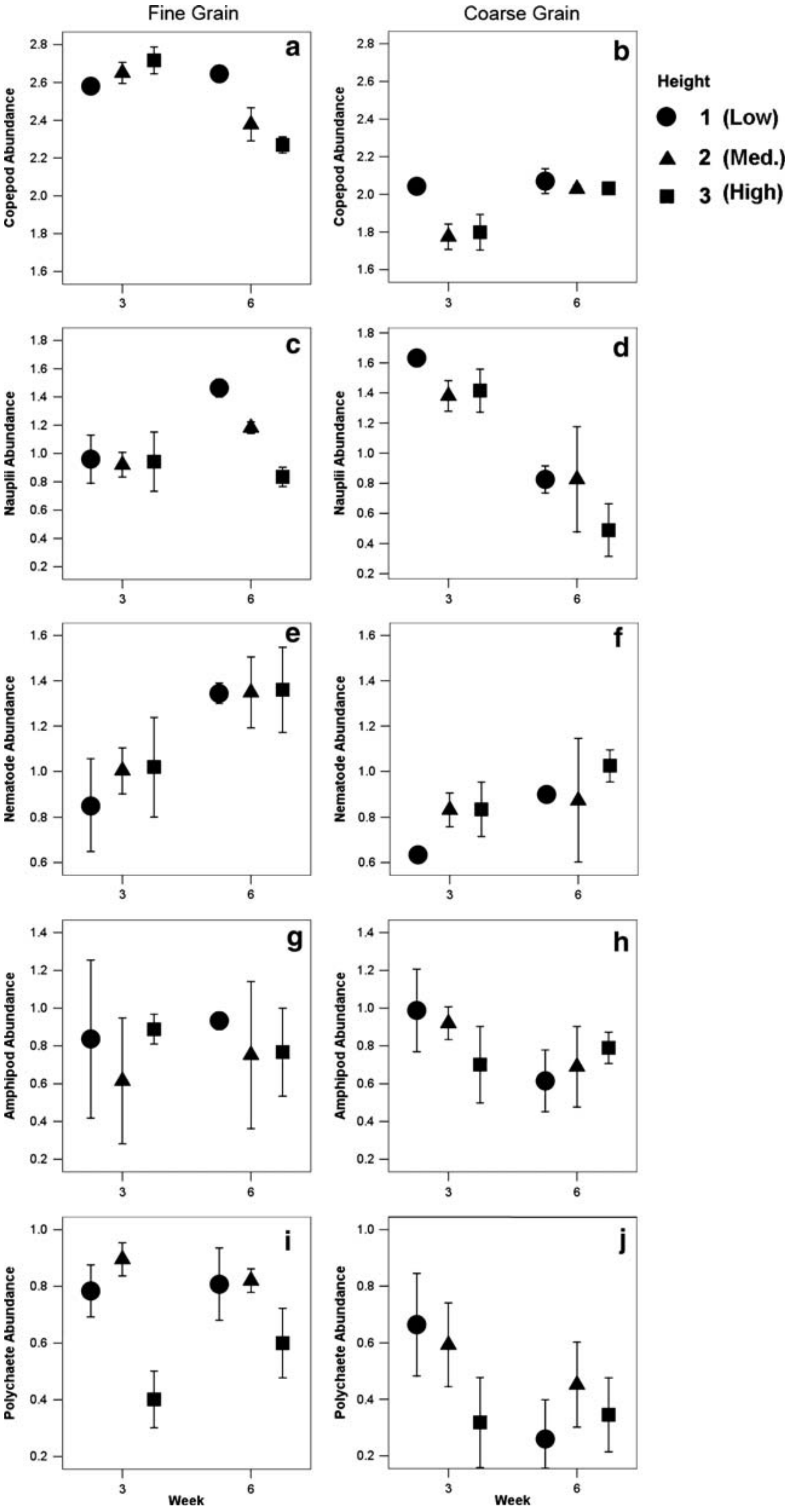
Amphipod abundance showed no significant relationship with colonization time for either the fine or coarse sediment treatments (DF:1, $F = 0.025$, $P = 0.877$ and DF:1, $F = 1.665$, $P = 0.221$, respectively; Fig. 3g, h), nor did it differ between sediment grain sizes (3 weeks: DF:8, $t = 0.00$, $P = 1.00$; 6 weeks: DF:8, $t = 1.437$, $P = 0.189$; Fig. 4) or with respect to distance of the substrate from the ocean floor for either the fine or the coarse sediment treatments (DF:2, $F = 0.259$, $P = 0.776$ and DF:2, $F = 0.094$, $P = 0.911$, respectively). Thus, as for the nauplii and nematodes, amphipod colonization appears not to have been hampered by increasing distance from the ocean floor.

Polychaete abundance did not change significantly over time for either the fine or coarse sediment treatments (DF:1, $F = 0.389$, $P = 0.544$ and DF:1, $F = 1.831$, $P = 0.201$, respectively; Fig. 3i, j). Overall polychaete abundance was greater in the fine sediment treatments versus the coarse sediment treatments, although this relationship was only significant after 6 weeks (3 weeks: DF:8, $t = 1.302$, $P = 0.229$; 6 weeks: DF:8, $t = 3.368$, $P = 0.010$; Fig. 4). Polychaetes from the fine sediment were more abundant in the lower-hanging treatments than in cages suspended higher in the water column (DF:2, $F = 7.924$, $P = 0.006$). This was not found for polychaetes colonizing the coarse sediment treatments (DF:2, $F = 0.802$, $P = 0.471$) which had overall lower abundances compared to the fine sediment regardless height in the water column.

Part two: surveying vertical distribution of meiofauna in the water column

Each cylinder of the PCD sieved approximately 400,000 cc of seawater along the 50-m transect line. Planktonic calanoid copepods and various types of

Fig. 3 Mean abundances of the five taxa that colonized the sediment baskets in the greatest densities (±1 SE, log + 1 transformed) between the two colonization times (3 and 6 weeks), three height treatments and two sediment grain sizes (fine and coarse)



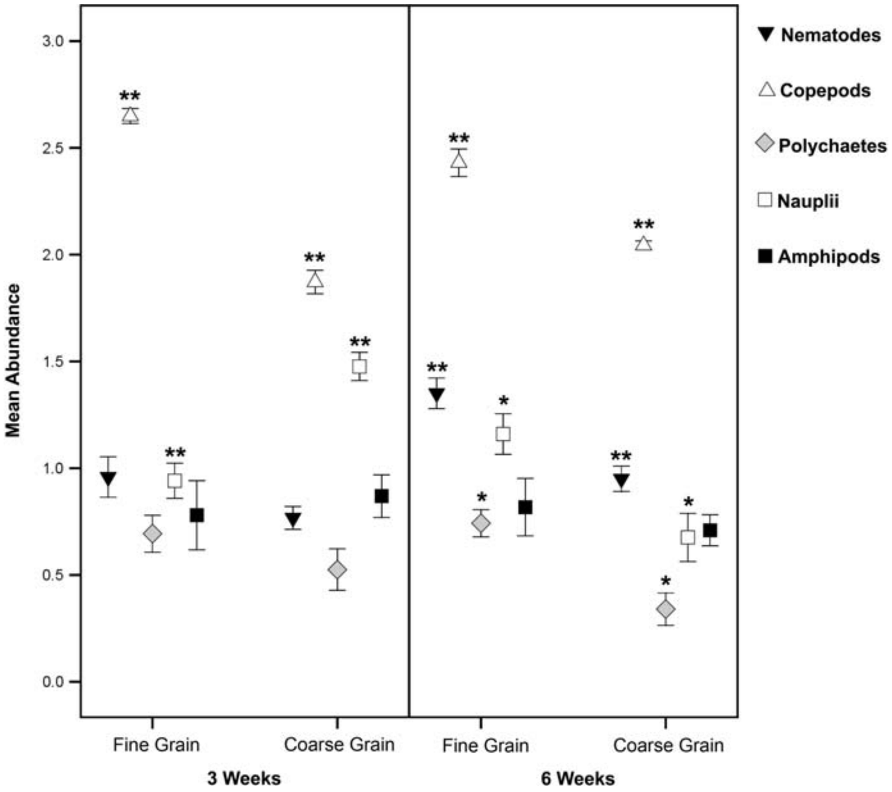


Fig. 4 Mean abundances for the five main groups (log + 1 transformed, ±1 SE) between the two sediment grain sizes. Paired *t*-test significance values denoted as ** $P < 0.01$, * $P < 0.05$

crustacean larvae vastly dominated the taxa collected by the PCD and are not considered further in this study of benthic meiofauna. Harpacticoid copepods (154, approximately 1/2,600 cc of seawater), polychaetes (93, approx. 1/4,300 cc of seawater) and nematodes (69, approx. 1/5,800 cc of seawater) were far less abundant in the plankton samples (Table 3). Cladocerans (104, approximately 1/3,850 cc of seawater) were also encountered in similar abundances as the meiofauna and are included in the study as a planktonic comparison. Fourteen nematode genera were identified from those collected in the water column (only 39 of the 69 specimens could be identified due to poor condition, Table 4). Over half of them (52%) belong to the Chromadoridae, a family comprised of epigrowth feeders. There did not appear to be a predominance of any particular genus as most were represented by one or two specimens.

Table 3 Fauna from the plankton samples collected in the summer of 2006 excluding highly abundant normally planktonic animals (e.g. calanoid copepods and crustacean larval stages)

	Protected	Exposed	Total
Harpacticoids	86	68	154
Polychaetes	78	15	93
Nematodes	45	24	69

Damaged and otherwise unidentifiable nematodes are not listed here

Harpacticoid copepods, although present at every height sampled, tended to occur most abundantly in plankton samples collected closest to the ocean floor (Fig. 5), although this difference was not significant (DF:6, $F = 2.280$, $P = 0.060$). Nematodes were also present at least once per height sampled (across exposure classes) and abundances were significantly greater in the samples closer to the ocean floor than those high in the water column (DF:6, $F = 3.013$, $P = 0.018$). Polychaetes were also present at least once per height treatment (across exposure classes) and did not show any relationship between abundance and height in the water column (DF:6, $F = 1.748$, $P = 0.141$). Cladocerans were not found in the samples closest to the ocean floor and instead showed a greater abundance in samples higher in the water column (DF:6, $F = 2.656$, $P = 0.033$) as might be expected for typically planktonic animals. There was

Table 4 Abundances of nematode genera from the plankton collected in summer of 2006

Site	Height	E/P	Enoplea								
			Actinolaimidae	*Anticoma*	Oxystominidae	*Halailaimus*	Oncholaimidae	*Viscosia*	*Viscosia carnleyensis*	Trefusiidae	*Trefusia*
E3	0.5	E									
E3	1.5	E									
E2	2.5	E									
E2	4.5	E									1
E1	5.5	E									
P1	1.5	P									
P1	6.5	P									
P3	1.5	P						1	1		
P3	2.5	P	1								
P3	4.5	P									
P3	5.5	P	1								
P2	0.5	P									
P2	1.5	P		1		1					

Site	Height	E/P	Chromadorida							
			Chromadorina	*Chromadorina laeta*	*Neochromadora*	*Parapinnanema*	*Prochromadorella neapolitana*	*Spilophorella*	Desmodoridae	*Desmodora*
E3	0.5	E				1		2		1
E3	1.5	E			1					
E2	2.5	E	1							
E2	4.5	E								
E1	5.5	E				1				
P1	1.5	P	2							
P1	6.5	P			1					
P3	1.5	P								
P3	2.5	P								
P3	4.5	P	1							
P3	5.5	P								
P2	0.5	P		1	9		1	2		
P2	1.5	P	2							

Table 4 continued

Site	Height	E/P	Monhysterida			Areolamida			
			Xyalidae	*Daptonema*	*Theristus*	Axonolaimidae	*Odontophora*	Comesomatidae	*Sabatieria hilarula*
E3	0.5	E			1				1
E3	1.5	E							
E2	2.5	E							
E2	4.5	E							
E1	5.5	E							
P1	1.5	P							
P1	6.5	P							
P3	1.5	P							
P3	2.5	P							
P3	4.5	P							
P3	5.5	P							
P2	0.5	P		1			1		1
P2	1.5	P							

Heights represent plankton collectors positioned at 1 m intervals from 0.5 to 6.5 m above the ocean floor. Exposed locations are denoted with an “E” while protected sites are indicated by “P”. Only plankton-samples that yielded nematodes are listed here. See Fig. 1 for location of study sites. Damaged, missing and otherwise unidentifiable nematodes are not listed here

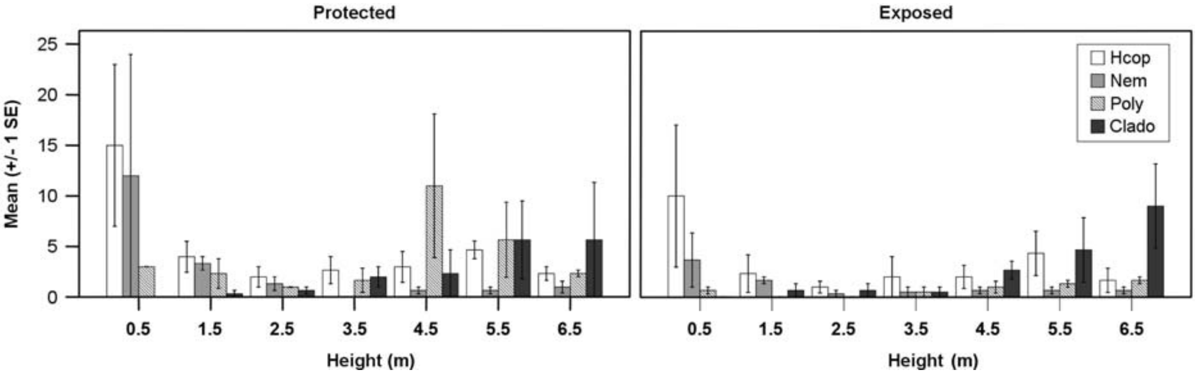


Fig. 5 Relative abundances of the four major taxa found in plankton samples between exposed and sheltered locations and heights in the water column collected at 1 m intervals from 0.5 to 6.5 m. *Hcop* harpacticoid copepods, *Nem* nematodes, *Poly* polychaetes, *Clado* cladocerans

no significant difference in abundance of harpacticoid copepods (DF:1, $F = 2.082$, $P = 0.157$), nematodes (DF:1, $F = 0.247$, $P = 0.622$) or cladocerans (DF:1, $F = 0.182$, $P = 0.672$) between the exposed and protected sample sites, although nematodes and harpacticoids were generally more abundant lower in the water column of protected versus exposed sites (Fig. 5). Polychaetes were more abundant in plankton samples collected from protected sites than from more exposed sites (DF:1, $F = 14.43$, $P = 0.001$).

Discussion

Part one: colonization rates of coarse and fine azoic sediment suspended at varying heights above the ocean floor in a low-energy environment

Colonization in a protected site

The sediment baskets were quickly colonized by a variety of meiofauna despite the relatively sheltered study location and presumably low rates of suspension of benthic materials by currents. Harpacticoid copepods were found in the greatest abundances followed by nauplii, nematodes, amphipods and polychaetes. Previous work on colonization by meiofauna has also shown that copepods establish fastest and in the greatest numbers (e.g. Thistle, 1980; Alongi et al., 1983; Chandler & Fleeger, 1983; Aarnio & Bonsdorff, 1992). In their colonization study, Fonseca-Genevois et al. (2006) found that copepods quickly established only after 1 day followed by nematodes, turbellarians, ostracods and other meiofaunal taxa.

Effect of increasing distance from ocean floor

It was surprising to find that nematodes, usually considered poor active dispersers, had attained their greatest abundances in cages farthest from the ocean floor. Even by the end of the study, nematodes were as or more abundant in baskets higher up in the water column than in those further down. The nematode genera found most abundantly throughout the study showed no obvious relationship to sediment height but instead were spread evenly across height treatments. There were however many less abundant genera that were absent from either high or low treatments. Nematodes that were never encountered in the highest sediment treatments were *Acanthonchus*, *Anticoma*, *Araeolaimus*, *Symplocostoma* and the species *Sabatieria hilarula*. Conversely, nematodes that were never found in the lowest sediment treatments were *Hypodontolaimus*, *Chromadorita*, *Ptycholaimellus*, *Axonolaimus*, *Deontostoma*, *Desmosolex* and *Diplolaimella*. The occurrence of such an array of nematode genera in only the higher treatments is striking and suggests that these nematodes were not arriving via active vertical migration. Furthermore, we found only two genera in common between the baskets and background sediment which support the notion that nematodes were not arriving solely from below. It is more probable that these colonizers arrived after becoming suspended by some external force. Fonseca-Genevois et al. (Brazil, 2006) also reported that *Acanthonchus*, *Chromadorina*, *Oncholaimus*, *Ptycholaimellus* and *Viscosia* colonized new habitats suspended above the ocean floor and attributed their arrival to periodic upwelling events. Despite the protected nature of our study site, it was still subjected to regular tidal cycles which may have carried nematodes from exposed environments outside the inlet to the sediment cages. The inlet also experienced high recreational boat traffic throughout the experiment which may also have contributed to nematode passive dispersal. Finally, it is important to recognize that in addition to colonization over time, reproduction by early arriving individuals may have also contributed to increases in abundances over the 6-week study.

Similarly, abundance of nauplii and small amphipods showed no relationship to distance from the ocean floor. They were also likely transported passively to the sediment baskets via external forces. In contrast, harpacticoid copepods and polychaetes colonized the three height treatments in a manner more indicative of active vertical dispersal from the sediment below. Juvenile polychaetes were found in greatest abundance in the fine sediment treatments closest to the ocean floor. They remained scarce in the high-hanging treatments throughout the study. This suggests that juvenile polychaetes likely arrived at the low-hanging treatments via short-range active dispersal. Although only significant in the coarse sediment, by the end of the study harpacticoids also tended to be more abundant in the low-hanging treatments. It is likely that many harpacticoid copepods, capable of actively departing the sediment (Alldredge & King, 1980, 1985; Bell et al., 1988; Kurdziel & Bell, 1992; Walters and Bell, 1994; Teasdale et al., 2004), arrived at the baskets under their own power.

Effect of grain size

Sediment size was an important factor affecting meiofaunal colonization and/or establishment. Abundances of copepods, nematodes and juvenile polychaetes were lower in the coarse than the fine sediments throughout the study. Whether these taxa actively chose fine over coarse gravel as demonstrated by Ullberg and Ólafsson (2003a, b) or were simply not retained by the larger interstitial spaces of the coarse sediment is uncertain. Veit-Köhler (2005) also found harpacticoid abundances to be greatest in fine-grained sediments, although total organic matter rather than grain size per se was considered the limiting factor. However, there is a point at which sediment becomes too fine for copepods as interstitial spaces become too small or clogged with silt. Reports have shown that copepod abundance peaks in sandy sediment (0.5–1.5 mm grain size) but declines sharply as mud/silt content increases (Wigley & McIntyre, 1964; Challis, 1969). The fine sediment cages in our study became lightly fouled with silt and other material over the duration of the study (visual inspection upon collection). This might explain the early and abundant colonization by copepods of the clean fine-sediment followed by a decline in overall abundance as the interstitial spaces became clogged. Conversely, siltation may have contributed to the increase in nematodes in the fine sediment cages over the duration of the study, as nematode abundance tends to be greatest in fine to muddy sediments (Heip et al., 1985). Although nematode density tends to be greater in finer sediments, greater diversities have been recorded in coarse sediments (Heip et al., 1985). We found no such pattern in this study. Instead, seven genera were found only in fine sediment, another seven only in coarse sediment, while the remaining 15 genera were found in both fine and coarse sediment. Few studies have investigated colonization preferences by polychaete larvae, and those that have mention little about effects of sediment size. Bhaud (1990) reported that larvae of a terebellid polychaete settled in the presence of sediment fine enough to be manipulated and used in tube building. However, we could find no other reports of polychaetes reaching greater abundances in fine versus coarse sediment. Finally, although we studied the effects of distance, time and sediment grain size independently, it is likely that these factors interact in nature to influence meiofaunal colonization of new sediments.

Part two: surveying vertical distribution of meiofauna in the water column

Vertical distribution

Harpacticoid copepods, nematodes and juvenile polychaetes, though meiofauna and typical within sediment, were encountered throughout the water column. Harpacticoids were most abundant and present in all samples. Nematodes and juvenile polychaetes were also found at every height sampled but their numbers were far fewer than the harpacticoids. Both nematode and harpacticoid copepod abundances tended to decline the higher the samples were collected in the water column. This was not surprising given that these taxa are almost exclusively benthic. Even though some meiofauna are capable of limited active dispersal, passive suspension via water currents or bioturbation likely caused epifaunal and shallow infaunal meiofauna to arrive in the water column. With the exception of the chromadorid nematodes *Neochromadora* and *Prochromadorella,* which were found in slightly greater abundances, there appeared to be no predominance of particular nematode genera in the water column. These genera and *Oncholaimus* sp. are known to occur in the upper 2 cm of sediment (see, for example, Sharma & Webster, 1983) and thus are more likely to be suspended in the water column by turbulence than nematodes that reside deeper in the sediment. Gobin & Warwick (2006) found chromadorids, cyatholaimids and microlaimids to be most successful in colonizing new substrates. Abundance of juvenile polychaetes, however, did not vary with position of the sampler in the water column. Instead polychaetes were found fairly evenly across all height samples in the protected site. In our basket-colonization study, we found juvenile polychaetes abundant only close to the sediment in the protected site. Perhaps polychaetes extend higher into the water column in the summer (plankton study) than in the fall (basket study) which would account for this discrepancy.

Exposed versus protected

It has been frequently suggested that meiofauna depend on external forces to become suspended in the water column and carried to distant habitats (Hagerman & Rieger, 1981; Mott & Harrison, 1983; Fleeger et al., 1984; Fegley, 1985; Armonies, 1988; Palmer, 1988; Bertelsen, 1998; Powers, 1998). One would thus expect to encounter more meiofauna in the water column of high-energy environments than of more protected ones. However, we found almost no difference between the abundance of meiofauna collected from the exposed and the protected sites. The one exception was a greater abundance of juvenile polychaetes in the protected sites. Perhaps, the levels of exposure were too similar to elicit a difference in suspended meiofauna. The tides may also cause sufficient mixing to disperse meiofauna evenly throughout both exposure classes. Whatever the cause, this study did not find evidence for more abundant suspended meiofauna in higher-energy environments.

Conclusion

In less exposed habitats, the transport of meiofauna via water currents is likely enhanced by taxa that are able to actively enter the water column. Once in the water column, even relatively small currents can transport the animals to distant habitats. However, for how long and over what distance can these benthic organisms remain suspended in the water column? Is there evidence of meiofauna in the water column of the open ocean? How long can meiofauna live suspended and on what do they subsist? Answers to these questions may help further our understanding of how these small benthic animals have reached their current levels of global ubiquity.

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