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Drifting algae as a means of re-colonizing defaunated sediments in the Baltic Sea. A short-term microcosm study

Nina Larissa Arroyo*, Katri Aarnio & Erik Bonsdorff
Environmental and Marine Biology and Husö Biological Station, Åbo Akademi, FIN-20500, Åbo, Finland
*(*Author for correspondence: Tel.: +358-2-2154070; Fax: +358-2-2153428; E-mail: nlarroyo@mundiva.es)*

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Abstract

We conducted a microcosm experiment to evaluate the capability of fauna inhabiting or being transported by drifting filamentous algae to colonize defaunated sediment. We expected meiofauna would perform a quicker and more effective re-colonization of disturbed areas by means of the algal mats than their macrofaunal counterparts. Similarly, within meiofauna, we expected more mobile taxa such as ostracods and harpacticoids to colonize the sediment more readily than other more sedentary ones such as nematodes. Naturally drifting algae were collected from the field and placed in 1 l aquaria on top of 5 cm of defaunated sediment. After 3 and 6 days, one core sample (5 cm deep) was taken from each aquarium; the first 2 cm were sliced into 2 mm layers, and the remaining fraction into 1 cm layers. The sediment remaining in the aquaria was sieved through a 0.5 mm sieve to collect the re-colonizing macrofauna. The dominant macrofaunal taxa inhabiting the algae were juvenile bivalves and gastropods, with *Cerastoderma glaucum* accounting for the majority of the bivalves and *Hydrobia* sp. for most of the gastropods. After 3 and 6 days, the most abundant macrofaunal taxa colonizing the sediment were *Cerastoderma glaucum*, *Hydrobia* sp. and gammarid amphipods. Higher abundances were found after 6 days than after 3, though differences were not significant for any of the major taxa. Meiofauna inhabiting the algae were dominated by rotifers, nematodes, ostracods, chironomid larvae and harpacticoid copepods. Contrary to our predictions, nematode and harpacticoid species inhabiting the drifting algae were not driven to sediment re-colonization but remained in the algae. Our results indicate that some benthic animals may indeed benefit from drifting algal mats as a means of dispersal and re-colonization of previously defaunated sediments in relatively short periods of time. Also, they may contribute to explain some of the trends found in other studies, regarding species increase under drifting algae and the recovery patterns found in areas often exposed to algal conglomerates.

Introduction

Re-colonization is critical for the survival of fragmented populations and is ultimately responsible for the recovery of disturbed areas in both marine and terrestrial habitats, being indispensable to the success of conservation of endangered metapopulations (Fahrig & Merriam, 1994). In marine benthic habitats, re-colonization of previously disturbed areas has been shown to be species-specific and to occur rapidly whenever suitable conditions in the colonizable area are restored (Bonsdorff, 1989; Colangelo & Ceccherelli, 1994; Christie & Berge, 1995; Gamenick et al., 1996; Guerrini et al., 1998; Cristoni et al., 2004). Distance to the source pool of colonists and size of the disturbed areas have also been found to be a limiting factor determining long-lasting recovery of populations (Bonsdorff, 1980; Thrush et al., 1996; Whitlach et al., 1998; Cristoni et al., 2004).

Benthic fauna have shown to increase their dispersal distances by associating themselves with highly mobile habitats such as cyanobacterial mats (Vopel & Arlt, 1995), sediment rafts (Hicks, 1988), artificial substrates (Myers, 1993; Aliani & Molcard, 2003), drift debris (Barnes, 2002) or drifting macroalgae (Yeatman, 1962; Ingólfsson, 1995; Brooks & Bell, 2001; Ólafsson et al., 2001). Particularly, the latter have proven to be an efficient transport system through long distances (Yeatman, 1962; Ólafsson et al., 2001) and to act as mobile corridors between different patches of phytal or sediment areas (Norkko et al., 2000; Brooks & Bell, 2001; Salovius & Bonsdorff, 2004; Salovius et al., 2005). These algal accumulations may hence aid in decreasing the degree of isolation between patches within a landscape and *ergo* the recovery time from disturbance events, or favouring genetic flow between populations and therefore enhancing diversity and their survival over long periods (Lawton, 1993; Brown et al., 1996).

Increased eutrophication during the last decades has caused an exponential rise in the amount of filamentous macroalgae standing stock in coastal areas worldwide (Duarte, 1995; Pihl et al., 1995; Raffaelli et al., 1998; Berglund et al., 2003). These algae detach at the end of their lifecycle or due to storms, gather and form algal mats of varying size and density which may eventually sink, covering large areas of the sea bottom or disintegrate progressively. Their noxious and/or beneficial effects on the benthic fauna are widely documented (Hull, 1987; Bonsdorff, 1992; Everett, 1994; Norkko & Bonsdorff, 1996a, b; Thiel & Watling, 1998; Raffaelli, 2000; Österling & Pihl, 2001; Franz & Friedman, 2002; Wetzel et al., 2002). In general, most studies have found dense coverage by macroalgal mats over extended periods of time to have detrimental effects on the benthic infauna, mainly as a consequence of induced hypoxia and anoxia (Hull, 1987; Raffaelli et al., 1991; Bonsdorff, 1992; Norkko & Bonsdorff, 1996b; Österling & Pihl, 2001), while moderate or low levels of algal coverage have been found to enhance recruitment (Isaksson & Pihl, 1992; Raffaelli et al., 1998) and provide an alternative habitat to many benthic and pelagic species (Shaffer et al., 1995; Norkko et al., 2000; Salovius & Kraufvelin, 2004; Salovius et al., 2005). However, despite the high abundance and diversity of benthic fauna often encountered among these algal mats, and the fact that many animals use them as an escape way in cases of severe hypoxia or anoxia of the underlying sediments, to our knowledge, no study has specifically addressed the potential role of these conglomerates as potential donors of macro- and meiofauna to previously disturbed areas. In shallow waters, were these algal assemblages disintegrate more readily (Salovius & Bonsdorff, 2004), and fluctuations of the algal mats or in sulphidic and anoxic conditions are more dynamic due to increased movement through storms or water currents (Diaz & Rosenberg, 1995), the beneficial effects in terms of dispersal of populations may have a fundamental importance for benthic community dynamics and the maintenance of population abundance and diversity between disturbed and undisturbed patches.

The aim of our study was to evaluate the capability of macro- and meiofauna inhabiting or being transported by naturally occurring drifting algal mats to colonize previously defaunated sediment over short periods of time. Because meiobenthic communities are in general less vulnerable than macrobenthic ones to extreme disturbances induced by eutrophication (Villano & Warwick, 1995; Tagliapietra et al., 1998) or hypoxia (Meyers et al., 1987; Vopel et al., 1996; Modig & Ólafsson, 1998), and considering their rapid colonization and turnover rates, we expected that they would perform a quicker and more effective re-colonization of disturbed areas by means of the algal mats than their macrofaunal counterparts. Similarly, within meiofauna, we expected more mobile taxa such as ostracods and harpacticoids to colonize the sediment more readily than other more sedentary ones such as nematodes.

Material and methods

Experimental set-up

A microcosm experiment was conducted in 2002 (July 26–August 2) by using 1.0 l aquaria containing a 5 cm layer of defaunated sediment and seawater (approx. 5 psu.). The sediment was sampled from a shallow (1 m) sand bottom bay in the northwestern Åland archipelago, northern Baltic Sea (60°17′N, 19°49′E) and had a medium grain size of 0.125–0.25 mm and organic content of 0.34%. Defaunation was achieved first by sieving the sediment through a 0.5 mm mesh in order to remove macrofauna, and freezing at −18 °C for 48 h to kill any remaining fauna. Then the sediment was stirred completely, after which a 5 cm thick layer was put into each aquarium and the sediment allowed to settle for 2 days. Filtered (10 μm) seawater was added to the aquaria (depth of overlying water: 10 cm). Following water addition, all aquaria were equipped with an aerating device (bubbling through individual syringes in each aquarium) and left undisturbed for 3 days. The experiment was kept on a 12–12 h light–dark regime.

Approximately 25 g wwt of drift algae (including animals) were put in all aquaria, and two experimental times considered: 3 days (time 1) and 6 days (time 2), with 5 replicates each. The algae were sampled from the same area as the sediment with a push net, and kept in aerated seawater until start of the experiment (no longer than 48 h). To determine the initial sediment meiofauna density and composition, five cores (from now on referred to as controls, even if we are aware that they are not strict control samples of the experimental ones) were taken from five independent aquaria from which only macrofauna had been removed at the start of the experiment. After 3 and 6 days, respectively, the algae were removed carefully from each aquarium and placed in plastic bags for further processing. Then, one core sample (ø 2.9 cm) was taken from the underlying sediment and sliced. Cores were dug in the middle of the aquaria to avoid edge effect. The first 2 cm were sliced into 2 mm layers, and the remaining fraction into 1 cm layers. The remaining sediment was sieved through a 500 μm sieve to retrieve the colonizing macrofauna. At the end of each experimental time, and before removing the algae, we measured temperature, pH and salinity in the water of each of the aquaria. Also, oxygen samples were taken from all aquaria under the algae to see whether hypoxic or anoxic conditions prevailed above the sediment layer. This was done by inserting a syringe through a perforated hole filled with silicone, which was previously drilled on each aquarium right on top of the sediment layer. All samples were retrieved during day-time, during the 12-h light period.

Sample processing

The algae were rinsed and all animals separated into meio- and macrofaunal fractions, by using 0.5 mm and 63 μm mesh sieves. The animals extracted from the algae and all core samples were fixed in 4% buffered formalin and dyed with Rose Bengal. All samples were sorted under a stereomicroscope. All macrofauna were identified to the lowest taxonomic level possible and counted. Meiofauna were identified to high-taxa level, nematodes and harpacticoids to genus and species level, respectively, and all counted.

Statistical and numerical analyses

We examined whether there were changes in the amount of total macro- and meiofauna and different taxa in the algal samples and colonizing the sediment over time, by performing a Student *t*-test between samples from time 1 (after 3 days) and time 2 (after 6 days). Data were first checked for normality and homoscedasticity and transformed (log $(x + 1)$) duly, in order to comply with these parametric assumptions.

We compared ‘re-colonized’ sediment meiobenthic community structure with that of control samples. Because macrofauna was sieved from control samples prior to sediment inclusion in the aquaria, no comparisons were performed between control samples and ‘re-colonized’ sediment for this group.

Due to differences in the amount and uniformity of the sediment between aquaria in the lower 2 cm, only the first 3 cm were used in our comparisons.

Results

Environmental variables

Results of hydrographical analyses are summarized in Table 1. Temperature increased progressively with time and compared with control

Table 1. Summary of results of hydrographical parameters measured in the aquaria during the experiment

	Control	3 days	6 days
O_2/mg/l	7.9 ± 1.3	3.5 ± 3.7	4.8 ± 1.9
pH	7.9 ± 0.3	6.9 ± 0.04	7.6 ± 0.09
Salinity	5.3 ± 0.07	5.36 ± 0.08	5.57 ± 0.05
Temperature	19.8 ± 0.3	21.9 ± 0.1	22.4 ± 0.04

Values stand for mean ($N = 5$) ± standard deviation of the mean, respectively.

aquaria, as well as salinity. Oxygen content and pH decreased after 3 days but then recovered higher values in time 2. In general, aquaria were vary variable as regards oxygen levels, and while 2 of them showed anoxia after 3 days and one hypoxia, only one of them presented hypoxic levels under the algae after 6 days.

Macrofauna

The dominant macrofaunal taxa inhabiting the algae were juvenile bivalves and gastropods, with *Cerastoderma glaucum* Poiret, 1789 accounting for the majority of the bivalves and *Hydrobia* sp. for most of the gastropods (Table 2). Both of these species were also present as adults. Other representative species were the isopods *Idotea viridis* Slabber, 1775 and *Jaera albifrons* Leach 1814, the bivalve *Mytilus edulis* L., 1758, the gastropods *Theodoxus fluviatilis* L., 1758 and *Limapontia capitata* Muller, 1774, the nemertine *Prostoma obscurum* Schultze, 1851 and gammarid amphipods (Table 2). Total macrofaunal abundance in the algae did not vary significantly over time ($p > 0.05$). Neither did that of the major taxa, though most of them showed an increase in their abundance over time (Table 2).

Macrofauna from the algae effectively colonized the underlying sediment already after 3 days. At both experimental times (3 and 6 days), the most abundant macrofaunal taxa colonizing the sediment were *Cerastoderma glaucum* and *Hydrobia* sp. individuals, and gammarid amphipods, though individuals from some other taxa present in the algae were also found (Table 2). Higher abundances were found after 6 days than after 3, though these were not significant for any of the major taxa or total macrofauna numbers

Table 2. Macrofauna recovered from the algae (indiv. per 25 g) and the sediment (ii per 500 cm^3) samples during the experiment

Taxa	Algae		Sediment	
	3 days	6 days	3 days	6 days
Cerastoderma glaucum	52 ± 25	77 ± 32	3 ± 1	7 ± 5
Gammaridae	3 ± 2	5 ± 4	2 ± 0.7	3 ± 2
Hydrobia sp.	3 ± 3	2 ± 4	1 ± 0.54	3 ± 2
Idotea viridis	0.4 ± 0.5	0.8 ± 1	1	
Insects	0.2 ± 0.4			
Jaera albifrons	3 ± 4	2 ± 2		
Juv. Gastropods	7 ± 6	16 ± 8		
Limapontia capitata.	2 ± 2	2 ± 4		
Macoma balthica		0.2 ± 0.4		1
Mytilus edulis	2 ± 1	0.4 ± 0.5	1	1
Prostoma obscurum	1 ± 1	0.8 ± 1	1	
Theodoxus sp.	0.4 ± 0.9	0.4 ± 0.9	2 ± 0.7	1 ± 0.5
Tricoptera	0.2 ± 0.4			

Values stand for mean ($N = 5$) ± standard deviation of the mean, respectively.

($p > 0.05$). The macrofaunal taxa which colonized the sediment did so regardless of the low oxygen levels present in some of the jars.

Meiofauna

At both experimental times, the dominant taxa inhabiting the aquarium algae were rotifers (46 and 40% at times 1 and 2, respectively), nematodes (14 and 11%), ostracods (11 and 14%), chironomid larvae (9 and 10%) and harpacticoid copepods (8 and 9%) (Table 3). Ciliates were observed in the algae only after 6 days. Meiofaunal abundance in the algae did not vary significantly between times 1 and 2 ($p > 0.05$). Neither did that of most of the major taxa ($p > 0.05$), although most of them showed an increase in their abundance. Only cladocerans were significantly more abundant after 6 days (t-test: $t = -2.7998$, d.f. = 8; $p < 0.05$), while nematode abundance showed a non-significant decline after the first week (Table 3).

The most abundant meiofaunal taxa in the sediment were nematodes (66 and 67% of total abundance after 3 and 6 days, respectively), rotifers (19 and 12%), and harpacticoid copepods (8 and 10%). Other relevant taxa were nauplii, ostracods, and chironomid larvae. Juvenile bivalves, gastropods and gammarids, oligochaetes and turbellarians also appeared but in low numbers (Table 3). The t-test for independent samples showed a significant decline in global meiofaunal abundance after 6 days compared to 3 days ($t = 2.9788$, d.f. = 8; $p = 0.018$). However, none of the main taxa showed this decline, and only nematodes showed a close to significant decrease in their abundance after 6 days ($p = 0.053$).

Most taxa concentrated in the upper sediment layers, though many reached the bottom of the aquaria. Especially nematodes, harpacticoids and ostracods appeared well represented in the bottom layers, while rotifers, nauplii and cladocerans appeared mainly in the uppermost layers (Fig. 1).

Nematodes

The nematode assemblage in the algae was dominated by *Adoncholaimus thalassophygas* De Man, 1876, which accounted for 71% of total nematode abundance (both at time 1 and 2), followed by *Anoplostoma* (6 and 2% at time 1 and 2, respectively), *Theristus* (4 and 8%) and *Daptonema* (5 and 7%) (Table 3).

Nematodes in the sediment were dominated by *Anoplostoma* (34 and 33%), *Axonolaimus* (12 and 10%), *Tripyloides* (9% in both times), *Chromadorita*, *Dichromadora* and *Adoncholaimus* (all accounting for 7 and 8% at time 1 and 2, respectively). All genera appeared in both habitat types except *Desmolaimus* and *Eumorpholaimus*, which were only found in low numbers in the sediment (Table 3). At time 1, nematodes were evenly found in all layers, while at time 2 they concentrated in the deeper ones (Fig. 2). *A. thalassophygas* were mostly found in the first centimeter of the sediment, while *Anoplostoma* were evenly found in all layers after 3 days, but were more abundant in the bottom layers at the end of the experiment (Fig. 2).

Copepods

Copepods in the algae were represented by members of the orders Cyclopoida and Harpacticoida. The harpacticoid community associated with the drifting algae was dominated by *Mesochra rapiens* Schmeil, 1894 and *M. aestuari* Gurney, 1921 (together accounting for 57 and 61% at times 1 and 2, respectively, of total copepod abundance), followed by *Onychocamptus mohammed* (Blanchard & Richard, 1891) (20 and 26%) and *Nitokra spinipes* Boeck, 1864 (6 and 5%). There appeared very occasionally also other species such as *Paraleptastacus spinicauda* (T. & A. Scott, 1895), *Huntemannia jadensis* Poppe, 1884 and *Tachidius discipes* Giesbrecht, 1882 (Table 3).

The dominating harpacticoids in the sediment were *Paraleptastacus spinicauda*, *Huntemannia jadensis* and *Tachidius discipes*. Harpacticoid species abundant in the algal samples were practically absent in the sediment (Table 3). Cyclopoids appeared in the sediment samples after 6 days, remaining mainly in the upper layers of the sediment (Fig. 3). All other species appeared more or less uniformly distributed throughout the sediment column though after 6 days, together with a reduction in numbers, a displacement of most of the copepods towards the upper layers could be observed (Fig. 3).

Table 3. Meiofauna recovered from the algae (indiv. per 25 g) and the sediment (indiv. per core, recolonized and controls) during the experiment

Taxa	Algae		Sediment		
	3 days	6 days	3 days	6 days	Control
Cyclopoids	3 ± 2	4 ± 1	0	1 ± 0.9	0
Ciliates		16 ± 15	2 ± 1	0.2 ± 0.44	220 ± 233
Cladocerans	9 ± 6	40 ± 21	0.2 ± 0.44	2 ± 2	0.4 ± 0.54
Chironomids	98 ± 33	119 ± 39	2 ± 1	3 ± 1	1 ± 1
Harpactioids	88 ± 19	100 ± 45	23 ± 10	20 ± 6	77 ± 15
Huntemannia jadensis	2 ± 2	2 ± 1	5 ± 1	4 ± 2	10 ± 3
Mesochra	57 ± 19	63 ± 39	0.2 ± 0.4	0.4 ± 0.5	1 ± 0.8
Nitokra spinipes	6 ± 2	5 ± 2			
Onychocamptus mohammed	19 ± 5	26 ± 6	0.6 ± 1	0.4 ± 0.5	
Paraleptastacus spinicauda	2 ± 0.7		11 ± 5	7 ± 0.9	30 ± 13
Pseudobradya	2 ± 0.7	1 ± 1			
Tachidius discipes	2 ± 0.8		3 ± 3	3 ± 3	11 ± 4
Ectinosomatidae			0.2 ± 0.4		
Mites	13 ± 6	15 ± 5			
Nauplii	4 ± 4	13 ± 8	9 ± 3	10 ± 6	33 ± 22
Nematodes	145 ± 46	123 ± 87	185 ± 51	123 ± 29	537 ± 115
Adoncholaimus thalassophygas	97 ± 30	89 ± 63	15 ± 6	9 ± 5	35 ± 13
Anoplostoma	7 ± 8	3 ± 4	63 ± 22	40 ± 17	162 ± 46
Ascolaimus	2 ± 3		4 ± 2	5 ± 4	23 ± 18
Axonolaimus	3 ± 5	7 ± 11	24 ± 15	14 ± 6	79 ± 63
Chromadorita	6 ± 5	4 ± 4	15 ± 10	9 ± 6	25 ± 8
Daptonema	10 ± 11	6 ± 6	8 ± 5	3 ± 3	26 ± 14
Desmolaimus			4 ± 2	3 ± 2	18 ± 3
Dichromadora	2 ± 3		14 ± 6	9 ± 5	81 ± 31
Eleutherolaimus		0.4 ± 0.8	0.8 ± 2	3 ± 4	1 ± 2
Enoplolaimus	3 ± 3	2 ± 4	11 ± 3	10 ± 5	34 ± 31
Eumorpholaimus			0.4 ± 0.9		5 ± 6
Metalinhomoeus					0.9 ± 2
Oncholaimus	2 ± 2	0.4 ± 0.8	0.4 ± 0.9		4 ± 3
Paracanthoncus	0.7 ± 1	0.5 ± 1	4.8 ± 2.5	2.7 ± 2.9	7 ± 2
Sphaerolaimus		0.4 ± 0.8	0.8 ± 1.2	2.2 ± 3.8	4 ± 5
Theristus	6 ± 6	13 ± 17	3 ± 4	3 ± 5.5	28 ± 17
Tripyloides	2 ± 3	2 ± 4	16 ± 4	11 ± 6	34 ± 14
Oligochaetes	1		0.2 ± 0.4	0.2 ± 0.4	13 ± 7
Ostracods	117 ± 30	160 ± 84	4 ± 3	4 ± 1	6 ± 2
Rotifers	602 ± 541	466 ± 276	52 ± 32	24 ± 26	79 ± 108
Turbellarians	4 ± 2	3 ± 2	0.2 ± 0.4	0.4 ± 0.9	36 ± 13

Values stand for mean ($N = 5$ except for nematodes in the algae, $N = 4$ and in the control samples, $N = 3$) ± standard deviation of the mean, respectively.

Comparison with control samples

Our results on copepod and nematode identification at species level indicated that meiofauna found in re-colonized sediment samples could not be entirely ascribed to animals coming from the algae. Hence, both interpretation of meiofaunal re-colonization into the sediment and comparison

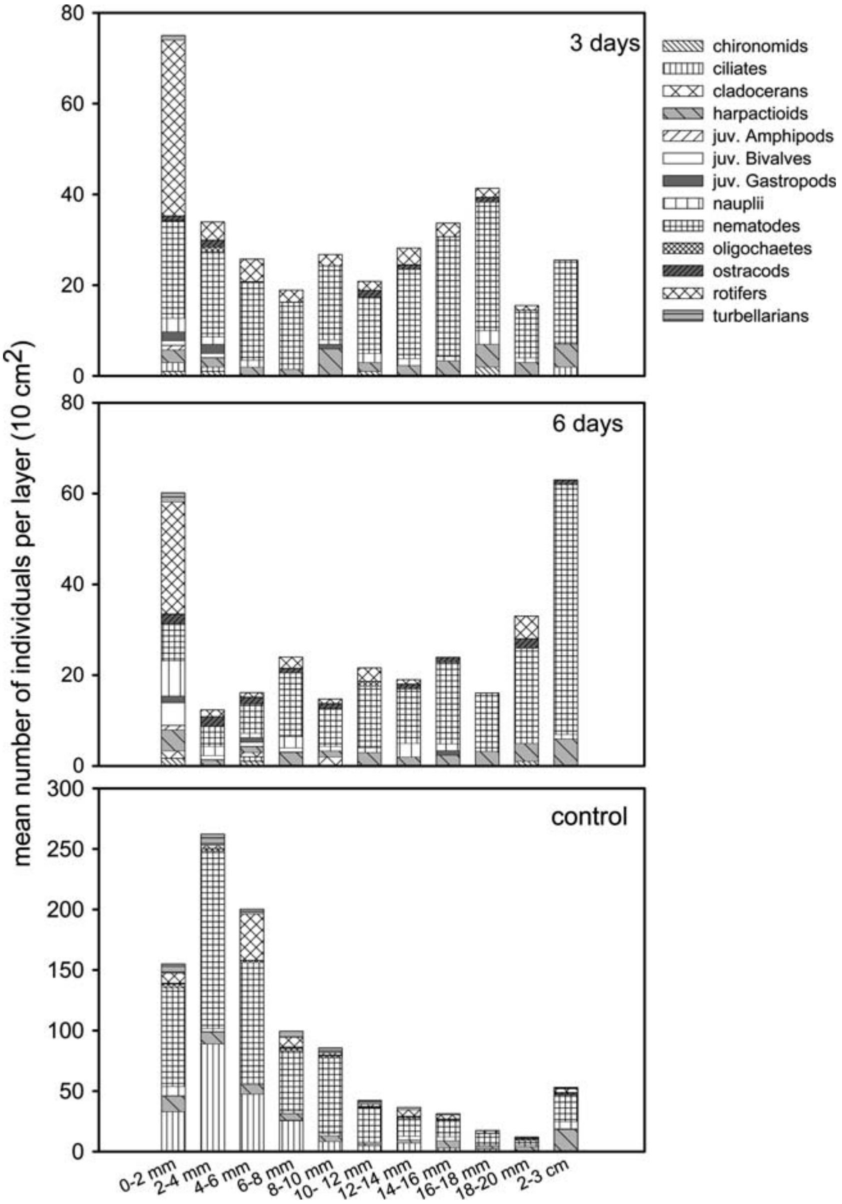

Figure 1. Distribution of meiofaunal taxa in the different core layers in control samples and after 3 and 6 days in the re-colonized sediment.

between re-colonized and control samples had to be performed cautiously, since other taxa could also have remained in the sediment despite defaunation. All meiofaunal taxa, which appeared in the re-colonized samples, were also represented in the control ones in equal or higher numbers (Table 3). The only groups, which showed higher abundances in the re-colonized sediment than in control samples, were juvenile gammarids, cladocerans and juvenile bivalves and gastropods (Table 3), though significance of these comparisons, due to the above-mentioned reasons was not tested. Distribution of the different taxa in the sediment column was more or less even in re-colonized and control samples, though some groups, such as juvenile bivalves and gastropods showed higher abundances in the upper re-colonized layers compared to control ones, particularly after

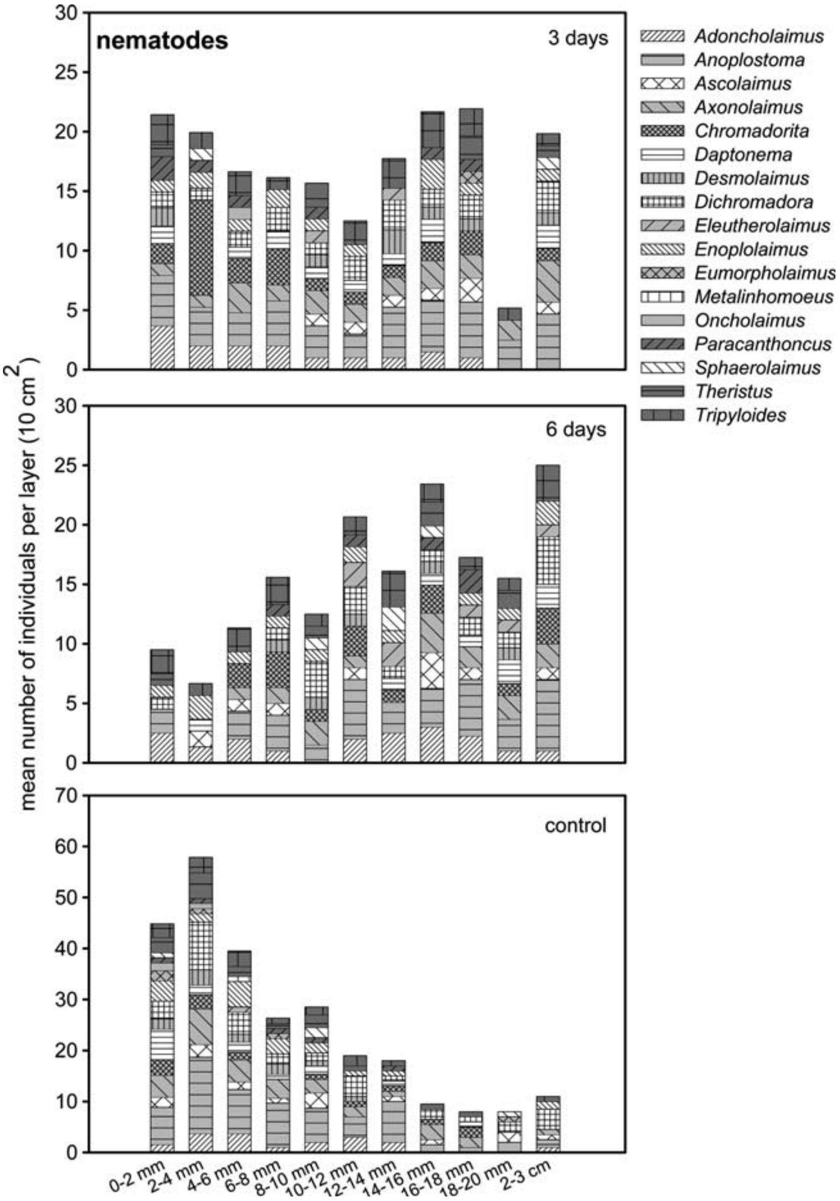

Figure 2. Distribution of nematodes in the different core layers in control samples and after 3 and 6 days in the re-colonized sediment.

6 days, when they were more abundant (Fig. 1). Some taxa, which appeared well represented in the control samples, such as ciliates, oligochaetes, and turbellarians showed low abundances in the re-colonized sediment (Table 3).

The same nematode genera were present in the re-colonized samples and in the control ones, where *Anoplostoma* was also the most abundant species. The vertical distribution in the sediment differed between control samples and the re-colonization ones (Fig. 2). In control sediment, most nematodes gathered in the uppermost layers, while in the re-colonized samples they were distributed evenly throughout the sediment column after 3 days, and mainly in the deeper layers after 6 days. *Anoplostoma* was most abundant in the

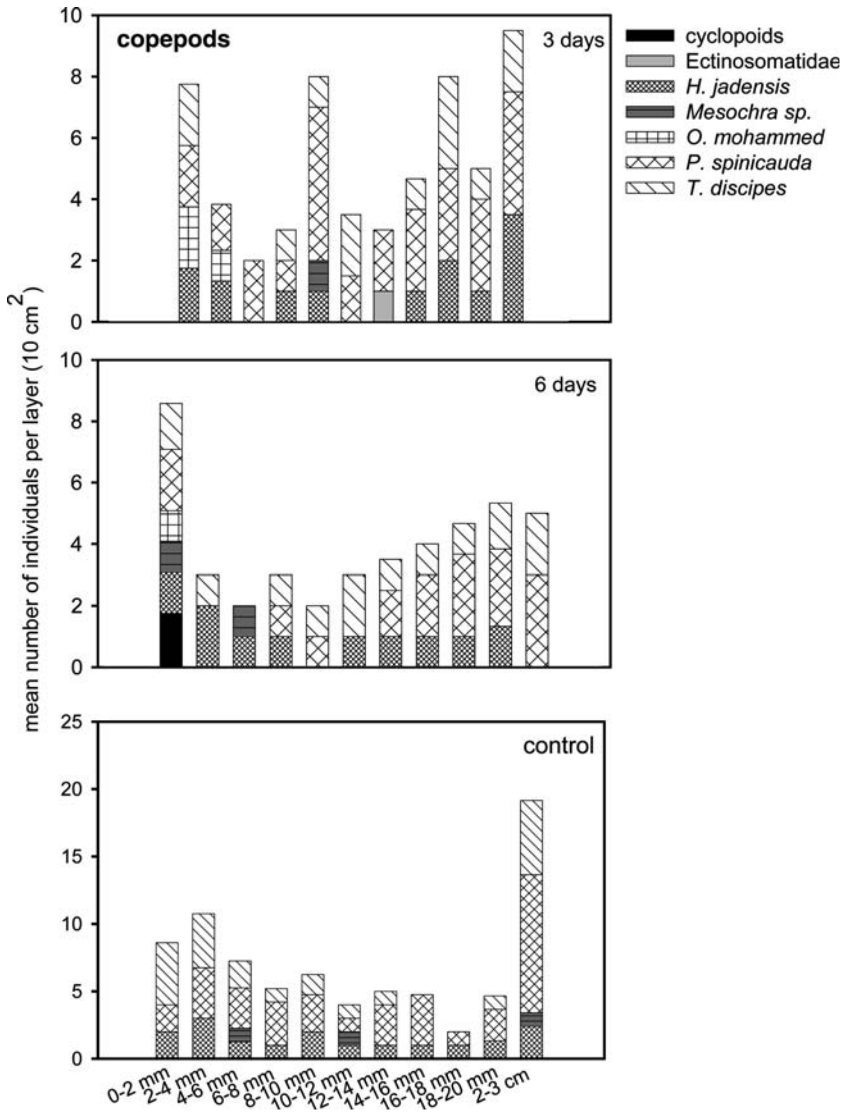

Figure 3. Distribution of copepods in the different core layers in control samples and after 3 and 6 days in the re-colonized sediment.

uppermost layers in control samples while in the re-colonized sediment it gathered in the deeper layers, particularly after 6 days (Fig. 2).

Almost all harpacticoid species represented in the re-colonized samples were also present in the control ones. Only *O. mohammed* and Ectinosomatidae, which appeared in the re-colonized samples, were absent in the control ones (Table 3). Similarly, cyclopoids which appeared in re-colonized samples after 6 days, were not present in the control samples. Distribution of the different species in the sediment column in control samples was also similar to that found in re-colonized ones, the three dominant species being evenly distributed all over the sediment column and a more evident dominance of *P. spinicauda* being noticeable in the deeper layers (Fig. 3).

Discussion

Our results indicate that some benthic animals may indeed benefit from drifting algal mats as a means of dispersal and re-colonization of previously defaunated sediments in relatively short periods of time. Also, they may contribute to explain some of the trends found in other studies, regarding species increase under drifting algae and the recovery patterns found in areas often exposed to algal conglomerates. Some of the macrobenthic fauna associated with the algae in our experiment seemed to colonize the underlying defaunated sediment already after 3 days, their numbers increasing with time. Particularly *Cerastoderma glaucum*, *Hydrobia* sp., and gammarid amphipods appeared well represented in the sediment samples at the end of the experiment. These animals are often found in algal assemblages, and unlike other macrobenthic species, whose presence/abundance has been found to be notably reduced under drifting algal mats, they have been found to thrive under the algal conglomerates, which they may also use as a means of dispersal or alternative habitat (Aarnio & Mattila, 2000; Bolam et al., 2000; Norkko et al., 2000; Österling & Pihl, 2001; Salovius & Kraufvelin, 2004; Salovius et al., 2005). They are relatively tolerant to hypoxia, especially short-term pulses of reduced oxygen availability, feed on a variety of resources and may also take advantage of protection from predation under the algae and reduced competition with more sensitive species (Fenchel & Kolding, 1979; Soulsby et al., 1982, Raffaelli et al., 1998; Norkko et al., 2000; Salovius & Kraufvelin, 2004). The number of *Cerastoderma glaucum* has increased in certain sites of the Åland Islands in the past 10 years and it has been suggested that this could be a result of larvae settling among drifting algal mats at these sites or being transported to them with the drifting algae (Norkko et al., 2000). Our results show that this process is likely to occur since *Cerastoderma* sp. was the most effective colonizer of the sediment in our experiment.

Contrary to our predictions, nematodes and harpacticoids inhabiting the algae showed almost no tendency towards sediment re-colonization. Other meiobenthic taxa found in the re-colonized sediment and which were not present in control samples, or at least not in such high numbers, could have come from the drifting algae but results at species level with harpacticoids and nematodes, showing that species found in the sediment were unlikely to have come from the algae, may be extended to them. On the other hand, the increased presence of chironomids, bivalve and gastropod juveniles or juvenile amphipods in the re-colonized sediment is probably the result of colonization from the algae, since their numbers were higher in these samples compared to the control ones and the same process was observed for their adult, or larger counterparts.

The apparent 'lack of interest' of nematodes and harpacticoids in the available sediment in our experiment is probably a combined result of habitat specialization of the dominant species and the high food resources present among the algae compared to the underlying sediments. Oncholaimid nematodes have shown to be attracted to organic matter originating from decaying plant material (Jensen, 1987). While juvenile *Adoncholaimus* live on organic matter produced by microbes, adults are also omnivorous and predators (Lopez et al., 1979) and particularly *A. thalassophygas* has been shown to form dense populations in cyanobacterial mats (Vopel & Arlt, 1995). On the other hand, *Anoplostoma* is a cosmopolitan genus capable of surviving large fluctuations in environmental conditions (Surey-Gent, 1981) and it is usually found in large numbers in sediment, while it is scarce in algal habitats (Heip et al., 1985). As regards harpacticoids, *Mesochra* species are commonly found in phytal assemblages and particularly in drifting cyanobacterial and macroalgal mats (Vopel & Arlt, 1995; Ólafsson et al., 2001). They can be tolerant to hypoxic and sulphidic conditions and, as many canthocapmptids often appear associated with highly organically enriched habitats (Lang, 1948; Vopel & Arlt, 1995). On the other hand, *N. spinipes*, *T. discipes* and cyclopoids are active swimmers which show a preference to colonize sediments (or other environments) rich in diatoms, microbial or organic resources (Ólafsson et al., 2005, in press). Fegley (1988) suggested quicker re-colonization by harpacticoid copepods in naturally defaunated sediments compared to artificially defaunated ones to be a result of higher microbial compound existing among them. Particularly pre-treatment by freezing has been shown to affect growth and survival of benthic fauna, presumably due to the negative changes it produces in sediment characteristics (Aljetlawi et al., 2000). In our case, freezing may have also depleted the microbial fauna and flora of the sediment, and hence made it less attractive for the meiofauna, which chose to remain among the algae, where resources were more abundant.

We considered two possibilities explaining presence of meiofauna after defaunation: either they survived freezing and thrived in the sediment during the whole experimental time or died but given the short time between the defaunation process and the initiation of the experiment and our short experimental times, their corpses remained in the sediment when collected and fixed. To test the first possibility, we defaunated sediment from the same locality using the same freezing procedure. After two days, all meiofauna other than some nematodes from the genus *Adoncholaimus*, were dead. It is very likely therefore, that the second possibility was true, at least for most of the animals. The reduction in most meiofaunal groups after 6 days is consistent with this hypothesis, progressive degeneration and disappearance of the corpses accounting for it. Similarly, the random distribution of nematodes and harpacticoids in the sediment column, as opposed to the 'natural' stratification found in the control samples, reinforces the 'dead animals' theory. On the other hand, nauplii and members of the so-called 'soft meiofauna' (e.g., turbellarians, oligochaetes) in the re-colonized sediment could very likely have come from the algae, since it is improbable that their corpses would have remained intact for so long in the sediment. Their low levels of re-colonization, particularly that of the oligochaetes, as opposed to results from other studies which have found them not only to be very tolerant to stress induced by the algal mats but also to be pioneering colonizing species of disturbed sediments (Bonsdorff, 1980, 1989; Norkko & Bonsdorff, 1996b; Thiel & Watling, 1998; Bolam et al., 2000) is probably due to the fact that in our experimental setting colonization was only possible from the drifting algae, while these animals often crawl into the sediment from adjacent areas (Bonsdorff, 1980, 1989).

Results from our study support others which indicate that moderate levels of drifting algal mats may have positive effects on the benthic fauna, in showing that they may not only serve as an alternative habitat and means of dispersal for benthic animals but also as a donor of benthic species to sediment areas (Norkko et al., 2000; Ólafsson et al., 2001; Berglund et al., 2003; Salovius et al., 2005). The implications of these selective re-colonization ability may however be envisioned from a less optimistic perspective if we consider that the same species that are tolerant to hypoxia/anoxia induced by the drifting algae are the ones which are able to colonize it and be transported by it, and ultimately the ones which show the ability to re-colonize these previously defaunated sediments. If these processes continue over extended areas and periods of time, other less tolerant and less mobile species, may be displaced from their natural habitats, causing a general loss in species and functional diversity in the system. The bulk of the field evidence from our area suggests that frequently occurring dense aggregations of drifting filamentous algal mats (Vahteri et al., 2000) have primarily negative effects on the soft-sediment infauna (Bonsdorff, 1992; Norkko & Bonsdorff, 1996a, b, c), and mechanisms favouring hypoxia-tolerant species will in the long run be negative for overall biodiversity.

Finally, our results draw attention to a problem, which may cause or may have caused interpretation mistakes in the past. Studies testing survival of animals (particularly meiobenthic ones) over short periods of time in which samples are immediately fixed, should first be checked to see if animals were alive at the termination of the experiment, given that corpses (in a relatively good state) may remain even if the effect of the disturbance has been lethal. Also, our study shows the importance of performing analysis of meiofauna at species level (also macrofauna but this is more often the case), not only given the fact that more subtle differences in response of the different taxa are detected and a real image of the consequences for diversity are attained but also because methodological mistakes as the ones detected in our experiment may otherwise be overlooked.

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References

Aarnio, K. & J. Mattila, 2000. Predation by juvenile *Platichthys flesus* (L.) on shelled prey species in a bare sand and a drift algae habitat. Hydrobiologia 440: 347–355.

Aliani, S. & A. Molcard, 2003. Hitch-hiking on floating marine debris: macrobenthic species in the Western Mediterranean Sea. Hydrobiologia 503: 59–67.

Aljetlawi, A. A., J. Albertsson & K. Leonardsson, 2000. Effect of food and sediment pre-treatment in experiments with a deposit-feeding amphipod, *Monoporeia affinis*. Journal of Experimental Marine Biology and Ecology 249: 263–280.

Barnes, D. K. A., 2002. Biodiversity: invasions by marine life on plastic debris. Nature 416: 808–809.

Berglund, J., J. Mattila, O. Ronnberg, J. Heikkila & E. Bonsdorff, 2003. Seasonal and inter-annual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. Estuarine Coastal and Shelf Science 56: 1167–1175.

Bolam, S. G., T. F. Fernandes, P. Read & D. Raffaelli, 2000. Effects of macroalgal mats on intertidal sandflats: an experimental study. Journal of Experimental Marine Biology and Ecology 249: 123–137.

Bonsdorff, E., 1980. Macrozoobenthic re-colonization of a dredged brackish water bay in SW Finland. Ophelia Suppl-1: 145–155.

Bonsdorff, E., 1989. Infaunal colonization and its dependence on environmental variation – experimental evidence from the northern Baltic Sea. In Ryland, J. S. & P. A. Tyler (eds) 23rd European Marine Biology Symposium. Olsen & Olsen, Fredensborg Denmark: 349–356.

Bonsdorff, E., 1992. Drifting algae and zoobenthos – effects on settling and community structure. Netherlands Journal of Sea Research 30: 57–62.

Brooks, R. A. & S. S. Bell, 2001. Mobile corridors in marine landscapes: enhancement of faunal exchange at seagrass/ sand ecotones. Journal of Experimental Marine Biology and Ecology 264: 67–84.

Brown, J. H., G. C. Stevens & D. M. Kaufman, 1996. The geographic range: size, shape, boundaries and internal structure. Annual Review of Ecology and Systematics 27: 597–623.

Christie, H. & J. A. Berge, 1995. *In situ* experiments on recolonization of intertidal mudflat fauna to sediment contaminated with different concentrations of oil. Sarsia 80: 175–185.

Colangelo, M. A. & V. U. Ceccherelli, 1994. Meiofaunal recolonization of azoic sediment in a Po Delta lagoon (Sacca di Goro). Bolletino di Zoologia 61: 335–342.

Cristoni, C., M. A. Colangelo & V. U. Ceccherelli, 2004. Spatial scale and meiobenthic copepod re-colonization: testing the effect of disturbance size in a seagrass habitat. Journal of Experimental Marine Biology and Ecology 298: 49–70.

Diaz, R. L. & R. Rosenberg, 1995. Marine benthic hypoxia, a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology Annual Review 33: 245–303.

Duarte, C. M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41: 87–112.

Everett, R. A., 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. Journal of Experimental Marine Biology and Ecology 175: 253–274.

Fahrig, L. & G. Merriam, 1994. Conservation of fragmented populations. Conservation Biology 8: 50–59.

Fegley, S. R., 1988. A comparison of meiofaunal settlement onto the sediment surface and re-colonization of defaunated sandy sediment. Journal of Experimental Marine Biology and Ecology 123: 97–113.

Fenchel, T. & S. Kolding, 1979. Habitat selection and distribution patterns of five species of the amphipod genus Gammarus. Oikos 33: 316–322.

Franz, D. R. & I. Friedman, 2002. Effects of a macroalgal mat (*Ulva lactuca*) on estuarine sand flat copepods: an experimental study. Journal of Experimental Marine Biology and Ecology 271: 209–226.

Gamenick, I., A. Jahn, K. Vopel & O. Giere, 1996. Hypoxia and sulphide as structuring factors in a macrozoobenhthic community on the Baltic Sea shore: colonization studies and tolerance experiments. Marine Ecology Progress Series 144: 73–85.

Guerrini, A., M. A. Colangelo & V. U. Ceccherelli, 1998. Recolonization patterns of meiobenthic communities in brackish vegetated and unvegetated habitats after induced hypoxia/anoxia. Hydrobiologia 375/376: 73–87.

Heip, C., M. Vincx & G. Vranken, 1985. The ecology of marine nematodes. Oceanography and Marine Biology Annual Review 23: 399–489.

Hicks, G. R. F., 1988. Sediment rafting: a novel mechanism for the small-scale dispersal of intertidal estuarine meiofauna. Marine Ecology Progress Series 48: 69–80.

Hull, S. C., 1987. Macroalgal mats and species abundance: a field experiment. Estuarine Coastal and Shelf Science 25: 519–532.

Ingólfsson, A., 1995. Floating clumps of seaweed around iceland – natural microcosms and a means of dispersal for shore fauna. Marine Biology 122: 13–21.

Isaksson, I. & L. Pihl, 1992. Structural changes in benthic macrovegetation and associated epibenthic faunal communities. Netherlands Journal of Sea Research 30: 131–140.

Jensen, P., 1987. Feeding ecology of free-living aquatic nematodes. Marine Ecology Progress Series 35: 187–196.

Lang, K., 1948. Monographie der Harpacticiden volume 2: Hakan Ohlsson, Lund.

Lawton, J. H., 1993. Range, population abundance and conservation. Trends in Ecology and Evolution 8: 409–413.

Lopez, G., F. Riemann & M. Schrage, 1979. Feeding biology of the brackish-water oncholaimid nematode *Adoncholaimus thalassophygas*. Marine Biology 54: 311–318.

Meyers, M. B., H. Fossing & E. N. Powell, 1987. Microdistribution of interstitial meiofauna, oxygen and sulfide gradients, and the tubes of macro-infauna. Marine Ecology Progress Series 35: 223–241.

Modig, H. & E. Ólafsson, 1998. Responses of Baltic benthic invertebrates to hypoxic events. Journal of Experimental Marine Biology and Ecology 229: 133–148.

Myers, A. A., 1993. Dispersal and endemicity in gammaridean amphipoda. Journal of Natural History 27: 901–908.

Norkko, A. & E. Bonsdorff, 1996a. Rapid zoobenthic community responses to accumulations of drifting algae. Marine Ecology Progress Series 131: 143–157.

Norkko, A. & E. Bonsdorff, 1996b. Population responses of coastal zoobenthos to stress induced by drifting algal mats. Marine Ecology Progress Series 140: 141–151.

Norkko, A. & E. Bonsdorff, 1996c. Altered benthic prey-availability due to episodic oxygen deficiency caused by drifting algal mats. PSZN I: Marine Ecology 17: 355–372.

Norkko, J., E. Bonsdorff & A. Norkko, 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology 248: 79–104.

Ólafsson, E., A. Ingólfsson & M. B. Steinarsdóttir, 2001. Harpacticoid copepod communities of floating seaweed: controlling factors and implications for dispersal. Hydrobiologia 453/454: 189–200.

Ólafsson, E., J. Ullberg & N. L. Arroyo, 2005. The clam *Macoma balthica* prevents *in situ* growth of microalgal mats: implications for meiofaunal assemblages. Marine Ecology Progress Series, in press.

Pihl, L., I. Isaksson, H. Wennhage & P.-O. Moksnes, 1995. Recent increase of filamentous algae in shallow Swedish bays: effects on the community structure of epibenthic fauna and fish. Netherlands Journal of Aquatic Ecology 29: 349–358.

Raffaelli, D., 2000. Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. Helgoland Marine Research 54: 71–79.

Raffaelli, D., J. Limia, S. Hull & S. Pont, 1991. Interactions between the amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. Journal of the Marine Biological Association of the U.K. 71: 899–908.

Raffaelli, D., J. A. Raven & L. J. Poole, 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology Annual Review 36: 97–125.

Salovius, S. & E. Bonsdorff, 2004. Effects of depth, sediment and grazers on the degradation of drifting filamentous algae (*Cladophora glomerata* and *Pilayella littoralis*). Journal of Experimental Marine Biology and Ecology 298: 93–109.

Salovius, S. & P. Kraufvelin, 2004. Filamentous green alga *Cladophora glomerata* as a habitat for littoral macrofauna in the Northern Baltic Sea. Ophelia 58: 62–78.

Salovius, S., M. Nyqvist & E. Bonsdorff, 2005. Life in the fast lane: macrobenthos use temporary drifting algal habitats. Journal of Sea Research 53: 169–180.

Shaffer, J. A., D. C. Doty, R. M. Buckley & J. E. West, 1995. Crustacean community composition and trophic use of drift vegetation habitat by juvenile splitnose rockfish *Sebastes diplopora*. Marine Ecology Progress Series 123: 13–21.

Soulsby, P. G., D. Lowthion & M. Houston, 1982. Effects of macro-algal mats on the ecology of intertidal mudflats. Marine Pollution Bulletin 13: 162–166.

Surey-Gent, S. C., 1981. Distribution of Anoplostoma viviparum (Nematoda) in Southhampton water sediments. Marine Biology 62: 157–160.

Tagliapietra, D., M. Pavan & C. Wagner, 1998. Macrobenthic community changes related to eutrophication in *Pallude della Rosa* (Venetian Lagoon, Italy). Estuarine Coastal and Shelf Science 47: 217–226.

Thiel, M. & L. Watling, 1998. Effects of green algal mats on infaunal colonization of a New England mud flat- long-lasting but highly localized effects. Hydrobiologia 375/376: 177–189.

Thrush, S. F., R. B. Whitlach, R. D. Pridmore, J. E. Hewitt, V. J. Cummings & M. R. Wilkinson, 1996. Scale-dependant re-colonization: the role of sediment stability in a dynamic sandflat habitat. Ecology 77: 2472–2487.

Vahteri, P., A. Mäkinen, S. Salovius & I. Vuorinen, 2000. Are drifting algal mats conquering the bottom of the Archipelago Sea, SW Finland?. Ambio 29: 338–343.

Villano, N. & R. Warwick, 1995. Meiobenthic communities associated with seasonal cycle growth of *Ulva rigida* Agardh in the Palude della Rosa, Lagoon of Venice. Estuarine Coastal and Shelf Science 41: 181–194.

Vopel, K. & G. Arlt, 1995. The fauna of floating cyanobacterial mats in the oligohaline eulittoral zone off Hiddensee (South-west coast of the Baltic Sea). Marine Ecology 16: 217–231.

Vopel, K., J. Dehmlow & G. Arlt, 1996. Vertical distribution of *Cletocamptus confluens* (Copepoda, Harpacticoida) in relation to oxygen and sulphide microprofiles of a brackish water sulphuretum. Marine Ecology Progress Series 141: 129–137.

Wetzel, M. A., A. Weber & O. Giere, 2002. Re-colonization of anoxic/sulfidic sediments by marine nematodes after experimental removal of macroalgal cover. Marine Biology 141: 679–689.

Whitlach, R. B., A. M. Lohrer, S. F. Thrush, R. D. Pridmore J. E. Hewitt, V. J. Cummings & R. N. Zajac, 1998. Scale-dependent benthic re-colonization dynamics: life-stage based dispersal and demographic consequences. Hydrobiologia 375/376: 217–226.

Yeatman, H. C., 1962. The problem of dispersal of marine littoral copepods in the Atlantic Ocean, including some redescriptions of species. Crustaceana 4: 253–272.

Österling, M. & L. Pihl, 2001. Effects of filamentous green algal mats on benthic macrofaunal functional feeding groups. Journal of Experimental Marine Biology and Ecology 263: 159–183.