Mar Biol (2009) 156:709–724
DOI 10.1007/s00227-008-1122-9

ORIGINAL PAPER

The impact of seabed disturbance on nematode communities: linking field and laboratory observations

M. Schratzberger · N. Lampadariou · P. J. Somerfield · L. Vandepitte · E. Vanden Berghe

Received: 5 June 2008 / Accepted: 18 December 2008 / Published online: 9 January 2009

Abstract Physical disturbance is a key factor in controlling the spatial and temporal composition of shallow-water benthic communities. Like shallow waters, deeper waters are increasingly subject to a range of anthropogenic disturbances, which can lead to significant alterations in sedimentation patterns. These alterations often exceed naturally occurring changes. We used a combined analysis of six independent data sets arising from large-scale field surveys and small-scale laboratory experiments to investigate the effects of seabed disturbance on nematode communities. Disturbance response was documented as a function of disturbance type (coastal development, dredged material disposal, bottom trawling, glacial fjord) and intensity (low, medium, high). Natural and man-induced seabed disturbance exerted differential effects on exposed populations, generating changes in the taxonomic (genus) and functional (feeding type) attributes of their assemblages. The genus composition of nematode assemblages from geographically separate seas converged with increased level of various types of man-made disturbance. Assemblages present along a gradient of natural disturbance in a glacial fjord followed an opposite response vector, suggesting that community changes induced by anthropogenic activities, or experimental treatments simulating the principal impacts of these, inherently differ from disturbance of natural origin. Changes in trophic diversity and structure were primarily driven by factors confounded with physical disturbance, such as metal contamination. Coupling the results of analyses at multiple scales proved a useful means of providing deeper insights into the general response of ecological communities to environmental change.

Communicated by U. Sommer.

M. Schratzberger (✉)
Centre for Environment, Fisheries and Aquaculture Science,
Pakefield Road, Lowestoft NR33 0HT, UK
e-mail: michaela.schratzberger@cefas.co.uk

N. Lampadariou
Hellenic Centre for Marine Research,
Institute of Oceanography, P.O. Box 2214,
71003 Iraklion, Crete, Greece

P. J. Somerfield
Plymouth Marine Laboratory, Prospect Place,
West Hoe, Plymouth PL1 3DH, UK

L. Vandepitte · E. Vanden Berghe
Flanders Marine Institute, Wandelaarkaai 7,
8400 Oostende, Belgium

E. Vanden Berghe
Institute of Marine and Coastal Sciences, Rutgers University,
71 Dudley Road, New Brunswick NJ 08901, USA

Introduction

Disturbance is an important source of temporal and spatial heterogeneity in natural communities (review by Sousa 1984) and has been highlighted in maintaining species diversity by preventing competitive exclusion by dominant species in an assemblage (e.g. Connell 1978; Sousa 1979; Huston 1994; Death and Winterbourn 1995). Physical disturbance, i.e. processes that lead to the disruption of sediments (review by Hall 1994), is a key factor in controlling the spatial and temporal composition of benthic communities. Sediment movement, erosion and deposition are natural processes to which benthic organisms are adapted. Benthic infauna burrow upwards or downwards to maintain an ideal position in the sediment. Anthropogenic activities including coastal development, dredged material disposal and bottom trawling may cause widespread physical disturbance of the seabed and changes in sedimentation patterns in shelf seas. The rates and magnitudes of these alterations often greatly exceed those of natural occurrences.

The effects of physical seabed disturbance on benthic ecosystems have been investigated in the field (e.g. Alongi 1985; Lopez-Jamar and Mejuto 1988; Warwick et al. 1990; review by Jennings and Kaiser 1998; Boyd et al. 2000), in field manipulation experiments (Hagerman and Rieger 1981; Fegley 1988; Kern 1990; Armonies 1994; Commito and Tita 2002) and in laboratory studies performed with experimental communities in micro- or mesocosms (e.g. Maurer et al. 1986; review by Coull and Chandler 1992; Chandrasekara and Frid 1998). Results to date indicate that disturbance can influence the number of species that are affected, assuming that there is some ranking of susceptibility to disturbance or recovery from disturbance based on species-specific properties, such as population growth rates and tolerance to environmental change.

A common approach used to assess the impact of physical disturbance on the benthos is to sample the seabed along known or assumed disturbance gradients. Such field sampling designs allow an examination of links between disturbance and structure of benthic communities. However, it is usually difficult to distinguish disturbance-induced changes in community structure from natural changes, as in most cases information on the pre-disturbance status of the assemblage and the surrounding environment are rare. The small amount of seabed sampled relative to the sea areas under consideration, and variability in the abiotic environment, generally limit the capacity of such studies to establish definitive cause–effect relationships beyond the immediate site of impact.

Environmental factors can more easily be controlled in simplified, small-scale ecosystem models (microcosms), maintained in the laboratory for periods of weeks to months. Meiofauna assemblages, and in particular nematodes, are ideal for experiments on this scale (Warwick 1993) and they have been widely used to determine the effects of disturbances in aquatic ecosystems (review by Coull and Chandler 1992). The real world and the microcosm have their own distinct properties, which differ because of the effects of scaling, environmental heterogeneity and species composition (Leffler 1980). Microcosms are experimental units designed to contain important components and to exhibit important processes occurring in a whole ecosystem. They retain the essence of the natural system from which they were abstracted rather than simulate a specific ecosystem (Draggan and Reisa 1980; Giesy and Odum 1980).

Whilst short-term, small-scale laboratory experiments quantify the immediate effect of disturbance on faunal communities, larger-scale field surveys offer the capacity to examine the prolonged effect of an impact and its manifestation over several generations. Coupling the results from analyses at multiple scales can help to gain wider insights into the response of populations and their assemblages to environmental pressures, although each method is not without its own biases (Ellis et al. 2002; Palen et al. 2005; Rome et al. 2005; McCarthy et al. 2006).

Individual studies often yield useful quantitative data, but they give no indication in themselves of whether the magnitude and direction of an observed disturbance response differs between studies or not. Combined analysis of independent studies is a useful tool for exposing general patterns in community responses to different pressures and treatments, especially if care is taken to minimise confounding biases in the data (Dernie et al. 2003). This approach permits ecological questions to be examined on a much larger scale than would otherwise be possible, often revealing consistent patterns that would be unsupported by single studies (Collie et al. 2000).

In this article, we describe a combined analysis of selected data on the abundances of free-living nematodes from large-scale field surveys and controlled small-scale laboratory experiments to test the null-hypothesis (H_0) that the effects of disturbance on nematode assemblages from soft sediments are the same regardless of the type of physical disturbance. We specifically addressed two questions:

(1) Are there consistent patterns in the response of nematode communities to physical disturbance resulting from natural changes and man-made activities; i.e. can specific effects on the taxonomic and functional structure of nematode assemblages be discerned?
(2) How are changes in assemblage structure observed in the field related to observations from controlled laboratory experiments; i.e. can statistically significant field observations be linked to ecologically significant cause–effect relationships established in the laboratory?

We expected that increased level of disturbance would result in the elimination of disturbance-sensitive species due to the direct and indirect effects of the disturbance itself and their replacement by more disturbance-tolerant species due to release from competition (Medina et al. 2007). However, we had no a priori expectation in relation to the type of physical disturbance.

Material and methods

In any combined analysis, individual studies become anonymous along with all their assumptions, incompatibilities and possible inconsistencies. These are often the consequence of the wide variation in the design, the use of non-standard methods and inconsistent taxonomy and variability in habitat and environmental factors specific to each case study. Contrary to larger-sized ecosystem components, there are currently not enough comparable data in the published literature on the effects of seabed disturbance on nematode genera to warrant a meta-analysis. At present there is also a paucity of data linking field-collected observations to results from smaller-scale experiments. Following careful screening of relevant published studies, we therefore undertook a narrower and more refined analysis involving six case studies. Our selection was based upon a restricted habitat (i.e. soft sediments where the effects of physical disturbance as a consequence of waves and currents are less pronounced than in coarser, more exposed sediments), comparable sampling and processing protocols and use of consistent taxonomy.

Field investigations targeted soft-bottom, subtidal species assemblages in the Aegean Sea, the Irish Sea, the North Sea and the North Atlantic. Sampling stations were located either along a gradient or transect through areas of known natural disturbance or anthropogenic activity or randomly within areas characterised by different intensities of known anthropogenic activity. Experimental data originated from a series of microcosm experiments where nematode assemblages from estuarine mud were exposed to disturbance treatments simulating sediment deposition and resuspension. Study sites, sampling and experimental designs and sample processing techniques are described in detail in the relevant articles (Somerfield et al. 1995; Lampadariou et al. 1997; Schratzberger and Warwick 1998; Schratzberger et al. 2000; Schratzberger and Jennings 2002; Somerfield et al. 2006). The following sub-sections provide a short summary.

Field surveys

Coastal development (Lampadariou et al. 1997)

Heraklion harbour on the coast of Crete, in the South Aegean Sea (Fig. 1), is a small and shallow (5–22 m) harbour characterised by intense ferry boat activity and supporting small commercial fishing boats and yachts. Untreated domestic sewage is discharged into the harbour through five outfalls. In 1993, nematode communities were sampled on a grid of 17 stations, extending from the inner area to the outer harbour.

Dredged material disposal (Somerfield et al. 1995)

Nematode assemblages were sampled along a transect through a dredged material disposal ground in Liverpool Bay, on the west coast of the UK (Fig. 1). The transect ran approximately north–south through the disposal ground and followed the 10 m contour to minimise effects of depth on faunal patterns.

Bottom trawling (Schratzberger and Jennings 2002)

The effects of trawling disturbance on nematode communities were examined by comparing three beam-trawl fishing grounds in the Silver Pit area of the central North Sea (Fig. 1), at depths between 60 and 80 m, in two seasons. These areas were trawled with mean frequencies of 1, 4 and 6 times year^{-1}, respectively.

Glacial fjord (Somerfield et al. 2006)

Nematode communities in Kongsfjord, on the coast of Spitzbergen in the North Atlantic (Fig. 1), were sampled along an environmental gradient from the glaciers to the open sea. Factors varying along the gradient included sediment deposition, organic content and disturbance (e.g. glacial discharges of meltwater, ice and till).

Laboratory experiments

Deposition (Schratzberger et al. 2000)

In a laboratory experiment to disentangle the effects of contamination and frequency and amount of sediment deposition on meiofauna (Fig. 2), nematode assemblages were exposed to the simulated deposition of native, uncontaminated intertidal mud and non-native sediments from harbours in the Mersey and the Tees estuary (UK), both of which were contaminated with heavy metals.

Resuspension (Schratzberger and Warwick 1998)

A microcosm experiment (Fig. 2) was undertaken to evaluate the relative effects of continuous and episodic physical disturbance on the structure of nematode communities in intertidal mud.

Sample collection and processing

In the field surveys, replicate sediment samples were collected by means of corers (Craib, NIOZ, Reineck) or van Veen grab, deployed at random locations at each sampling station (Fig. 1). The top 5 cm of Craib cores were retained for faunal analyses; NIOZ cores, box cores and van Veen grabs were sub-sampled with smaller cores to a depth of 5 cm. Additional samples were obtained for the analysis of various sedimentary parameters. Faunal samples were fixed and preserved in formalin and environmental samples were frozen at −20°C pending analysis.

Sediment containing meiofauna was collected for the laboratory experiments from two muddy estuaries, one located at the southeast (Creeksea estuary), the other at the southwest coast (Lynher estuary) of the UK. Two types of

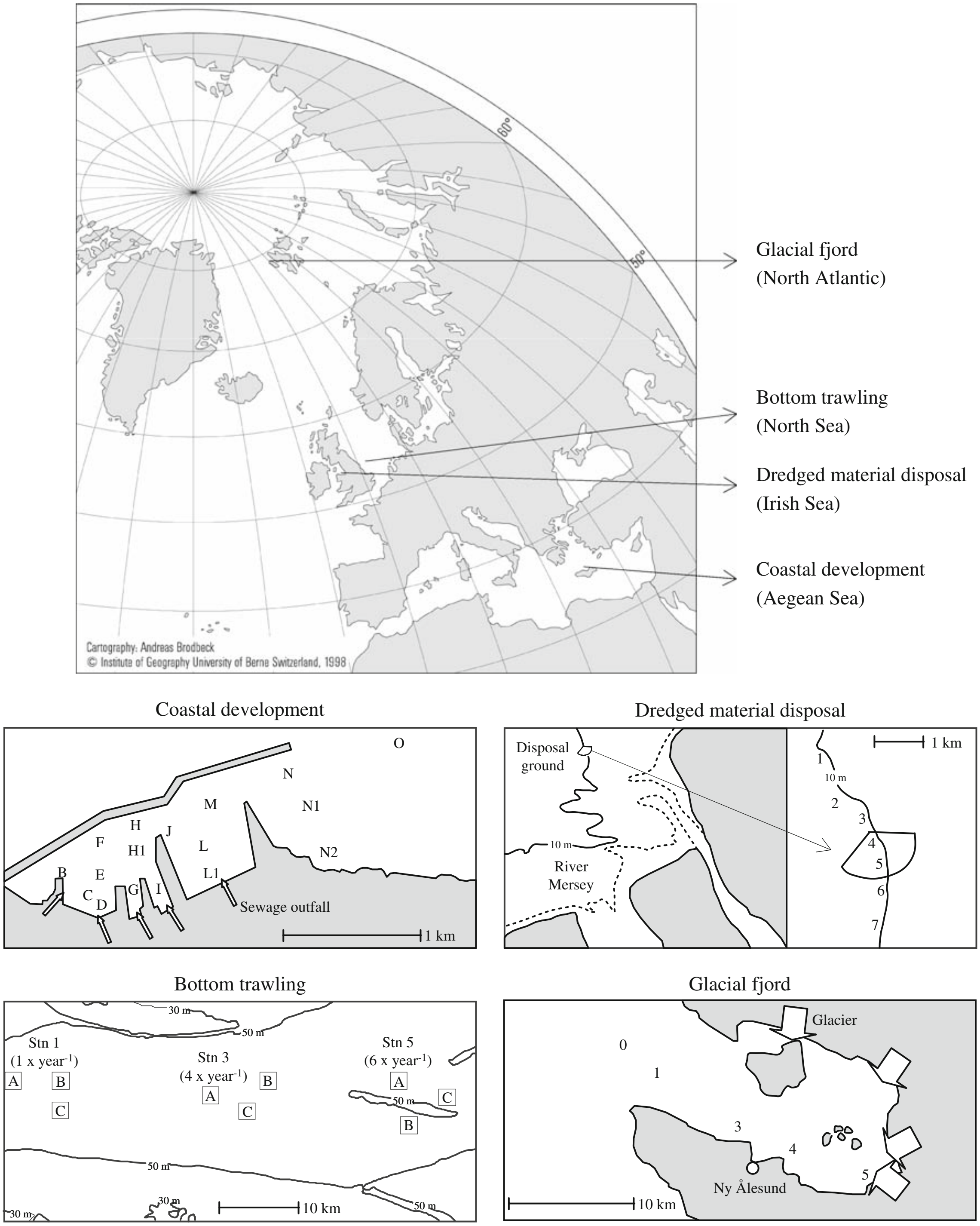


Fig. 1 Location of field sampling sites

microcosm designs were utilised (Fig. 2), glass cylinders, closed with a rubber bung at the bottom (deposition experiment) and glass bottles (resuspension experiment). Microcosms were filled with a weighed amount of field-collected, homogenised intertidal mud containing the meiofauna and topped up with filtered seawater of natural salinity. In the deposition experiment, weighed amounts of defaunated muddy sediment, including native intertidal sediment and non-native harbour sediment, were deposited onto field-collected sediment. Material was deposited in either one single dose at the beginning of the experiment or ten small doses throughout the study period. Defaunated harbour sediments varied in the level of heavy metal contamination. Resuspension was effected by leaving the microcosms on and off a

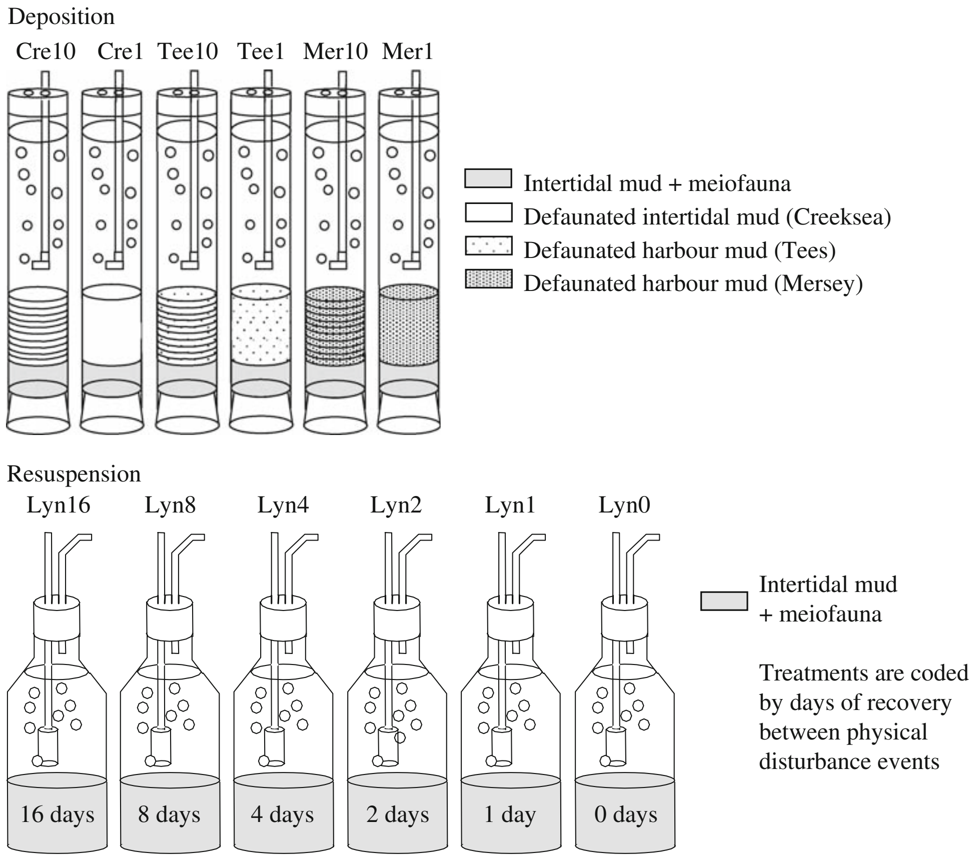


Fig. 2 Design of microcosms and experimental treatments

shaker for varying periods of time. All microcosms were run as closed systems with aeration for 2 months at a temperature between 15 and 20°C. Experiments were conducted in the dark to prevent microalgal growth. Entire microcosms were harvested at the end of each experiment and the sediment fixed and preserved in formalin.

After washing the samples onto a 63 µm sieve, meiofauna were extracted with Ludox (Somerfield and Warwick 1996; Somerfield et al. 2005). The extraction was repeated at least twice. The extracts were evaporated slowly to anhydrous glycerol and mounted, evenly spread, on slides for identification and counting. Nematodes comprised the dominant meiofauna taxon in all samples. The first 200 nematodes encountered in each sample or all nematodes present in either the entire or a specified volume percentage of the extract (containing approximately 200–300 individuals) were identified to genus or species level.

Data processing

The six data sets, combined, contained a total of 199 samples (Vandepitte et al. submitted). Working with the data set obtained at the dredged material disposal ground in Liverpool Bay, Somerfield and Clarke (1995) showed that aggregation of nematode species-level data to genus has little effect on overall patterns. Species abundances in the combined data set were therefore aggregated to genus prior to analysis to reduce the effects of region- and study-specific differences in species identities. The integrated data set contained abundances of 156 genera.

In order to explore faunal differences between different types of physical disturbance, sampling stations and experimental treatments were coded by level of disturbance (i.e. low, medium, high). Disturbance regimes (i.e. the areal extent of disturbance effects on a receiving assemblage) found at any one field sampling site, or simulated in any one laboratory experiment, are influenced by a variety of factors including local variation in the intensity, timing and spatial distribution of potentially disturbing forces, which can vary widely (review by Sousa 1984). The design of field surveys and laboratory experiments utilised in the combined analysis entailed the different spatial scales at which low, medium and high levels of disturbance were likely to occur. Comparable levels of disturbance caused by coastal development and dredged material disposal were expected to occur at smaller spatial scales (i.e. km) than those resulting from bottom trawling or glacial activity (i.e. tens of kilometres). The coding of field sampling stations and experimental treatments was therefore based on a continuum of disturbance rather than on distinct thresholds, taking into account the study-specific disturbance regimes. This continuum was based on various combinations of measures including proximity to known or assumed impacts and frequency of known impact/treatment (Tables 1, 2, 3, 4).

In addition to the varying level of disturbance, and associated changes in the substrate, nematodes at the field study sites were possibly influenced by other environmental gradients, such as differences in water depth or silt and contaminant content in the sediment (Tables 2, 3). Available information on ecological factors potentially affecting populations were included in univariate and multivariate regression and correlation analyses of relationships between nematode community structure and type and level of disturbance. There was insufficient co-variation of variables used in these analyses to warrant any exclusions (Quinn and Keough 2002).

Univariate analyses

To encapsulate variation in different aspects of community structure, three univariate measures were calculated. Hill's N_1 (Hill 1973) is an evenness measure and is used to indicate the diversity of genera in samples. An evenness measure was chosen as differences in sample sizes are considered to be less of a problem for estimates of evenness than for estimates of richness. The numbers of individuals identified should give reasonable and comparable, estimates. Taxonomic distinctness, Δ^+ (Clarke and Warwick 1998a; Clarke and Warwick 2001a; review by Warwick and Clarke 2001), is sample-size independent and measures the relatedness of genera within assemblages. The Index of Trophic Diversity (ITD; Heip et al. 1985) is another evenness measure, but this time it indicates the evenness of feeding groups (Wieser 1953), rather than taxonomic groups, within samples.

Relationships between environmental variables, assigned level of disturbance and univariate community attributes were investigated by stepwise multiple regression analysis with a forward direction (F to enter model was 1.00 and a P-value of <0.05 was considered to be statistically significant). The following variables were evaluated: water depth, silt content, assigned level of disturbance and cadmium, chromium, copper and lead concentration in the sediment. Since the coding of samples was based on a disturbance continuum, assigned disturbance level was treated as a continuous variable with values 1, 2 and 3 for low, medium and high disturbance levels, respectively (Quinn and Keough 2002). Forward selection began with no variables in the equations, then, one by one, the most significant variables (i.e. lowest P value) were added to the model. Tolerances of variables were used as an indication of colinearity among them. The aim of this type of analysis was to obtain a model that contained relatively few significant determinant variables with the highest coefficient of

Table 1 Type of seabed disturbance present at field sampling sites or simulated in laboratory experiments, mechanisms potentially affecting nematodes and categories used to assign level of disturbance to samples

Type of study	Seabed disturbance present/simulated	Mechanisms potentially affecting nematodes	Categories used to assign level of disturbance (Figs. 1, 2)
Coastal development survey	Seabed disturbance due to boat traffic and discharge of untreated domestic sewage	Increased turbidity, high rates of sedimentation and burial confounded with toxicity of contaminants in sewage	Distance to harbour entrance and sewage outfalls
Dredged material disposal survey	Deposition of clean and contaminated dredged material	Direct burial by dredged material often confounded with toxicity of contaminants in dredgings	Distance to disposal ground, prevailing currents
Bottom trawling survey	Irregular passage of trawls causing scouring, resuspension and deposition of surface sediment	Mortality or displacement and burial, changes in sediment structure and geochemistry	Trawling frequency (times $year^{-1}$)
Glacial fjord survey	Regular sediment deposition, discharges of meltwater, ice and till	High turbidity, frequent resuspension, sedimentation and burial by unconsolidated, easily eroded, sediments	Distance to glaciers
Deposition experiment	Deposition of clean and contaminated sediment	Burial by differing volumes of clean and contaminated sediment	Volume and frequency of deposition, type of deposited sediment
Resuspension experiment	Sediment resuspension and subsequent deposition	Resuspension and subsequent burial by unconsolidated sediment	Frequency of resuspension and subsequent deposition (times $experiment^{-1}$)

Table 2 Environmental variables measured and level of disturbance assigned to samples from large-scale field surveys in Heraklion harbour (Lampadariou et al. 1997) and at the Liverpool Bay disposal ground (Somerfield et al. 1995)

Station	Dist. level	Depth (m)	Silt (%)	Cu (ppm)	Cr (ppm)	Pb (ppm)	Cd (ppm)
Heraklion harbour (coastal development)[a]							
O	Low	22	1	1	81	16	0.99
N	Medium	14	10	7	123	33	0.90
N1	Medium	11	5	3	134	27	0.84
N2	Medium	6	2	2	131	59	0.90
B	High	5	48	70	132	64	1.39
C	High	8	7	18	93	43	1.62
D	High	9	42	31	138	118	1.39
E	High	11	6	6	111	22	0.90
F	High	7	12	20	107	34	1.10
H	High	10	23	26	130	42	1.22
H1	High	12	8	4	107	17	1.07
I	High	10	23	23	115	44	1.16
J	High	10	18	8	141	29	0.99
L	High	7	16	10	204	17	2.63
L1	High	5	51	76	195	26	3.62
M	High	13	6	10	132	23	0.73
Liverpool Bay disposal ground (dredged material disposal)[b]							
1	Low	10	7	53	79	209	0.16
2	Low	10	6	45	69	103	0.26
3	Low	10	10	46	69	97	0.35
7	Low	10	8	43	57	87	0.28
6	Medium	10	8	43	66	90	0.40
4	High	10	33	74	94	136	0.65
5	High	10	83	76	96	141	0.68

Station names as in Fig. 1

[a] Station G was omitted because it represented an area devoid of macrofuana (Karakassis et al. 1993) and because it could not be ascribed to any of the three disturbance levels

[b] Day grab samples were omitted

Table 3 Environmental variables measured and level of disturbance assigned to samples from the large-scale field surveys at Silver Pit fishing grounds (Schratzberger and Jennings 2002) and in Kongsfjord (Somerfield et al. 2006)

Station	Disturbance level	Depth (m)	Silt (%)
Silver Pit fishing grounds (bottom trawling)			
1A	Low	74	37
1B	Low	69	33
1C	Low	75	25
3A	Medium	72	37
3B	Medium	65	35
3C	Medium	70	36
5A	High	65	39
5B	High	63	42
5C	High	60	27
Kongsfjord (glacial fjord)			
0	Low	301	90
1	Low	363	96
3	Medium	290	94
4	Medium	133	93
5	High	80	95

Station names as in Fig. 1

determination (r^2). Partial correlation was used to explore the relationship between univariate indices and level of disturbance, while controlling for confounding variables. These included water depth (coastal development, bottom trawling, glacial fjord, all data sets combined) and silt, cadmium, chromium and copper concentration in the sediment (dredged material disposal). Preliminary analyses were performed to ensure that there was no violation of the assumptions of normality, linearity and homoscedasticity. Multiple regression analyses were carried out using Statistica version 6.0.

Multivariate analyses

The analysis of multivariate ecological data should include a robust unconstrained and/or constrained ordination, a rigorous statistical test of the hypothesis and a characterisation of species responsible for multivariate patterns (Anderson and Willis 2003). Unconstrained ordination techniques are useful for visualising broad community patterns across the entire data, as well as any differences in within-group variability and spread. Although group differences may be seen in an unconstrained ordination, they can be masked by high

Table 4 Treatments applied and level of disturbance assigned to samples from small-scale laboratory experiments (Schratzberger and Warwick 1998; Schratzberger et al. 2000)

Treatment	Disturbance level	Experimental treatment
Deposition[a]		
Cre10	Low	Deposition of clean native sediment in 10 doses of 0.6 cm
Tee10	Medium	Deposition of contaminated non-native sediment in 10 doses of 0.6 cm
Me10	Medium	Deposition of contaminated non-native sediment in 10 doses of 0.6 cm
Cre1	High	Deposition of clean native sediment in a single dose of 6 cm
Tee1	High	Deposition of contaminated non-native sediment in a single dose of 6 cm
Me1	High	Deposition of contaminated non-native sediment in a single dose of 6 cm
Resuspension[b]		
Lyn16	Low	Two days resuspension followed by 16 days of recovery
Lyn8	Low	Two days resuspension followed by 8 days of recovery
Lyn4	Medium	Two days resuspension followed by 4 days of recovery
Lyn2	Medium	Two days resuspension followed by 2 days of recovery
Lyn1	High	Two days resuspension followed by 1 day of recovery
Lyn0	High	Continuous resuspension

Treatment names as in Fig. 2

[a] Experimental controls and bottom (6–9 cm) and middle (3–6 cm) sediment layers were omitted

[b] Experimental controls and sand microcosms were omitted

variability and correlation structure among variables unrelated to group differences. A constrained ordination, on the other hand, does not allow an assessment of either total or relative within-group variability, but it does allow location differences between groups to be seen, if indeed any are discernible in multivariate space (Anderson and Willis 2003). We carried out preliminary analyses on the combined data set, applying both unconstrained and constrained ordination procedures. Results indicated that unconstrained ordination techniques such as non-parametric multi-dimensional scaling (MDS), based on appropriate resemblance measures (Clarke et al. 2006), provided a powerful tool for visualising patterns in nematode assemblage data (Clarke 1993; Clarke and Warwick 2001b).

Two-way analysis of similarities (ANOSIM; Clarke 1993) was performed on station- and treatment-averaged data to test for statistically significant effects of the factors "study type" (i.e. six study types averaged over three disturbance levels) and "disturbance level" (i.e. three disturbance levels averaged over six study types). Two-way similarities percentages analysis (SIMPER; Clarke 1993) with the same factors was used to identify genera or feeding types contributing to differences between a priori groups of samples.

BIOENV (Clarke and Ainsworth 1993) and BVSTEP analyses (Clarke and Warwick 1998b) were used to investigate relationships between water depth, sediment silt content, contaminant concentration, level of disturbance and community composition at the field sampling sites. Spearman rank correlations (ρ) between resemblance matrices derived from faunal data (based on Bray–Curtis similarity) and matrices derived from various sub-sets of environmental data (based on normalised euclidean distance) were used to identify suites of variables that best explained observed biotic patterns. The significance of the correlations was determined using a permutation procedure (Clarke et al. 2008). All multivariate analyses were performed using Primer version 6.1.5 (Clarke and Gorley 2006).

Results

Multiple regression analyses of relationships among univariate indices (N_1, ITD and Δ^+), environmental variables and assigned level of disturbance (Table 5) showed that best model predictions were achieved when analyses were performed separately for each data set (model predictions between 14 and 60% and 30 and 99% for the combined and separate data sets, respectively). In most cases, there was a strong partial correlation between genus or trophic diversity and level of disturbance, controlling for depth ($r > \pm 0.43$, $P < 0.01$) or for contaminants ($r > \pm 0.73$, $P < 0.02$). An inspection of the zero-order correlation ($r > \pm 0.48$ for depth and $r > \pm 0.92$ for contaminants) suggested that controlling for these two factors had little effect on the strength of the relationship between disturbance level and genus or trophic diversity, respectively. In contrast, a partial correlation between level of disturbance and taxonomic distinctness persisted marginally only when controlling for depth ($r = 0.47$, $P = 0.05$), whilst it was lost when controlling for contaminants ($r > \pm 0.04$, $P > 0.38$).

Multivariate correlation analyses (i.e. BIOENV and BVSTEP analyses; Table 6) showed that, in most cases, the assigned disturbance level was the single most important variable in determining the genus composition of nematode assemblages. Some contaminants, in combination with the assigned level of disturbance, influenced the trophic structure of nematode assemblages at sites exposed to coastal development and dredged material disposal. When the

Table 5 Sub-sets of variables that best explained the observed variation in genus diversity (N_1), taxonomic distinctness (Δ^+) and trophic diversity (ITD) as selected by the multiple regression modelling (variables are shown in order of importance)

	Percentage[a]	P	Variables
Genus diversity (N_1)			
Coastal development	74	<0.01	Disturbance level, Cu concentration
Dredged material disposal	86	<0.01	Disturbance level
Bottom trawling	60	0.01	Disturbance level
Glacial fjord	33	ns	–
All data sets combined	60	<0.01	Disturbance level, depth
Taxonomic distinctness (Δ^+)			
Coastal development	30	0.03	Disturbance level
Dredged material disposal	63	0.03	Cd concentration
Bottom trawling	54	ns	–
Glacial fjord	53	ns	–
All data sets combined	14	ns	–
Trophic diversity (ITD)			
Coastal development	72	<0.01	Silt content, Cr concentration, depth
Dredged material disposal	99	<0.01	Cd, Cu and Pb concentration
Bottom trawling	48	0.04	Disturbance level
Glacial fjord	44	ns	–
All data sets combined	25	<0.01	Disturbance level

Variables used include water depth, silt content, assigned disturbance level and, for coastal development and dredged material disposal only, also cadmium (Cd), chromium (Cr), copper (Cu) and lead (Pb) concentration in the sediment (see Tables 2 and 3)

ns not significant at $P < 0.05$

[a] Percent variance explained

Table 6 Spearman rank correlation (ρ) and significance level (P) between averaged faunal data and mean environmental variables (variables are shown in order of importance)

	ρ	P	Variables
Genus			
Coastal development	0.766	0.01	Disturbance level
Dredged material disposal	0.924	0.03	Disturbance level
Bottom trawling	0.580	0.01	Disturbance level
Glacial fjord	0.770	ns	–
All data sets combined[a]	0.470	<0.01	Depth, silt content
Feeding type (Wieser 1953)			
Coastal development	0.446	0.02	Disturbance level, Cd and Cu concention
Dredged material disposal	0.958	0.01	Disturbance level, Cd and Cu concentration
Bottom trawling	0.349	0.02	Disturbance level
Glacial fjord	0.488	ns	–
All data sets combined	0.300	<0.01	Disturbance level, silt content

Variables used include water depth, silt content, assigned disturbance level and, for coastal development and dredged material disposal only, also cadmium (Cd), chromium (Cr), copper (Cu) and lead (Pb) concentration in the sediment (see Tables 2 and 3). All heavy metal concentrations were log-transformed

ns not significant at $P < 0.05$

[a] Combination of disturbance level, depth, silt content: $\rho = 0.446$, $P = 0.01$

assigned disturbance level was excluded from the analyses, correlations between biotic and abiotic matrices were, however, still significant at $P < 0.05$ in some cases.

A combination of the genus and trophic diversity and taxonomic distinctness, expressed as N_1, ITD and Δ^+, respectively, summarises the impact of various types of seabed disturbance on nematode communities (Fig. 3):

(1) Low genus diversity at stations highly impacted by coastal development and dredged material disposal was coupled with a significantly increased taxonomic distinctness of nematode communities and decreased trophic diversity.
(2) In field situations where man-induced seabed disturbance was not confounded by contamination (i.e. bottom trawling), genus diversity decreased with increasing level of disturbance, while taxonomic distinctness and ITD appeared relatively unaffected.
(3) The negative relationship between nematode genus diversity and level of disturbance at anthropogenically impacted study sites corresponded with the trend observed in a microcosm experiment studying the confounded effects of burial and sediment contamination on nematode communities.
(4) The response of nematode assemblages to different frequencies of sediment resuspension and subsequent deposition in the laboratory was non-monotonic with highest trophic diversity (i.e. lowest ITD) and taxonomic distinctness at intermediate disturbance frequencies. Similar, though less pronounced, trends for taxonomic distinctness were apparent along a natural gradient of glacier-induced disturbance.

In all samples, genus diversity decreased with increasing level of disturbance (Fig. 3). Chromadorids (i.e. *Ptycholaimellus* in

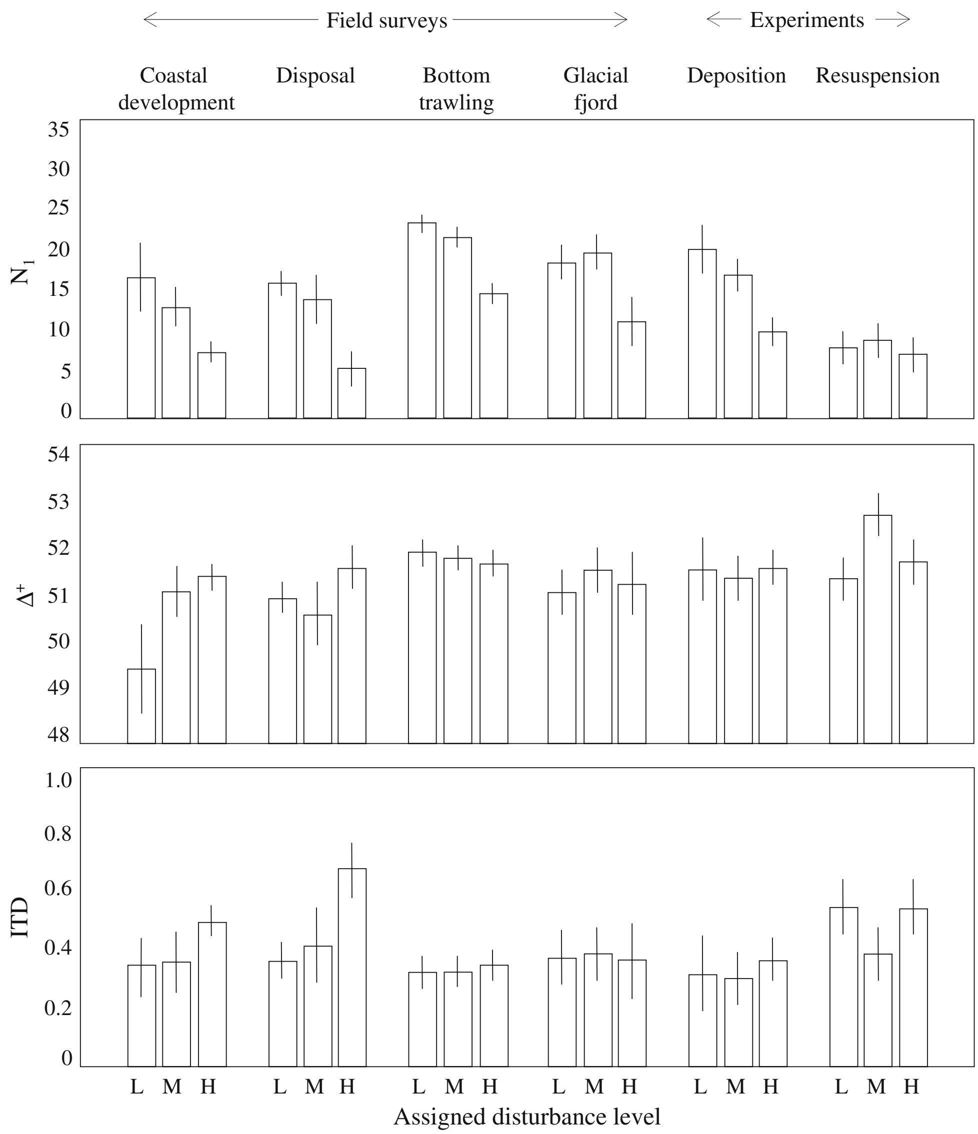


Fig. 3 Mean (±95% pooled confidence intervals) genus diversity (N_1), taxonomic distinctness (Δ^+) and Index of Trophic Diversity (ITD) of nematode assemblages from field surveys and laboratory experiments coded by level of disturbance

field samples and *Prochromadorella* in experimental microcosms) were absent from highly impacted samples as were several genera belonging to the cyatholaimids (field surveys) and some large enoplids (laboratory experiments).

In an MDS ordination (Fig. 4) based on the mean relative abundance of nematode genera, samples from large-scale field surveys in shallow shelf seas were located at the right-hand side of the plot, whereas those from deeper waters were found to the left. The separation of assemblages harvested from experimental microcosms and those collected in the field was most likely a result of inevitable differences in scaling, environmental heterogeneity, potential for recolonisation and composition of the communities studied (i.e. subtidal assemblages in field surveys and intertidal assemblages in the experiments). Results from two-way ANOSIM revealed a consistent effect of disturbance level on the genus composition of nematode assemblages (global *R* for disturbance level effect averaged over study types: 0.786, $P < 0.01$), against study-specific dissimilarities between communities (global *R* for study type effect averaged over disturbance levels: 0.792, $P < 0.01$). The genus composition of nematode assemblages from geographically separate seas became increasingly similar with increased level of various types of anthropogenic disturbance (Fig. 4). The response of nematodes from the deposition experiment followed the same trajectory. Conversely, communities present in treatments from the resuspension experiment and along a gradient of natural, glacier-induced disturbance followed an opposite response vector.

Taxonomic differences in nematode assemblages among groups of samples mainly resulted from changes in the relative abundance of genera that are frequently encountered in muddy intertidal and subtidal sediments, including *Sabatieria*, *Leptolaimus* and *Terschellingia* (SIMPER analysis). In general, proportions of *Sabatieria* increased with increasing level of disturbance but, as illustrated in Fig. 5, the

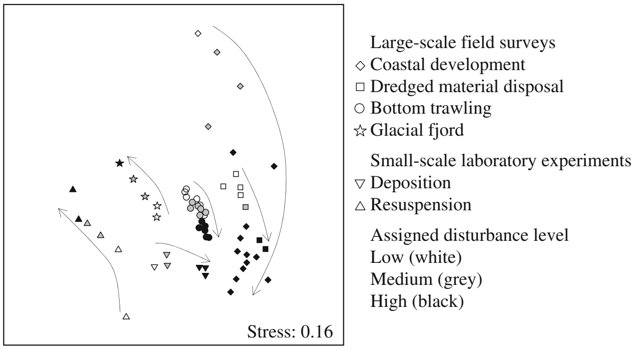
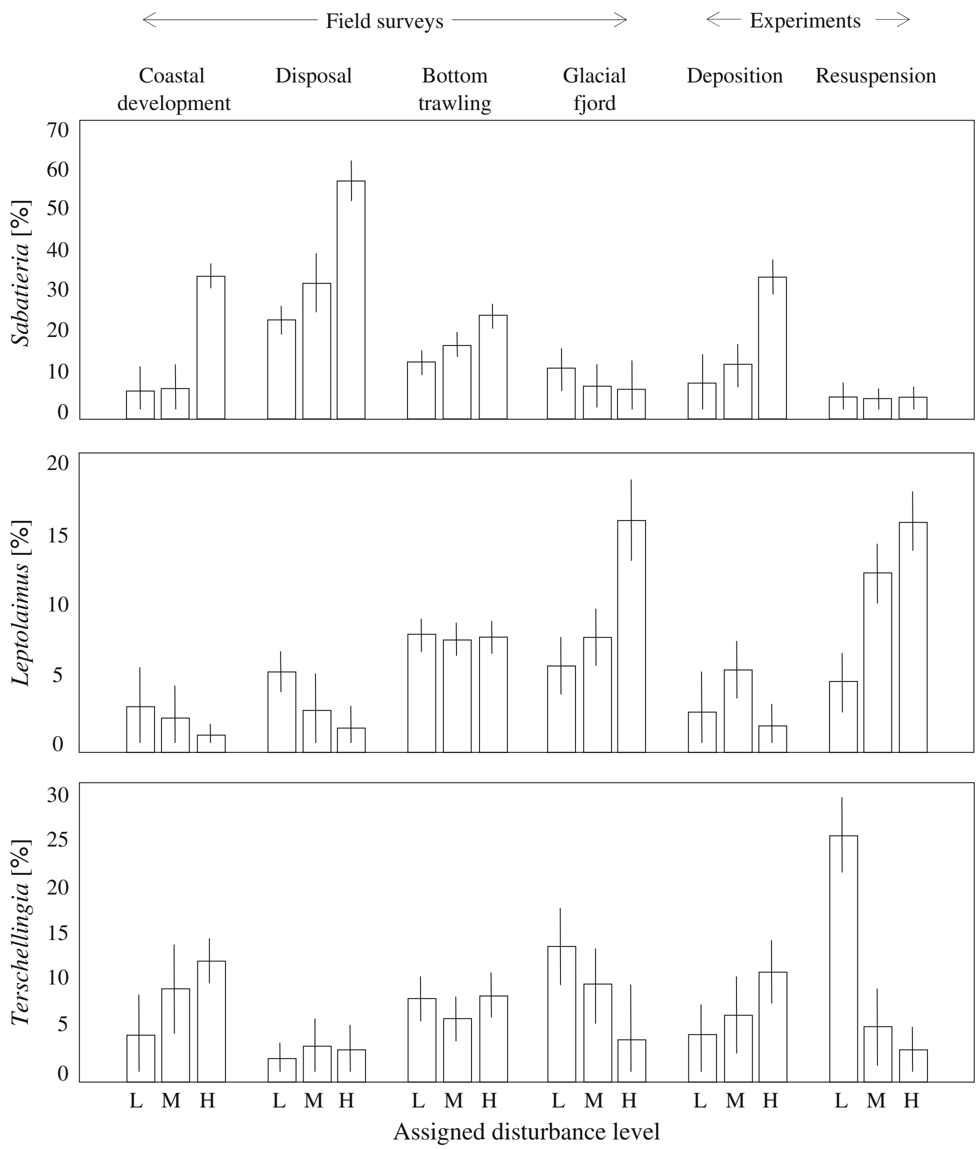


Fig. 4 Non-parametric multidimensional scaling (MDS) ordination of field surveys and laboratory experiments coded by level of disturbance. The plot is derived from a similarity matrix of relative abundance of genera. *Arrows* indicate community change in response to increasing level of disturbance

magnitude of this trend was study-specific. *Sabatieria*, and to a lesser degree *Terschellingia*, exhibited a consistent response to man-made disturbance at all field sampling sites. Increased dominance of these two genera with increasing level of disturbance was possibly due to their resilience to burial and/or their ability to survive in contaminated sediments (Fig. 5). The response of the three discriminating genera to repeated resuspension and subsequent deposition of sediment in experimental microcosms resulted in unaltered (*Sabatieria*), increased (*Leptolaimus*) or decreased (*Terschellingia*) dominance with increased level of disturbance (Fig. 5).

MDS based on the relative abundances of feeding types (Fig. 6) showed a graded change in community composition with increasing level of disturbance. Increasing levels

Fig. 5 Mean (±95% pooled confidence intervals) relative abundance of discriminating nematode genera from field surveys and laboratory experiments coded by level of disturbance



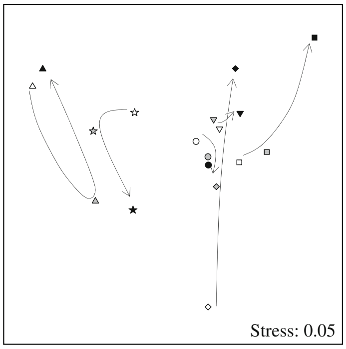


Fig. 6 Non-parametric multidimensional scaling (MDS) ordination of field surveys and laboratory experiments coded by level of disturbance. The plot is derived from a similarity matrix of relative abundance of feeding types (Wieser 1953). For clarity, the values within each of three disturbance levels were averaged for each field survey/laboratory experiment. *Arrows* indicate community change in response to increasing level of disturbance

of disturbance generally led to the decline of epigrowth feeders (global R for disturbance level effect averaged over study types: 0.348, $P < 0.01$). However, the direction of the community change differed between study types (global R for study type effect averaged over disturbance levels: 0.485, $P < 0.01$) and in particular between field situations where seabed disturbance was confounded by contamination (coastal development, dredged material disposal) and locations where this was not the case (bottom trawling, glacial fjord). The proportion of epigrowth feeders decreased in response to coastal development and dredged material disposal, increased with increasing level of bottom trawling and remained largely unaltered along the environmental gradient in a glacial fjord. Together with results from the correlation analyses (Table 6), this suggests that the decline of epigrowth feeders following coastal development and dredged material disposal might partly be a consequence of the susceptibility of this feeding type to heavy metal contamination rather than sediment movement. None of the trends observed in the field could be linked conclusively to results from the resuspension experiment where epigrowth feeders dominated nematode assemblages at intermediate levels of disturbance.

Discussion

Disturbance-induced changes in benthic systems are complex, factors affecting the system are not exclusive but interdependent (Fernandez-Duque and Veleggia 1993) and it is generally impossible to attribute observed changes to a single cause. Benthic communities vary in concert with numerous physical, chemical and geological processes that include both natural and man-induced effects. Generally, the richness of benthic invertebrates is highest in stable, undisturbed communities and depauperate populations occur in unstable regions of constant disturbance. The response of populations to modest or irregular disturbance, however, is variable (Gaston et al. 1998; Mackey and Currie 2001). In this article, we present results from the combined analysis of individual data sets investigating the response of nematode communities to seabed disturbance of different natural and anthropogenic origin. This form of analysis allowed us to determine whether multiple, independent studies reveal general relationships and whether any general relationships are influenced by one or more variables (e.g. type and level of seabed disturbance).

Only patterns of genus diversity were consistent, decreasing with increasing level of disturbance, regardless of the disturbance type (Table 7). Trends in taxonomic distinctness and trophic group diversity, in contrast, were more variable and depended on the nature and origin of the stress-generating factors. As such, the null-hypothesis is rejected. At sites exposed to coastal development and dredged material disposal, taxonomically closely related, epigrowth feeding genera such as *Sprinia* and *Desmodora* were highly susceptible to seabed disturbance, resulting in reduced genus diversity at greatly impacted stations. An increased ITD (i.e. decreased trophic diversity) at these stations was primarily due to increased dominance of non-selective deposit feeders. These included a range of genera, which are more taxonomically distinct than the epigrowth feeders that were lost from the system, leading to increased taxonomic distinctness values as the level of disturbance increased. Reductions in genus diversity as a result of bottom trawling were not manifested in changes of taxonomic distinctness and trophic diversity, indicating that genera were lost across taxonomic groups and functional guilds. Results from the resuspension experiment revealed that taxonomic distinctness did not change in an ordered fashion with increasing frequency of disturbance. Low and high frequency of disturbance were dominated by taxonomically closely related genera, whereas assemblages were more taxonomically distinct at intermediate levels of disturbance. A similar, though less pronounced, pattern was observed along a long-term natural disturbance gradient in a glacial fjord.

Studying various marine habitats including intertidal mud and sand as well as subtidal fine silts, coarse gravels and stones, Warwick and Clarke (1998) found that the taxonomic distinctness of nematodes from environmentally degraded locations was generally reduced in comparison with that of more pristine locations. Their data also revealed a positive relationship between taxonomic distinctness and trophic diversity; a reduction in trophic diversity generally led to a reduction in taxonomic distinctness. These findings are in contrast to the inconsistent trends revealed in this study, suggesting that measures of

Table 7 Main drivers for changes in the taxonomic and trophic diversity and composition of nematode communities in response to physical disturbance of the seabed

Community attribute	Response	Main driver of response
Genus diversity	Consistent decline with increased level of disturbance, irrespective of disturbance type or origin	Disturbance level
Genus composition	Assemblages exposed to various types of man-induced impacts and those present along a gradient of natural disturbance follow opposite response vectors	Disturbance level and origin
Trophic diversity	Decline in sediments where high levels of heavy metal contamination confound the effects of physical disturbance	Type of man-made activity
Feeding type composition	Dominance of non-selective deposit feeders and reduction of epigrowth feeders in sediments where high levels of heavy metal contamination confound the effects of physical disturbance	Type of man-made activity

taxonomic distinctness and functional diversity should be treated with caution before being recommended as universal diagnostic indicators of physical disturbance in benthic biota (review by Warwick and Clarke 2001; Wlodarsaka-Kowalczuk et al. 2005; Somerfield et al. 2006).

Are there consistent patterns in the response of nematode communities to physical disturbance resulting from natural changes and man-made activities?

Seabed disturbance at a harbour, a dredged material disposal site, a fishing ground and a glacial fjord affected genus composition differentially, although the patterns in genus diversity were consistent regardless of the type of disturbance. Communities present along the gradient of natural disturbance in a glacial fjord followed an opposite response vector to those present at anthropogenically impacted sites. This suggests that man-induced community changes might be intrinsically different from those of natural origin (Table 7). The difference may stem from the longer history of natural physical disturbance compared to relatively recent anthropogenic disturbances. Furthermore, the more episodic and unpredictable nature (i.e. high amplitude, low frequency) of many man-induced changes tends to differ from the chronic and predictable character (i.e. low amplitude, high frequency) of most natural disturbances.

Colonisation following seabed disturbance requires that the first arrivals can initiate new populations. After initial successful colonisation, the next stage is characterised by establishment of a viable, self-sustaining population. Whilst dispersal constraints determine the pool of potential colonists available at a particular time and place, environmental constraints subsequently restrict species establishment and mediate interactions between successful colonists (Schratzberger et al. 2008). Although responses of nematode communities to disturbance may be complex, generally disturbance leads to dominance by opportunistic genera (review by Heip et al. 1985 and case studies cited in the "Introduction"). Opportunistic genera often display a high phenotypic plasticity, illustrated by their ability to alter their growth rate, physiology or behaviour to better suit the environmental conditions with which they are faced. Our results provide empirical evidence that adaptive strategies of genera to physical disturbance of anthropogenic and natural origin might differ.

In the present study, *Sabatieria* proliferated at high levels of anthropogenic disturbance resulting from coastal development, dredged material disposal and bottom trawling. Species belonging to this genus are adapted to exploit newly available habitats or resources and are typically found in unpredictable and variable environments (Vincx 1990; Heip et al. 1990). Tietjen (1980) reported that *Sabatieria* species are well-adapted to different types of environmental change and Jensen (1984) showed that they are able to survive extended periods of anoxia. Dominance in anthropogenically impacted sediments suggests that this genus has evolved life-history characteristics (e.g. rapid growth rate, ability to adapt to a wide range of environmental conditions) that allow it to quickly establish itself in newly exposed habitats and persist in disturbed sediments where it may occur in high densities (Thistle 1981; Moore and Bett 1989; Somerfield et al. 1995).

In contrast, *Leptolaimus*, the genus dominating in the glacial bay where highest levels of natural physical disturbance were encountered, is not classified as truly opportunistic although high densities have been reported from some impacted sites and microcosms (Jayasree and Warwick 1977; Modig and Ólafsson 1998). Ullberg and Ólafsson (2003) hypothesised that the agility of small, surface-dwelling nematode genera (e.g. *Leptolaimus*) might be an evolutionary response towards higher levels of competence for coping with low amplitude, high frequency disturbance events. It appears that genera dominating in near-glacial sites are adapted to respond to frequent disturbance events rapidly by employing special life-history traits, such as high agility coupled with high dispersal potential (Lee et al. 2001; Commito and Tita 2002).

In terms of trophic diversity and structure, the response of nematode communities to disturbance originating from various types of man-made activities and natural processes was primarily driven by factors confounded with physical disturbance of the seabed (Table 7). That heavy metal contamination of the sediment was inversely related to trophic diversity supports a well-established, but seldom documented, paradigm amongst ecologists: pollution adversely affects community function (Rakocinski et al. 1997; Gaston et al. 1998). Much of this effect at the field locations of the present study was manifested in dominance of non-selective deposit feeders in contaminated sediments and a reduction of epigrowth feeders. This resulted in a less even mix of functional groups at impacted stations as illustrated by an increased ITD. In contrast, the type and frequency of seabed disturbance experienced at a North Sea fishing ground appeared to favour epigrowth feeding nematodes. The functional characteristics of epigrowth feeders were clearly suited to those conditions. The advantages of a survival strategy that combines a high productive potential, continuous asynchronous breeding and feeding position near the sediment surface at uncontaminated sites with high level of physical disturbance are clear: non-continuous dispersal and recolonisation of disturbed areas are possible (Nichols and Thompson 1985).

How are changes in assemblage structure observed in the field related to observations from controlled laboratory experiments?

A range of different mechanisms can cause mortality of nematodes at harbours, disposal sites and fishing grounds, including increased turbidity, high rates of sedimentation and sudden burial. In some cases (e.g. coastal development, dredged material disposal), these events can be confounded by sediment contamination. Similar trajectories were revealed for nematode communities responding to anthropogenic seabed disturbance in the field and experimental treatments simulating these (i.e. deposition experiment). Equally, comparable changes were observed of communities present in treatments from the resuspension experiment and along a gradient of natural, glacier-induced disturbance, suggesting that the response of nematodes to certain aspects of glacier-induced seabed disturbance was, to some extent, replicated successfully in the laboratory. At high-latitude fjords, chronic physical disturbance of natural origin is accompanied by low organic matter input. The activity of Arctic tidal glaciers results in high turbidity, high rates of inorganic particulate sedimentation and sedimentary instability in near-glacier marine basins. High sedimentation results in the formation of unconsolidated, easily eroded sediments, which are readily and frequently resuspended and redeposited (Wlodarsaka-Kowalczuk et al. 2005).

It would seem that the effects of both burial and heavy metal contamination were more pronounced at the sites exposed to man-induced seabed disturbance than in the glacial fjord where smaller amounts of virtually uncontaminated sediment are possibly resuspended and deposited more regularly. The use of multiple data sets and the agreement, to an extent, of the results derived from large-scale field surveys and small-scale laboratory experiments corroborates the idea that, although serving different purposes, both approaches combined can provide better insights into the complexity of ecological processes.

Outlook

Analysing a combined data set, including observations from already published studies, allowed us to compare the effects of different types of seabed disturbance on nematode assemblages. Although, to some degree, results may have arisen from the unbalanced nature of the data with many natural and anthropogenic seabed disturbances unrepresented, we were able to draw new conclusions that clearly go beyond the scope of the individual published papers.

Comparisons of the nature and effects of natural versus anthropogenic disturbance are necessary for understanding the ways in which anthropogenic activities influence benthic ecosystems and this clearly requires further field studies and experimental tests. As with most ecological issues of this kind, there is unlikely to be a simple answer, and elements of several explanations will probably pertain in different places and at different times. As evidenced from the outcome of this study, generalisations about attributes of assemblages prevailing at impacted locations are most likely to emerge from the combined analysis of independent, but comparable, data sets, an approach that is readily amenable to updating in the light of new data.

Acknowledgments This work is a contribution to the responsive mode project Manuela (Meiobenthic and nematode biodiversity: unravelling ecological and latitudinal aspects) within the EU FP6 Network of Excellence MarBEF (contract no. GOCE-CT-2003-505446). MS received financial support from Defra (project ME4118, Environmental indicators: a structured approach to the evaluation of impacts arising from human activities at sea). PJS acknowledges financial support from the UK NERC and Defra (project ME3109, Assessment of marine biodiversity linked to ecosystems).

References

Alongi DM (1985) Effects of physical disturbance on population dynamics and trophic interactions among microbes and meiofauna. J Mar Res 43:351–364

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511–525. doi:10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2

Armonies W (1994) Drifting meio- and macrobenthic invertebrates on tidal flats in Königshafen: a review. Helgol Wiss Meeresunters 48:299–320. doi:10.1007/BF02367043

Boyd SE, Rees HL, Richardson CA (2000) Nematodes as sensitive indicators of change at dredged material disposal sites. Estuar Coast Shelf Sci 51:805–819. doi:10.1006/ecss.2000.0722

Chandrasekara WU, Frid CLJ (1998) A laboratory assessment of the survival and vertical movement of two epibenthic gastropod species, *Hydrobia ulvae* (Pennant) and *Littorina littorea* (Linnaeus), after burial in sediment. J Exp Mar Biol Ecol 221:191–207. doi:10.1016/S0022-0981(97)00123-8

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser 92:205–219. doi:10.3354/meps092205

Clarke KR, Gorley RN (2006) PRIMER v6. user manual. Primer-E Ltd, Plymouth

Clarke KR, Warwick RM (1998a) A taxonomic distinctness index and its statistical properties. J Appl Ecol 35:523–531. doi:10.1046/j.1365-2664.1998.3540523.x

Clarke KR, Warwick RM (1998b) Quantifying structural redundancy in ecological communities. Oecologia 113:278–289. doi:10.1007/s004420050379

Clarke KR, Warwick RM (2001a) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar Ecol Prog Ser 216:265–278. doi:10.3354/meps216265

Clarke KR, Warwick RM (2001b) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. Primer-E Ltd, Plymouth

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and zero-adjusted Bray–Curtis coefficient for denuded assemblages. J Exp Mar Biol Ecol 330:55–80. doi:10.1016/j.jembe.2005.12.017

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J Exp Mar Biol Ecol 366:56–69. doi:10.1016/j.jembe.2008.07.009

Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–789. doi:10.1046/j.1365-2656.2000.00434.x

Commito JA, Tita G (2002) Differential dispersal rates in an intertidal meiofauna assemblage. J Exp Mar Biol Ecol 268:237–256. doi:10.1016/S0022-0981(01)00386-0

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310. doi:10.1126/science.199.4335.1302

Coull BC, Chandler GT (1992) Pollution and meiofauna: field, laboratory and mesocosm studies. Oceanogr Mar Biol Annu Rev 30:191–271

Death RG, Winterbourn MJ (1995) Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. Ecology 76:1446–1460. doi:10.2307/1938147

Dernie KM, Kaiser MJ, Warwick RM (2003) Recovery rates of benthic communities following physical disturbance. J Anim Ecol 72:1043–1056. doi:10.1046/j.1365-2656.2003.00775.x

Draggan S, Reisa JJ (1980) Controlling toxic substances: historical perspective and future research needs. In: Giesy JP (ed) Microcosms in ecological research. Technical Information Centre, US Department of Energy, Springfield, p 45

Ellis J, Cummings V, Hewitt J, Thrush S, Norkko A (2002) Determining effects of suspended sediment on condition of a suspension feeding bivalve (*Atrina zelandica*): results of a survey, a laboratory experiment and a field transplant experiment. J Exp Mar Biol Ecol 267:147–174. doi:10.1016/S0022-0981(01)00355-0

Fegley SR (1988) Experimental variation of near-bottom current speeds and its effect on depth distribution of sand-living meiofauna. Mar Biol (Berl) 95:183–191. doi:10.1007/BF00409004

Fernandez-Duque E, Veleggia C (1993) Meta-analysis: a valuable tool in conservation research. Conserv Biol 8:555–561. doi:10.1046/j.1523-1739.1994.08020555.x

Gaston GR, Rakocinski CF, Brown SS, Cleveland CM (1998) Trophic function in estuaries: response of macrobenthos to natural and contaminant gradients. Mar Freshw Res 49:833–846. doi:10.1071/MF97089

Giesy JP, Odum EP (1980) Microcosmology: introductory comments. In: Giesy JP (ed) Microcosms in ecological research. Technical Information Centre, US Department of Energy, Springfield, pp 1–13

Hagerman GM, Rieger RM (1981) Dispersal of benthic meiofauna by wave and current action in Bogue Sound, North Carolina, USA. Mar Ecol (Berl) 2:245–270. doi:10.1111/j.1439-0485.1981.tb00099.x

Hall SJ (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. Oceanogr Mar Biol Annu Rev 32:179–239

Heip C, Vincx M, Vranken G (1985) The ecology of marine nematodes. Oceanogr Mar Biol Annu Rev 23:399–489

Heip C, Huys R, Vincx M, Vanreusel A, Smol N, Herman R, Herman PMJ (1990) Composition, distribution, biomass and production of North Sea meiofauna. Neth J Sea Res 26:333–342. doi:10.1016/0077-7579(90)90095-X

Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427–432. doi:10.2307/1934352

Huston MA (1994) Biological diversity. Cambridge University Press, Cambridge

Jayasree K, Warwick RM (1977) Free-living marine nematodes of a polluted sandy beach in the Firth of Clyde, Scotland: description of seven new species. J Nat Hist 11:289–302. doi:10.1080/00222937700770211

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201–352. doi:10.1016/S0065-2881(08)60212-6

Jensen P (1984) Ecology of benthic and epiphytic nematodes in brackish water. Hydrobiologia 108:201–217

Karakassis I, Papadopoulou KN, Dafnomili EN, Plaiti W, Wilkinson M (1993) Preliminary study of the environmental contitions of Iraklion harbour. Proceedings of the 4th national symposium in oceanography and fisheries, Rhodes, Greece, pp 397–400

Kern JC (1990) Active and passive aspects of meiobenthic copepod dispersal at two sites near Mustang Island, Texas. Mar Ecol Prog Ser 60:211–223. doi:10.3354/meps060211

Lampadariou N, Austen MC, Robertson N, Vlachonis G (1997) Analysis of meiobenthic community structure in relation to pollution and disturbance in Iraklion harbour, Greece. Vie Milieu 47:9–24

Lee HJ, Vanhove S, Peck LS, Vincx M (2001) Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. Polar Biol 24:918–925. doi:10.1007/s003000100300

Leffler JW (1980) Microcosmology: theoretical applications of biological models. In: Giesy JP (ed) Microcosms in ecological research. Technical Information Centre, US Department of Energy, Springfield, pp 14–29

Lopez-Jamar E, Mejuto J (1988) Infaunal benthic recolonisation after dredging operations in La Coruna Bay, NW Spain. Cah Biol Mar 29:37–49

Mackey RL, Currie DJ (2001) The diversity–disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492

Maurer D, Keck RT, Tinsman JC, Leathem WA, Wethe C, Lord C, Church TM (1986) Vertical migration and mortality of marine benthos in dredged material: a synthesis. Int Rev Ges Hydrobiol 71:49–63

McCarthy JM, Hein CL, Olden JD, vander Zanden MJ (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. Freshw Biol 51:224–235. doi:10.1111/j.1365-2427.2005.01485.x

Medina MH, Correa JA, Barata C (2007) Micro-evolution due to pollution: possible consequences for ecosystem responses to toxic stress. Chemosphere 67:2105–2114. doi:10.1016/j.chemosphere.2006.12.024

Modig H, Ólafsson E (1998) Responses of Baltic benthic invertebrates to hypoxic events. J Exp Mar Biol Ecol 229:133–148. doi:10.1016/S0022-0981(98)00043-4

Moore CG, Bett BJ (1989) The use of meiofauna in marine pollution impact assessment. Zool J Linn Soc 96:263–280. doi:10.1111/j.1096-3642.1989.tb01831.x

Nichols FH, Thompson JK (1985) Persistence of an introduced mudflat community in South Francisco Bay, California. Mar Ecol Prog Ser 24:83–97. doi:10.3354/meps024083

Palen WJ, Williamson CE, Clauser AA, Schindler DE (2005) Impact of UV-B exposure on amphibian embryos: linking species physiology and oviposition behaviour. Proc R Soc Lond B Biol Sci 272:1227–1234. doi:10.1098/rspb.2005.3058

Quinn G, Keough M (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Rakocinski CF, Brown SS, Gaston GR, Heard RW, Walker WW, Summers JK (1997) Macrobenthic responses to natural and contaminant-related gradients in northern Gulf of Mexico estuaries. Ecol Appl 7:1278–1298. doi:10.1890/1051-0761(1997)007[1278:MRTNAC]2.0.CO;2

Rome MS, Young-Williams AC, Davis GR, Hines AH (2005) Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). J Exp Mar Biol Ecol 319:129–145. doi:10.1016/j.jembe.2004.06.014

Schratzberger M, Jennings S (2002) Impacts of chronic trawling disturbance on meiofaunal communities. Mar Biol (Berl) 141:991–1000. doi:10.1007/s00227-002-0895-5

Schratzberger M, Warwick RM (1998) Effects of physical disturbance on nematode communities in sand and mud: a microcosm experiment. Mar Biol (Berl) 130:643–650. doi:10.1007/s002270050286

Schratzberger M, Rees HL, Boyd SE (2000) Effects of simulated deposition of dredged material on structure of nematode assemblages: the role of contamination. Mar Biol (Berl) 137:613–622. doi:10.1007/s002270000386

Schratzberger M, Maxwell TAD, Warr K, Rogers SI (2008) Spatial variability of infaunal nematode and polychaete assemblages in two muddy subtidal habitats. Mar Biol (Berl) 153:621–642. doi:10.1007/s00227-007-0836-4

Somerfield PJ, Clarke KR (1995) Taxonomic levels, in marine community studies, revisited. Mar Ecol Prog Ser 127:113–119. doi:10.3354/meps127113

Somerfield PJ, Warwick RM (1996) Meiofauna in marine pollution monitoring programmes: a laboratory manual. Ministry of AgricultureFisheries and Food, Directorate of Fisheries Research, Lowestoft

Somerfield PJ, Rees HL, Warwick RM (1995) Interrelationships in community structure between shallow-water marine meiofauna and macrofauna in relation to dredging disposal. Mar Ecol Prog Ser 127:103–112. doi:10.3354/meps127103

Somerfield PJ, Warwick RM, Moens T (2005) Chapter 6: Meiofauna techniques. In: Eleftheriou A, McIntyre A (eds) Methods for the study of marine benthos, 3rd edn. Blackwell Science Ltd, Oxford, pp 229–272

Somerfield PJ, Cochrane SJ, Dahle S, Pearson TH (2006) Free-living nematodes and macrobenthos in a high-latitude glacial fjord. J Exp Mar Biol Ecol 330:284–296. doi:10.1016/j.jembe.2005.12.034

Sousa WP (1979) Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. Ecology 60:1225–1239. doi:10.2307/1936969

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391. doi:10.1146/annurev.es.15.110184.002033

Thistle D (1981) Natural physical disturbances and communities of marine soft bottoms. Mar Ecol Prog Ser 6:223–228. doi:10.3354/meps006223

Tietjen JH (1980) Population structure and species composition of the free-living nematodes inhabiting sands of the New York Bight Apex. Estuar Coast Mar Sci 10:61–73. doi:10.1016/S0302-3524(80)80049-1

Ullberg J, Ólafsson E (2003) Effects of biological disturbance by *Monoporeia affinis* (Amphipoda) on small-scale migration of marine nematodes in low-energy soft sediments. Mar Biol (Berl) 143:867–874. doi:10.1007/s00227-003-1139-z

Vandepitte L, Vanaverbeke J, Vanhoorne B, Hernandez F, Campinas-Bezerra T, Mees J, Vanden Berghe E (2008) The MANUELA database: an integrated database on meiobenthos from European marine waters. Meiofauna Marina (submitted)

Vincx M (1990) Diversity of the nematode communities in the Southern Bight of the North Sea. Neth J Sea Res 25:181–188. doi:10.1016/0077-7579(90)90019-D

Warwick RM (1993) Environmental impact studies on marine communities: pragmatical considerations. Aust J Ecol 18:63–80. doi:10.1111/j.1442-9993.1993.tb00435.x

Warwick RM, Clarke KR (1998) Taxonomic distinctness and environmental assessment. J Appl Ecol 35:532–543. doi:10.1046/j.1365-2664.1998.3540532.x

Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. Oceanogr Mar Biol Annu Rev 39:207–231

Warwick RM, Platt HM, Clarke KR, Agard J, Gobin J (1990) Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. J Exp Mar Biol Ecol 138:119–142. doi:10.1016/0022-0981(90)90180-K

Wieser W (1953) Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Ark Zool 4:439–484

Wlodarsaka-Kowalczuk M, Pearson TH, Kendall MA (2005) Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Mar Ecol Prog Ser 303:31–34. doi:10.3354/meps303031