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Impacts of chronic trawling disturbance on meiofaunal communities

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Abstract Bottom trawling causes chronic and widespread disturbance to the seabed in shelf seas. Meiofauna may be impacted directly or indirectly by this disturbance, since the passage of trawls causes immediate mortality or displacement, changes sediment structure and geochemistry and affects the abundance of predators or competitors. Since meiofauna make a significantly greater contribution to benthic production than the larger macrofauna, there are compelling reasons to assess their response to chronic trawling disturbance. In this study, we determined the effects of trawling disturbance, season, sediment type and depth on the structure and diversity of nematode communities. Our analyses were based on comparisons between nematode communities in three beam-trawl fishing areas in the central North Sea. These areas were trawled with mean frequencies of 1 (low disturbance), 4 (medium) and 6 (high) times year⁻¹ respectively. Our analyses showed that trawling had a significant impact on the composition of nematode assemblages. In two sampling seasons, the number of species, diversity and species richness of the community were significantly lower in the area subject to high levels of trawling disturbance than in the areas subject to low or medium levels of disturbance. However, levels of disturbance at the 'low' and 'medium' sites may have been insufficient to cause marked long-term changes in community structure. Many of the observed changes were consistent with responses to other forms of physical disturbance. The extent to which the observed changes in community structure reflect changes in the production of the nematode community remains

unknown, although overall abundance was not significantly affected by trawling disturbance.

Introduction

Bottom trawling causes chronic and widespread disturbance to soft-sediments in shelf seas (Gislason 1994; Jennings and Kaiser 1998; Lindeboom and de Groot 1998; Hall 1999; Kaiser and de Groot 2000). In areas subject to frequent trawling disturbance, the biomass, diversity and production of benthic macrofauna is reduced, with larger and habitat forming species showing greater sensitivity than smaller free-living species. As a result, trawled areas are characterised by smaller-bodied, short-lived infaunal species with high rates of population growth while untrawled areas are characterised by larger sessile and emergent species (Collie et al. 1997; Kaiser et al. 2000; Jennings et al. 2001). The rates of recovery for benthic communities following intensive trawling disturbance may range from weeks to years, with rates of recovery depending on rates of immigration, recruitment and growth. Overall rates of recovery tend to be faster on mobile sediments where there are high levels of natural disturbance (Collie et al. 2000).

Most existing studies of trawling impacts have examined changes in community structure due to experimental trawling (e.g. Currie and Parry 1996; Hansson et al. 2000; Lindegarth et al. 2000) or have compared fished and unfished sites in previously unfished or lightly fished areas (e.g. Hall et al. 1990; Tuck et al. 1998; McConnaughey et al. 2000). These studies have focused on impacts on larger macrofauna and habitat forming species, primarily because reductions in their abundance and diversity are an important conservation issue. However, the meiofauna, those animals that pass through a 500 µm sieve but are retained in a 63 µm sieve, make a significantly greater contribution to the processing of carbon by benthic communities because they are abundant and have higher rates of reproduction

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and growth than the larger macrofauna. Moreover, the meiofauna have high diversity and lack pelagic larvae. For these reasons, meiofauna are widely regarded as ideal organisms to study the potential ecological effects of anthropogenic impacts such as pollution (review: Coull and Chandler 1992). However, even though trawling causes chronic and widespread disturbance to marine sediments, the only studies of trawling impacts on meiofauna are experimental, and the effects of chronic trawling disturbance on real fishing grounds are not known (Schratzberger et al. 2002).

Schratzberger et al. (2002) used a BACI experimental design to investigate the short-term effects of beam trawling on the diversity, biomass and community structure of meiofauna. Experiments at two locations in the southern North Sea showed that there were no short to medium-term (1–392 days after experimental trawling) trawling impacts on meiofaunal diversity or biomass, but that there were mild effects on community structure. Any impacts due to trawling were minor in relation to seasonal changes in the meiofaunal communities. The results of the study, coupled with a post-hoc power analysis, suggested that meiofauna were more resilient to beam trawling disturbance than macrofauna. Their relative resilience may have been a consequence of low mortality rates due to trawling and their high rates of population increase following trawling. However, small-scale experimental studies of this type are unlikely to represent the chronic impacts of trawling disturbance on real fishing grounds.

A major impediment to the study of trawling impacts is the paucity of trawling disturbance data at small spatial and long temporal scales (Rijnsdorp et al. 1998). As a result, relatively few studies have examined

trawling or dredging impacts across quantifiable gradients of disturbance (Collie et al. 1997; Thrush et al. 1998; Kaiser et al. 2000; Veale et al. 2000; Piet et al. 2001). One method for quantifying trawling disturbance on relatively small scales is to use records of vessels sighted by aircraft that patrol the fishing grounds around the United Kingdom. The crew on these aircraft record the description and location of all vessels they see fishing. Relative trawling disturbance can be estimated as the number of actively fishing trawlers sighted per unit of search effort per unit area (Jennings et al. 2001).

The aim of the present study is to assess the response of meiofaunal nematode communities to chronic trawling disturbance on real fishing grounds. We use over-flight records to identify sites that are subject to different levels of trawling disturbance, and predict the relative contribution of trawling disturbance, season, sediment type and water depth to any significant differences between nematode communities.

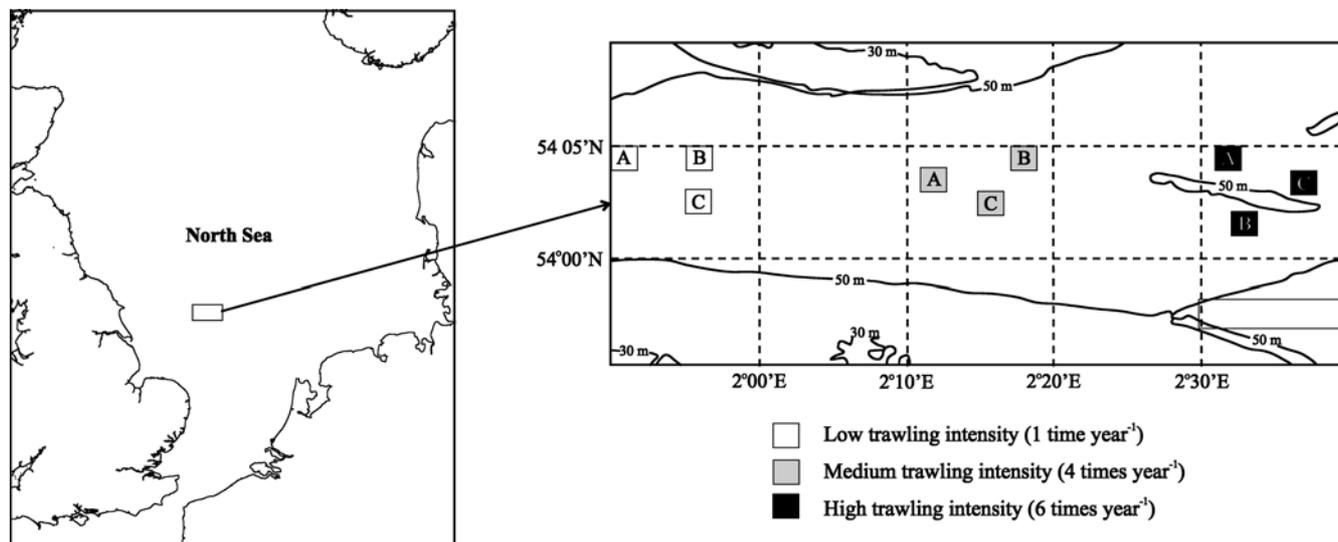
Material and methods

Study site and estimation of trawling disturbance

We studied the impacts of trawling on nematode communities in the Silver Pit, central North Sea (Fig. 1). The Silver Pit is predominantly 60–80 m deep with a muddy-sand substratum; parts of the Silver Pit are intensively fished by beam trawlers. We selected three study areas of 5×6 nautical miles (c. 9.3×11.1 km) that were subject to different levels of fishing effort.

The mean levels of trawling disturbance in each study area were determined from records of beam trawler sightings per unit of aircraft search effort (SPUE). Within each area, we calculated beam trawler SPUE on an annual basis for the years 1994–2000. Sightings were the number of times that a beam trawler was recorded in the area, and search effort was the number of times that an aircraft visited the area. We assumed that beam trawler SPUE was directly and linearly proportional to trawling effort and trawling disturbance. We converted our SPUE data to a mean frequency of beam trawling for each area, based on the assumption that the average beam trawler fishing in the Silver Pit will tow two 12-m-wide beams at a speed of 6 knots (11.1 km hour⁻¹), and that 267,264 m² of seabed will be disturbed each hour. Thus an annual

Fig. 1 Study areas [5×6 nautical mile (c. 9.3×11.1 km) boxes] and sampling sites (1×1 nautical mile boxes; 1 nautical mile² = 3.43 km²) in the Silver Pit region of the central North Sea. The broken lines show the boundaries of the areas for which trawling disturbance was assessed



SPUE of 1 (beam trawler always sighted at the site) will equate to the entire area being trawled, on average, 22.73 times each year. Side-scan sonar observations of trawl tracks within the study areas suggest that track frequency and SPUE are correlated and that tracks cross the more heavily fished sites in many directions (T.A. Dinmore and S. Jennings, unpublished data). We expected trawling effort to be spatially heterogeneous in this area of relatively homogeneous substratum because beam trawlers tend to fish on the 'tows' that are recorded in their navigation systems and known to be free of obstructions that could damage the trawl gear. Indeed, previous studies have shown that trawling effort in the southern and central North Sea is heterogeneous on many scales (Rijnsdorp et al. 1998).

Sampling of meiofauna

Meiofauna were sampled at three sites in each of the three study areas (hereafter referred to as low, medium and high disturbance areas). Each site (designated A, B or C) was defined by a box of 1 nautical mile (1.85 km) north to south by 1 nautical mile (1.85 km) east to west. Meiofauna samples were collected with a NIOZ corer in November 2000 and April 2001, at four haphazardly chosen locations in each site. The NIOZ corer takes a circular core of 0.1 m² to a depth of > 30 cm. The surface of sediment samples collected with a NIOZ corer is relatively undisturbed, and the corer retains a few centimetres of the overlying water. A 5.5-cm internal diameter perspex tube (surface area 23.76 cm²) was pushed into the NIOZ sediment core until the top of the tube was level with the water surface in the NIOZ core. The water overlying the sediment in the perspex tube was siphoned into a 63 µm sieve and washed into a sample pot. The top of the perspex tube was then sealed with a rubber bung and sediment around the tube was excavated so that the tube containing the sediment could be removed. The top 5 cm of the sediment in the tube was transferred into the sample pot and fixed with 10% formalin in filtered seawater.

In November 2000, sediment samples were also taken from the NIOZ cores with a 5.5-cm-diameter perspex tube. These were frozen pending particle size analysis. After thawing, sediment samples were wet sieved through a 500 µm sieve, and the fraction greater than 500 µm was oven dried at 90 °C for 24 hours. This fraction was then dry sieved at 0.5 φ intervals, down to 1 φ (500 µm) and weighed on a top pan balance (precision = 0.01 g). The fraction smaller than 500 µm was freeze dried and analysed on a Coulter LS 130 Laser sizer. The laser sizer results were combined with the dry sieve results to give the full particle size distribution. The mean particle size diameter and sorting coefficient were calculated from these results (Dyer 1986).

Meiofauna sample processing

In the laboratory, samples were decanted five times onto a 63 µm sieve, and meiofauna were extracted with Ludox using the procedures of McIntyre and Warwick (1984) and Somerfield and Warwick (1996). The extraction was repeated 3 times. Subsamples of 15% of the extracted material (containing 145–396 nematodes) were evaporated slowly in anhydrous glycerol and mounted on slides for identification and counting. Nematodes, comprising the dominant meiofauna taxon, were identified to genus or species level following Platt and Warwick (1983, 1988) and Warwick et al. (1998).

Data analyses

Correlation-based principal components analysis (PCA) was applied to ordinate measured environmental variables that were not significantly correlated (mean particle diameter, sorting coefficient, water depth and trawling intensity). The positions of samples in the ordination were defined in relation to axes representing the full set of environmental variables that were measured, one axis for each variable. The first principal component axis (PC1) was then defined

as the direction in which the variance of sample points projected perpendicularly onto the axis was maximised and the second principal component (PC2) was defined as the axis perpendicular to PC1 (Clarke and Warwick 1994).

The total number of individuals, total number of species, Shannon-Wiener-Index (H'), species richness (Margalef's d) and evenness (Pielou's J) were calculated to describe nematode assemblage structure. Bartlett's and Cochran's tests were used to test for homogeneity of variance. The effect of both "trawling intensity" and "sampling season" on univariate indices was investigated using a two-way analysis of variance (ANOVA) and one-way ANOVA was applied to assess differences between samples collected at the same station in November 2000 and April 2001. To further explore statistically significant differences, the Tukey HSD multiple comparisons test was used in pair-wise comparisons of sampling stations.

Ordination by non-metric multidimensional scaling (MDS) using the Bray-Curtis similarity measure was applied to untransformed species abundance data to summarise patterns in the composition of nematode assemblages. Analysis of similarities (ANOSIM), an analogue of univariate ANOVA, was used to test for significant differences between groups of multivariate samples from different areas (low, medium and high trawling intensity). Two-way crossed ANOSIM was used to test for statistically significant effects of the factors "trawling intensity" and "sampling season" on nematode assemblage structure. A one-way ANOSIM was also completed for each sampling season separately to assess the significance of differences in the composition of nematode communities between sites and areas.

The similarity percentages programme (SIMPER) was applied to identify the species primarily providing the discrimination between sample clusters observed in the MDS ordinations and the relationships between multivariate biotic patterns and environmental variables were assessed using the BIO-ENV programme. Spearman rank correlations (ρ) between a similarity matrix derived from the biotic data and matrices derived from various subsets of environmental data were calculated, thereby defining suites of environmental variables which best explain the biotic structure.

Univariate analyses were performed using the software package STATGRAPHICS Plus version 3.3 and multivariate analyses were carried out using the software package PRIMER version 5.2.3 (Clarke and Warwick 1994; Clarke and Gorley 2001).

Results

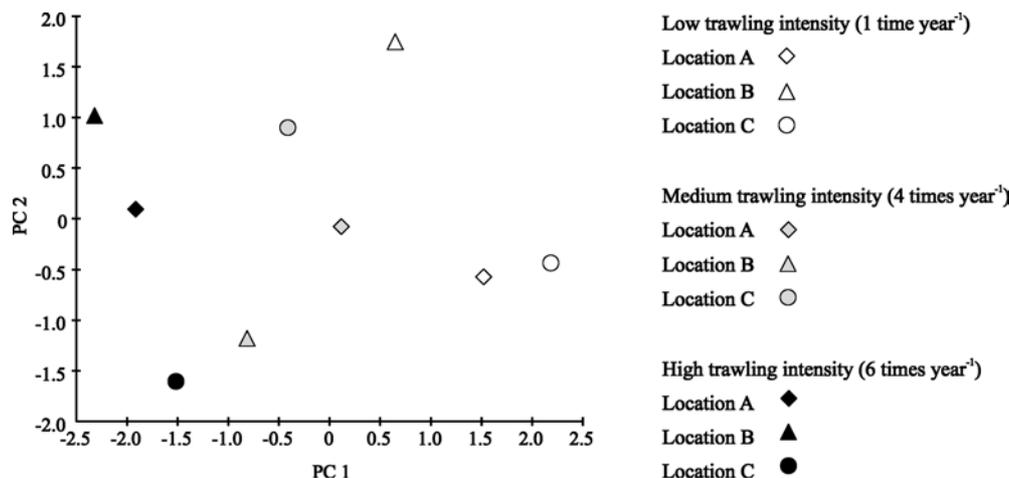
Environmental variables

The analysis of sediments showed that the sediments at all study sites could be classified as sandy muds and muddy sands with mean particle diameters between 36 and 81 µm (Table 1). Differences in mean particle diameter ($F=0.54$, $P=0.60$) and sorting coefficient ($F=0.17$, $P=0.85$) among areas were not statistically significant at $P<0.05$. Water depth, however, was significantly greater in the low trawling disturbance area than in the area where trawling disturbance was high ($F=7.81$, $P=0.02$).

The ordination of environmental data by PCA (including mean particle diameter, sorting coefficient, water depth and trawling intensity) showed that sampling locations clustered mainly by trawling intensity (Fig. 2). Differences between the sites A, B and C within the low, medium and high disturbance areas were mainly related to differences in the sorting coefficient. Seventy-seven percent of the total variation was explained by the first

Table 1 Mean environmental variables \pm SE ($n=5$) for all study sites

	Mean (μm)	Sorting coefficient	Sand (%)	Mud (%)	Water depth (m)	Trawling disturbance (times year ⁻¹)
Low A	53.46 \pm 9.81	2.42 \pm 0.08	63.18 \pm 3.95	36.82 \pm 3.94	74.1 \pm 1.7	0.98
Low B	55.55 \pm 10.42	2.26 \pm 0.10	67.41 \pm 4.62	32.60 \pm 4.62	69.1 \pm 0.5	0.98
Low C	80.95 \pm 15.20	2.36 \pm 0.10	74.91 \pm 2.23	25.09 \pm 2.23	74.8 \pm 1.3	0.98
Medium A	51.69 \pm 31.54	2.38 \pm 0.15	62.85 \pm 10.85	37.14 \pm 10.85	71.7 \pm 0.5	4.11
Medium B	43.47 \pm 11.46	2.04 \pm 0.13	53.38 \pm 5.94	29.96 \pm 5.94	64.7 \pm 1.1	4.11
Medium C	38.73 \pm 9.00	1.92 \pm 0.10	51.96 \pm 3.76	30.88 \pm 4.09	69.7 \pm 1.5	4.11
High A	39.13 \pm 11.23	2.37 \pm 0.20	63.92 \pm 3.85	38.69 \pm 6.60	64.8 \pm 0.3	6.14
High B	35.73 \pm 3.64	2.32 \pm 0.09	57.78 \pm 3.26	42.23 \pm 3.26	63.4 \pm 2.0	6.14
High C	78.11 \pm 25.08	2.39 \pm 0.13	73.33 \pm 6.47	26.67 \pm 6.46	60.2 \pm 0.6	6.14

Fig. 2 Principal components analysis ordination of environmental data from November 2000. Only the non-correlated variables mean particle diameter, sorting coefficient, trawling intensity and water depth are included in the ordination

two principal components, indicating that the two-dimensional ordination gave an appropriate representation of the similarity between sampling areas.

Nematode diversity and assemblage structure

There were statistically significant differences in mean univariate indices of assemblage structure (except

evenness) among areas (low, medium, high trawling intensity) sampled in the same season. However, differences among areas sampled in different seasons (November 2000, April 2001) and trawling intensity \times sampling season interactions were not significant at $P < 0.05$ (Tables 2, 3, Fig. 3).

Total nematode abundance was significantly higher in the area exposed to medium levels of trawling disturbance than in either of the other areas. The numbers

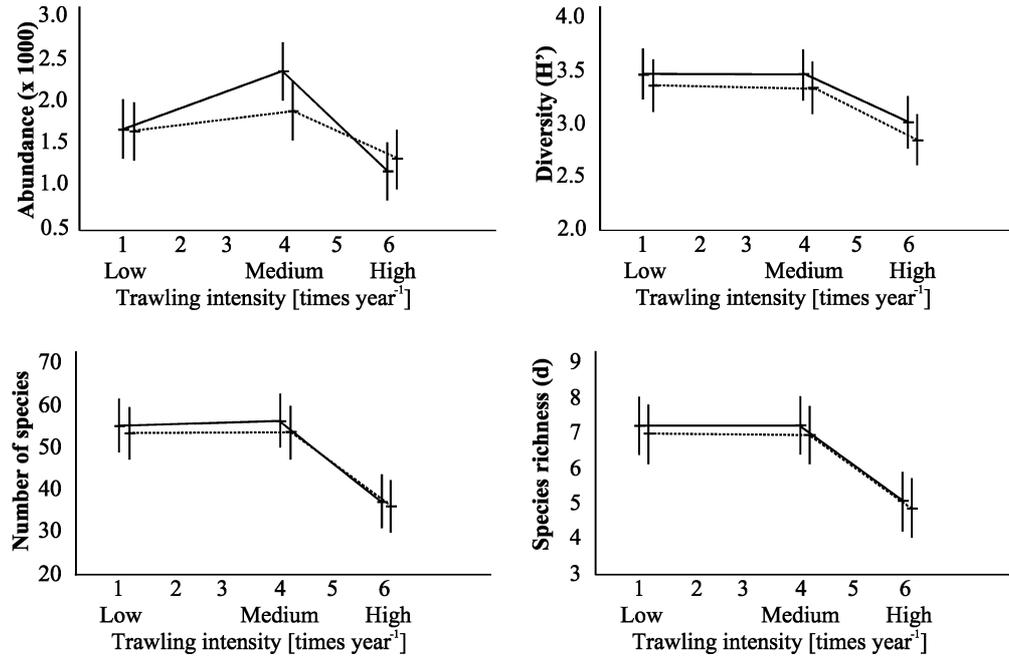
Table 2 Mean univariate indices \pm SE ($n=4$) for the nematode assemblages in all study sites in November 2000 and April 2001

	Abundance	Number of species	Diversity (H')	Richness (d)	Evenness (J')
Low A November	1,743 \pm 224	58 \pm 4	3.44 \pm 0.11	7.61 \pm 0.57	0.85 \pm 0.02
Low B November	1,716 \pm 286	49 \pm 9	3.25 \pm 0.39	6.38 \pm 1.15	0.84 \pm 0.06
Low C November	1,528 \pm 280	53 \pm 4	3.53 \pm 0.05	7.13 \pm 0.36	0.89 \pm 0.02
Medium A November	2,554 \pm 931	54 \pm 3	3.34 \pm 0.10	6.85 \pm 0.44	0.84 \pm 0.02
Medium B November	2,642 \pm 787	60 \pm 4	3.53 \pm 0.06	7.49 \pm 0.34	0.86 \pm 0.02
Medium C November	1,781 \pm 687	52 \pm 6	3.36 \pm 0.13	6.81 \pm 0.53	0.85 \pm 0.01
High A November	1,340 \pm 652	33 \pm 7	2.82 \pm 0.06	4.47 \pm 0.66	0.81 \pm 0.03
High B November	1,074 \pm 425	35 \pm 5	2.96 \pm 0.12	4.83 \pm 0.47	0.84 \pm 0.01
High C November	964 \pm 380	39 \pm 2	3.07 \pm 0.20	5.52 \pm 0.43	0.84 \pm 0.05
Low A April	1,922 \pm 895	58 \pm 10	3.55 \pm 0.05	7.60 \pm 0.86	0.88 \pm 0.03
Low B April	1,600 \pm 160	44 \pm 5	2.92 \pm 0.20	5.83 \pm 0.64	0.77 \pm 0.03
Low C April	1,230 \pm 387	52 \pm 10	3.46 \pm 0.20	7.18 \pm 1.16	0.88 \pm 0.01
Medium A April	2,044 \pm 266	56 \pm 6	3.35 \pm 0.15	7.25 \pm 0.66	0.83 \pm 0.04
Medium B April	1,715 \pm 540	53 \pm 9	3.33 \pm 0.21	6.99 \pm 0.96	0.84 \pm 0.02
Medium C April	1,848 \pm 640	48 \pm 8	3.26 \pm 0.16	6.19 \pm 0.82	0.85 \pm 0.01
High A April	1,386 \pm 526	30 \pm 7	2.50 \pm 0.05	4.01 \pm 0.81	0.74 \pm 0.04
High B April	1,048 \pm 145	33 \pm 5	2.80 \pm 0.17	4.53 \pm 0.69	0.81 \pm 0.03
High C April	1,331 \pm 315	41 \pm 3	2.99 \pm 0.07	5.61 \pm 0.17	0.81 \pm 0.03

Table 3 Results from the two-way ANOVAs for mean univariate indices

	Trawling intensity		Sampling season		Trawling × season	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
Abundance	16.25	< 0.01	1.09	0.32	1.74	0.22
Number of species	26.71	< 0.01	0.74	0.41	0.06	0.94
Diversity (<i>H'</i>)	13.35	< 0.01	1.99	0.18	0.10	0.90
Richness (<i>d</i>)	20.42	< 0.01	0.47	0.51	0.00	1.00
Evenness (<i>J'</i>)	3.12	0.08	2.61	0.13	0.50	0.62

Fig. 3 Means ± 95% pooled confidence intervals of mean univariate indices for the nematode assemblages. Solid line November 2000, dotted line April 2001



of species, diversity and species richness of nematodes were significantly lower in the most heavily trawled area than in the areas trawled less intensively.

A total of 122 nematode species were recorded in November 2000 and 136 in April 2001. Approximately half the recorded species occurred in all areas, but some species were restricted to fewer areas (Table 4). In November 2000, 18% of all species recorded were found only in the area subject to medium levels of trawling disturbance, and in April 2001, 21% of all nematodes recorded were only found in the area exposed to low trawling intensity (Table 4).

The MDS analysis was based on replicates collected at each site in November 2000 and April 2001 (Fig. 4). In November 2000, the sites within the area exposed to

low levels of trawling disturbance were represented in an intermediate position between the sites subject to medium and high intensities of trawling disturbance. In April 2001, the sample sites were represented as a series that reflected the levels of trawling disturbance to which they were exposed.

The results from the two-way crossed ANOSIM tests indicated a statistically significant effect of trawling intensity ($R=0.436$, $P<0.01$) and sampling season ($R=0.116$, $P<0.01$) on nematode assemblage structure. However, the outputs from the one-way ANOSIM analyses (Table 5) and MDS ordinations (Fig. 4) showed that differences in nematode assemblage structure due to trawling intensity were greater than the seasonal differences. In November 2000, the highest dissimilarity in

Table 4 Number of nematode species present in individual sampling areas. Proportion in parentheses

	November 2000	April 2001
Total number of species	122	136
Number of species present in all areas	66 (54%)	66 (49%)
Number of species present in the low intensity area only	8 (7%)	29 (21%)
Number of species present in the medium intensity area only	22 (18%)	10 (7%)
Number of species present in the high intensity area only	1 (1%)	4 (3%)
Number of species present in the low and medium areas only	13 (11%)	14 (10%)
Number of species present in the low and high areas only	7 (6%)	9 (7%)
Number of species present in the medium and low areas only	5 (4%)	4 (3%)

Fig. 4 Non-parametric multi-dimensional scaling ordination for nematode assemblages collected in November 2000 and April 2001 (based on untransformed species abundance data)

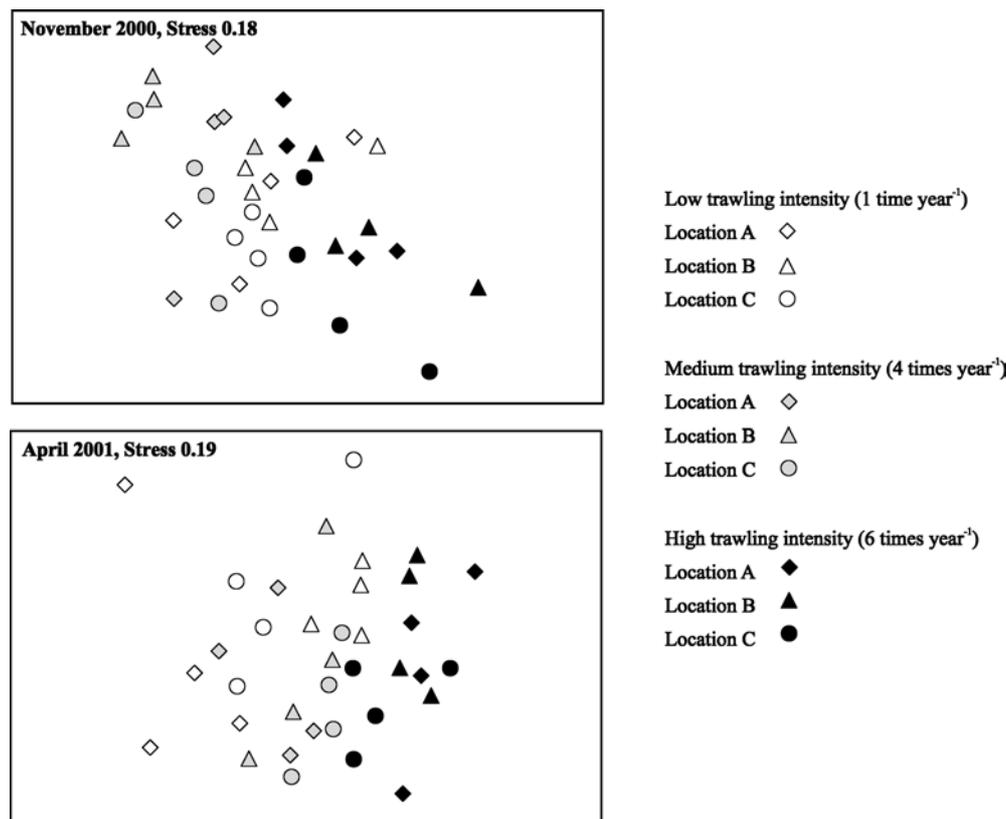


Table 5 Mean dissimilarities (%) between nematode assemblages collected from areas differing in trawling intensity based on untransformed species abundance data. *R*-values in parentheses. Sampling season: low intensity 46 (0.096); medium intensity 44 (0.155); high intensity 46 (0.096); all significant to $P < 0.05$

Trawling intensity					
	Low November	Medium November		Low April	Medium April
Medium November	49 (0.547)*		Medium April	51 (0.309)*	
High November	49 (0.491)*	55 (0.523)*	High April	53 (0.320)*	50 (0.489)*

* $P < 0.05$

nematode assemblage structure was observed between areas subject to medium and high levels of trawling disturbance. In April 2001, the greatest dissimilarity was between the areas subject to low and high levels of disturbance.

The species that were responsible for the main differences between assemblages in the areas subject to different levels of disturbance included the chromadorids *Prochromadorella ditlevseni*, *Actinonema pachydermatum*, *Sabatieria punctata*, *Richtersia inaequalis*, *Aponema torosa* and *Leptolaimus elegans*, and the monhysterids *Cobbia trefusiaeformis*, *Daptonema setosum*, *Metalinhomoeus longiseta* and *Terschellingia longicaudata*. The abundance of all discriminating species, except *Cobbia trefusiaeformis* and *Terschellingia longicaudata* differed significantly between areas. Differences between seasons and trawling intensity \times sampling season interactions, however, were not significant at $P < 0.05$ for all species except *Daptonema setosum* (Table 6). *Prochromadorella ditlevseni* and

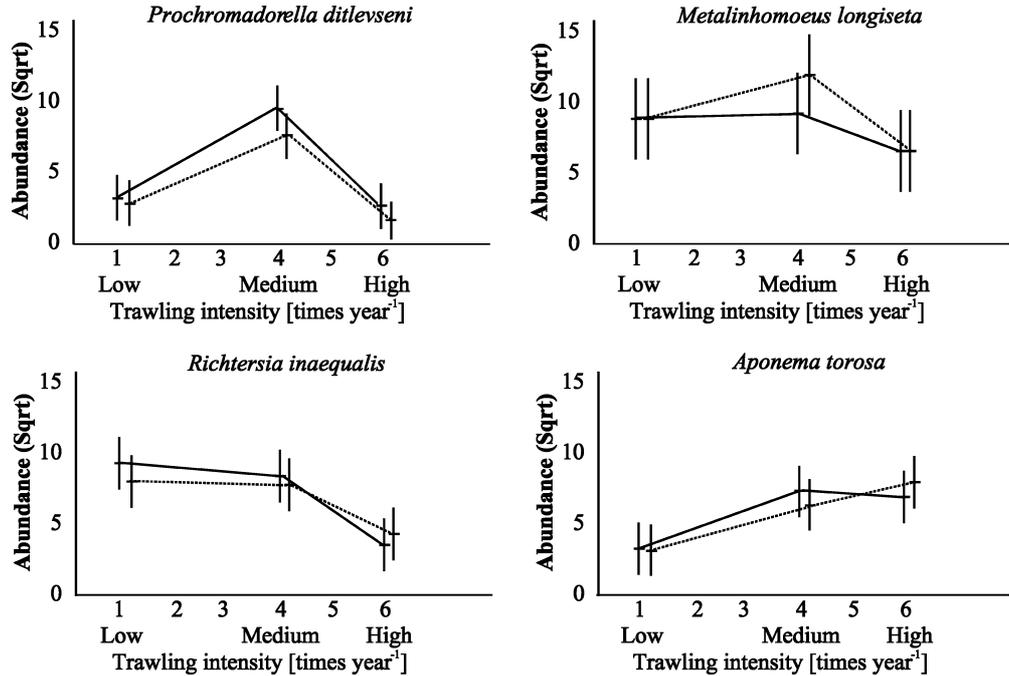
Actinonema pachydermatum (not shown) were significantly more abundant in the area subject to medium levels of trawling disturbance (Fig. 5). The abundance of *Richtersia inaequalis* and *Leptolaimus elegans* (not shown) was significantly lower in the area subject to high levels of trawling disturbance (Fig. 5). *Metalinhomoeus longiseta* and *Daptonema setosum* (not shown) exhibited a significantly higher abundance in the area subject to medium levels of trawling disturbance while *Aponema torosa* and *Sabatieria punctata* (not shown) showed an opposing trend with significantly higher abundance in the areas subject to medium and high levels of trawling disturbance (Fig. 5).

The combined results of the SIMPER and MDS analyses for the November 2000 samples suggested that the differences between assemblage structure in the area subject to medium disturbance and in the areas subject to high and low disturbance were mainly due to the large number of species that occurred exclusively in the area subject to medium levels of disturbance and to

Table 6 Results from two-way ANOVA for square-root transformed mean abundance of selected discriminating nematode species

	Trawling intensity		Sampling season		Trawling × season	
	F-ratio	P-value	F-ratio	P-value	F-ratio	P-value
<i>Prochromadorella ditlevseni</i>	45.62	< 0.01	3.45	0.09	0.66	0.54
<i>Actinonema pachydermatum</i>	12.24	< 0.01	1.32	0.27	3.59	0.06
<i>Sabatieria punctata</i>	5.38	0.02	1.79	0.21	2.70	0.11
<i>Richtersia inaequalis</i>	18.18	< 0.01	0.10	0.75	0.79	0.47
<i>Aponema torosa</i>	12.66	< 0.01	0.24	0.64	1.66	0.23
<i>Leptolaimus elegans</i>	8.04	0.01	0.17	0.69	1.54	0.25
<i>Cobbia trefusiaeformis</i>	0.15	0.86	1.35	0.27	0.58	0.57
<i>Daptonema setosum</i>	7.73	0.01	2.50	0.14	11.72	0.02
<i>Metalinhomoeus longiseta</i>	4.64	0.03	0.68	0.43	0.68	0.52
<i>Terschellingia longicaudata</i>	0.42	0.66	0.19	0.67	0.45	0.65

Fig. 5 Means ± 95% pooled confidence intervals of mean square-root transformed abundance data from selected discriminating nematode species. Solid line November 2000, broken line April 2001



the generally greater abundance of other common species in this area. By April 2001, nematode assemblages in the area subject to medium disturbance were more similar to those sampled in the area subject to high disturbance. This change was driven predominantly by the disappearance of species that were previously observed in the area subject to medium disturbance and a reduction in the abundance of discriminating species such as *Sabatieria punctata* and *Daptonema setosum* (Fig. 6, Table 6).

Relationship between environmental variables and assemblage structure

The results of the correlation analyses between nematode assemblage structure and environmental variables are presented in Table 7. The BIO-ENV analyses demonstrated that trawling intensity was the single most important factor in determining nematode assemblage structure in both sampling seasons.

Discussion

Our comparison of nematode assemblages in areas subject to different levels of beam trawling disturbance showed that trawling had a significant impact on nematode community structure. During both sampling seasons, the number of species, diversity and species richness of the assemblages were significantly lower in the area subject to high levels of trawling disturbance than in the areas subject to low or medium levels of disturbance. The results of this study contrasted with the results of a previous small-scale experimental study, where seasonal impacts on assemblage structure were greater than those attributed to trawling, and shows why uncritical extrapolation of results from small-scale studies to larger scales should be avoided (Schratzberger et al. 2002). Our results also suggest that the levels of disturbance at the ‘low’ and ‘medium’ sites may have been insufficient to cause marked long-term changes in assemblage structure.

Fig. 6 *Sabatieria punctata* and *Daptonema setosum*. Means \pm 95% pooled confidence intervals of mean square-root transformed abundance data. Solid line November 2000, broken line April 2001

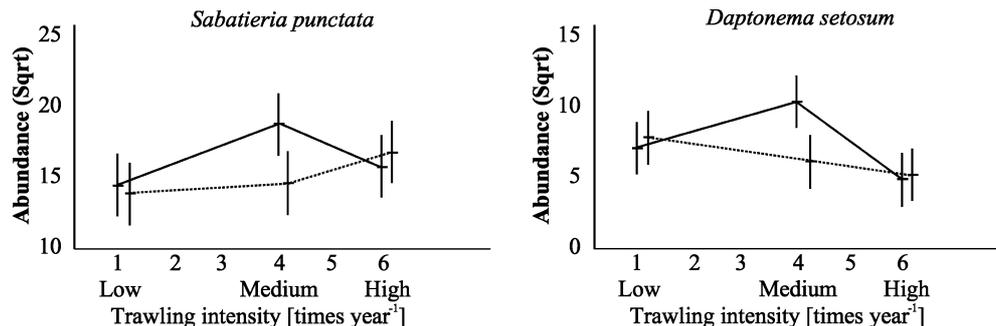


Table 7 Spearman rank correlations (ρ) between averaged nematode assemblage structure and averaged environmental variables

Variable	November 2000	April 2001
Mean particle diameter	0.236	0.232
Sorting coefficient	-0.334	-0.097
Trawling intensity	0.368	0.368
Water depth	0.296	0.157

Trawling has two major effects on the environment. First, organisms in the path of the net may be removed, killed or damaged (e.g. Bergman and van Santbrink 2000). Second, the trawl gear disturbs the sediment surface (e.g. Schwinghamer et al. 1996, 1998). The disturbance of the sediment surface may have a number of secondary sub-effects, both positive and negative. Positive effects could result from the turn-over of the sediment surface and the release of buried organic matter and nutrients in areas where populations of bioturbating macrofauna have been reduced by the direct impacts of trawling (Duplisea et al. 2001). The positive effects may have allowed populations of opportunistic nematode species such as *Sabatieria punctata* and *Aponema torosa* to proliferate. The negative effects of frequent trawling disturbance, however, appeared to be more important for most nematode species, and changes to the habitat are likely to have resulted in the reduction in species richness and the decreased abundance of otherwise abundant species such as *Richtersia inaequalis* and *Leptolaimus elegans*. Moreover, since the biomass and production of larger benthic infauna (bivalves and spatangoids) is significantly reduced in the more frequently trawled areas of the Silver Pit (Jennings et al. 2001), we reasonably expect reduced working of sediment by bioturbating macrofauna, with effects on oxygenation of sediment and carbon fluxes (Duplisea et al. 2001). These changes are also expected to influence the structure of nematode assemblages.

In contrast to the univariate analyses, multivariate analyses of the species abundance data revealed seasonal differences in the composition of nematode assemblages. In the area subject to medium disturbance, the abundance of the non-selective deposit feeders *Sabatieria punctata* and *Daptonema setosum* was higher in November 2000 than in April 2001. As typical inhabitants of muddy intertidal and subtidal sediments, both

Sabatieria spp. and *Daptonema setosum* are adapted to decreased oxygen concentrations, high organic loadings and high sulphide concentrations (Jensen et al. 1992; Hengelberg and Jensen 1993; Soetaert and Heip 1995; Soetaert et al. 1995; Vopel et al. 1996). They often persist in conditions that are unsuitable for other nematode species, such as those that live in well-oxygenated sediments (Tietjen 1980; Vopel and Arlt 1995; Somerfield et al. 1995; Boyd et al. 2000). Some nematode species, including *Prochromadorella ditlevseni* and *Actinonema pachydermatum* were consistently more abundant in the area subject to medium levels of trawling disturbance than in areas subject to lower and higher trawling intensity. This suggests that these nematode species may have been affected by local differences between sampling areas rather than the impacts of trawling, or that they were beneficiaries of intermediate levels of disturbance.

Physical characteristics of the environment, such as sediment particle size and depth, have an important influence on meiofauna community structure. The use of multiple sampling areas and sites in our study helped us to assess the extent to which the differences in nematode assemblages among sites and areas could be attributed to the physical environment. The areas subject to low, medium and high levels of trawling disturbance differed little in terms of sediment granulometry, and mean particle diameter or sorting coefficient did not account for observed differences in nematode assemblage structure. Water depth, however, did contribute to observed differences among areas in November 2000, possibly because it determined the amount or quality of phytoplankton-derived carbon reaching the seafloor. While natural processes other than bottom-trawling may cause physical disturbance to sediments (e.g. wave and tidal actions), the intensity of such disturbances is likely to decrease with increasing depth. Because our study was conducted in an area where natural physical disturbance was relatively low, it is unlikely that natural physical disturbance was responsible for the impoverished nematode fauna in the most frequently trawled area.

Both the direct and indirect effects of intensive trawling disturbance appear to have significant effects on the nematode assemblages of real fishing grounds. However, as with other large-scale studies of the effects of fishing on community structure (Hall 1999), our analyses did not allow us to distinguish between the direct and indirect effects of trawling. Moreover, it is not clear

how the observed changes in assemblage structure will affect functional processes such as production, even though meiofauna are known to be key contributors to total production in many benthic communities. Thus, while the 'standing stock' biomass of meiofauna is generally lower than that of macrofauna, total production is higher (Giere 1993) and, in undisturbed environments, meiofauna (dominated by nematodes and harpacticoid copepods, as in the present study) may consume twice the carbon, and produce four times as much carbon, as the macrofauna (Warwick and Price 1979).

Changes in biomass and production at real fishing grounds may be costly and difficult to detect, since a previously published power analysis has already shown that there was only a 65% probability of detecting an order of magnitude change in nematode biomass at the levels of replication we used (Schratzberger et al. 2002). However, our data suggest that the effects of trawling on nematode assemblages are much more subtle than those on larger macrofauna in the central North Sea (Bergman and van Santbrink 2000; Jennings et al 2001; Piet et al. 2001) and, given the high rates of recruitment and growth in meiofauna, meiofauna are expected to account for a much larger proportion of the total benthic biomass and production in heavily trawled areas.

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