Large-scale responses of nematode communities to chronic otter-trawl disturbance

Hilmar Hinz, Jan G. Hiddink, James Forde, and Michel J. Kaiser

Abstract: Nematodes, because of their small size and short life cycles, are thought to be less affected by direct trawling mortality compared with the larger macrofauna. However, nematodes may still be indirectly affected by the physical disturbance of trawling through changing sediment characteristics and food web structure. We determined whether nematode communities on two muddy fishing grounds located in the North Sea and Irish Sea were affected by chronic otter-trawl disturbance and quantified these effects. Nematode abundance, production, and genus richness declined in response to trawling within both areas. Nematode biomass did not respond to trawling intensity. Genus composition was affected by trawling only in the North Sea. The responses in abundance of individual nematode genera to increasing trawling intensity were negative as well as positive. These results indicate that despite their size and fast life cycle, nematodes are affected by intensive trawling on muddy fishing grounds. The loss in secondary production from nematodes can have far-reaching consequences for the integrity of the benthic food web. As bottom trawl fisheries are expanding into ever deeper muddy habitats, the results presented here are an important step towards understanding the global ecosystem effects of bottom trawling.

Résumé : On croit que les nématodes, à cause de leur petite taille et de leur cycle biologique court, subissent moins de mortalité directe due au chalutage que la macrofaune de plus grande taille. Cependant, les nématodes peuvent néanmoins être affectés indirectement par les perturbations physiques causées par le chalutage par la modification des caractéristiques des sédiments et de la structure du réseau alimentaire. Nous déterminons si les peuplements de nématodes sur deux aires de pêche à fond boueux dans la mer du Nord et la mer d'Irlande sont affectés par la perturbation chronique due à l'utilisation de chaluts à panneaux et nous en mesurons les effets. L'abondance, la production et la richesse générique des nématodes diminuent en réaction au chalutage dans les deux régions. La biomasse des nématodes ne change cependant pas en fonction de l'intensité du chalutage. La composition générique n'est affectée par la chatulage que dans la mer du Nord. Les variations des abondances individuelles des différents genres de nématodes en réaction à une augmentation de l'intensité du chalutage peuvent être négatives ou positives. Nos résultats indiquent donc que, malgré leur petite taille et leur cycle biologique court, les nématodes sont perturbés par le chalutage intensif sur les aires de pêche à fond boueux. La perte de production secondaire provenant des nématodes peut avoir des conséquences de longue portée sur l'intégrité du réseau alimentaire benthique. Puisque la pêche au chalut pénètre de plus en plus dans les habitats boueux plus profonds, les résultats de notre étude constituent une étape importante dans la compréhension des effets du chalutage de fond sur l'écosystème global.

[Traduit par la Rédaction]

Introduction

Towed bottom fishing gears, such as beam trawls and otter trawls, are regarded as one of the greatest and most widespread sources of anthropogenic physical disturbance to soft sediments in shelf seas (Jennings and Kaiser 1998; Bergman and van Santbrink 2000; Kaiser et al. 2006). Research over the past two decades has demonstrated that these fishing activities can have far-reaching negative effects on the biodiversity, biomass, and production of benthic communities (Jennings and Kaiser 1998). The majority of studies thus far have focussed primarily on the impacts of trawling on larger benthic macrofauna, because they are thought intrinsically vulnerable to trawl disturbance and because they are relatively easy to sample and identify. In contrast, meiofauna are considered less vulnerable to the direct physical impacts of trawling because of their size and higher intrinsic rates of productivity (Duplisea et al. 2002). Nevertheless, these smaller organisms may be affected indirectly by the physical disturbance of trawl gear through habitat disruption and changes in the macrofauna composition, abundance, and biomass. Previous studies have shown that bottom trawling can modify sediment sorting, grain size, and organic matter profiles; increase silt content; and cause loss of surficial sediment through resuspension and the winnowing of fines (Palanques et al. 2001; Brown et al. 2005; Trimmer et al.

Received 16 May 2007. Accepted 5 December 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 18 March 2008. J20005

H. Hinz,[1] J.G. Hiddink, J. Forde, and M.J. Kaiser. School of Ocean Sciences, University of Wales, Bangor, Menai Bridge, Anglesey, LL59 5AB, United Kingdom.

[1] Corresponding author (e-mail: h.hinz@bangor.ac.uk).

Can. J. Fish. Aquat. Sci. **65**: 723–732 (2008) doi:10.1139/F08-002

2005). This physical disruption of the sediments has been demonstrated to ultimately result in a loss of habitat quality for benthic organisms (Watling et al. 2001).

In marine sediments, nematodes are usually numerically dominant and account for 60%–95% of the total meiofauna (Coull 1999). The entire life cycle of many meiofauna can be completed in a matter of weeks (Gee and Warwick 1984), resulting in a much higher production to biomass ratio of meiofauna compared with macrofauna. Thus, despite their negligible biomass, meiofauna can make an important contribution to overall benthic productivity (Alongi and Robertson 1995; Schwinghamer et al. 1998). Meiofauna feed upon bacteria, detritus, diatoms, and algal mats and represent an important source of food for higher trophic levels, such as macrofauna and fish (Coull 1999). In addition, meiofauna have been shown to indirectly affect the microbiota by stimulating bacterial growth and consequently enhance rates of mineralization and nutrient regeneration (Heip et al. 1985). While nematodes are an important ecosystem component in all habitats, they are probably more active in sediments with high amounts of organic matter, such as muddy sediments (Coull 1999).

Little research has been conducted on the response of meiofaunal communities to fishing (Engel and Kvitek 1998; Pranovi et al. 2000; Schratzberger and Jennings 2002) despite their ecologically important role to marine food webs (Gerlach 1971, 1978). For ecosystem-based approaches to fisheries management (Link 2002), the effects of fishing on meiofauna need consideration.

To understand the effects of trawling disturbance at the scale of the fishery, it is necessary to study areas subjected to real fisheries where disturbance occurs on large scales over long time periods. Within the present study, we investigated if nematode communities were affected by chronic otter-trawl disturbance and quantified the response of nematode abundance, biomass, production, and genus composition to chronic otter-trawling. The effects of otter-trawling were investigated at a scale relevant to fishery management with a much higher level of replication than earlier comparative studies, which has been made possible by the advent of high resolution over-flight and satellite monitoring of fishing vessels. We compared the impact of otter trawling on two muddy fishing grounds in the North Sea (Fladen Ground) and the Irish Sea (off the Cumbrian coast) separated by approximately 800 km. Such regional comparisons are useful because they highlight the generality of responses to similar agents of disturbance at a regional scale.

Materials and methods

Study areas

The long-term effects of chronic trawling on benthic meiofauna was investigated in two fishing grounds located in the North Sea (Fladen Ground, Fig. 1*b*) and Irish Sea (off the Cumbrian coast, Fig. 1*c*). The main bottom trawling activity that occurs on both fishing grounds is otter-trawling for gadoid fish and Norway lobster (*Nephrops norvegicus*). In addition, shrimps of the genus *Pandalus* are targeted on the Fladen Ground. The fisheries in both areas operate mainly in spring and early summer. The offshore fishery of the Fladen Ground generally consists of fishing vessels of over 24 m in length that operate for more than a day at a time. In the Irish Sea, because of the proximity to the coast, vessels tend to be day boats under 20 m in length. Both areas are characterized by mild hydrodynamic conditions and consequently comprise muddy sediment deposits with a high silt and clay content (>50%). The areas were selected for investigation because they were of a similar habitat type and had a strong spatial gradient in trawling intensities (Table 1).

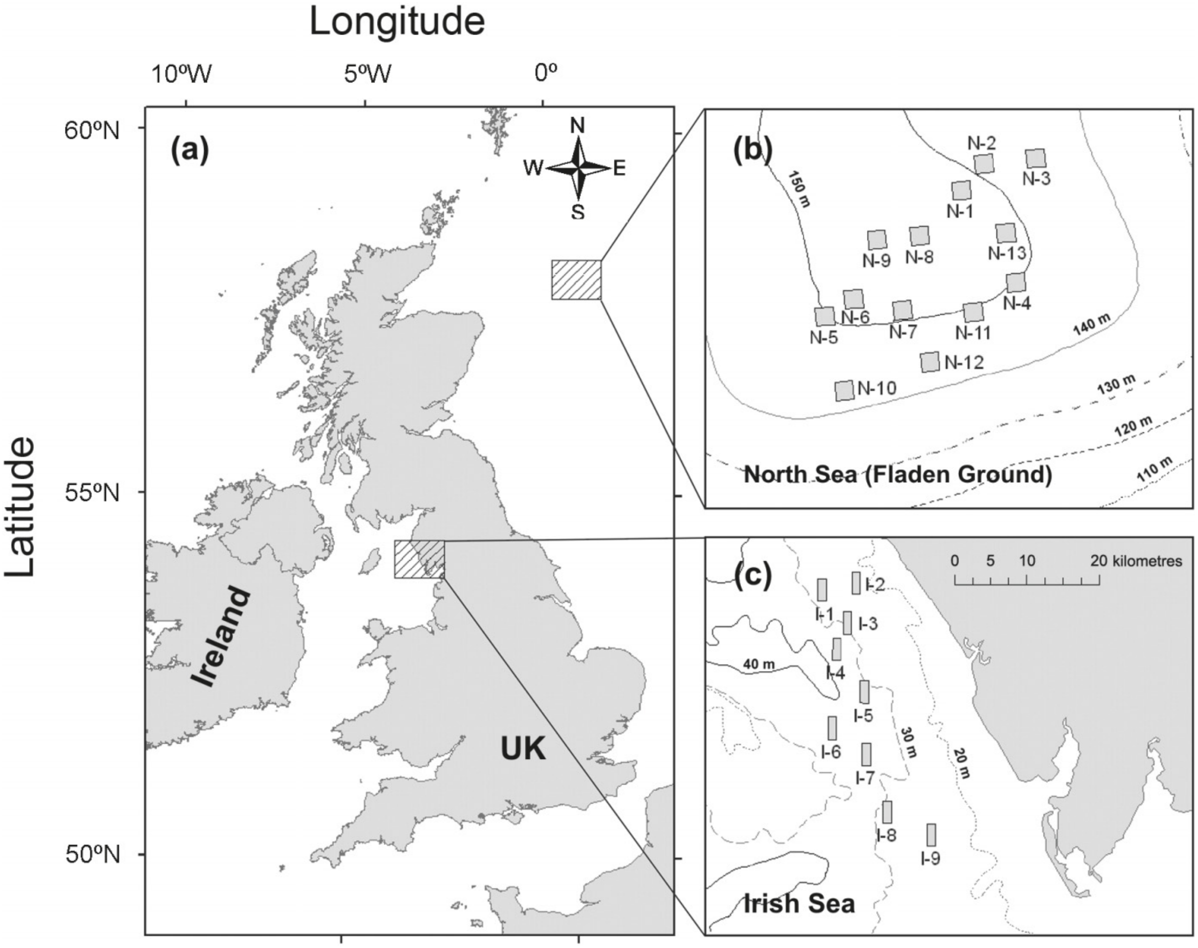
Estimation of fishing effort

The estimation of trawling intensities over the two respective fishing grounds was based on different data sources and therefore required different methodologies. In the North Sea, satellite data from the European Community Vessel Monitoring System (VMS) was used to calculate fishing effort. Vessels over 24 m are required to report their location via satellite at 2 h intervals. Only vessels that undertake fishing trips under 24 h or that exclusively fish within 12 nautical miles (1 nautical mile = 1.852 km) of the shoreline are exempted (Dann et al. 2002). The operational status of vessels (e.g., fishing, steaming, or stationary) was identified from two consecutive positions. Vessels travelling at a speed over 8 knots (1 knot = 1.852 $km \cdot h^{-1}$) were considered to be steaming and were excluded from the analysis. Similarly, stationary vessels were eliminated as they were assumed not to be fishing. The spatial distribution of fishing vessels was processed within a GIS, and fishing frequency was calculated on a scale of 9 km^2 cells over the extent of the fishing ground. For calculations of trawling intensities, as times trawled per year, an average trawling speed of 2.5 knots and an average gear width of 60 m for otter trawls was used. Trawling intensities on the Fladen Ground were calculated for the period from July 2000 to December 2003. Sampling of the nematode communities on the Fladen Ground was carried out in June 2004.

Owing to the exemption of certain fishing vessels to the reporting process of positional information (see above), VMS data were not available for the fleet operating in the Irish Sea. Almost the entire area of the fishing ground is located within the 12 nautical mile limit, and fishing vessels are below the minimum size for which VMS is mandatory. To estimate fishing effort, over-flight data and logbook records of hours spent fishing per ICES rectangle collected by the UK's Sea Fisheries Inspectorate were used. Spotter planes regularly survey the UK's Exclusive Economic Zone to monitor UK and foreign fishing vessels. Flights over the Irish Sea occur on a weekly basis and record the geographical position, gear type, and activity of fishing vessels indiscriminate of vessel size. From these data, the spatial distribution of active fishing vessels fishing with relevant bottom gears was established for a 5-year period from October 2000 to October 2004. Sampling of the nematode communities off the Cumbrian coast was carried out in November 2004.

As the spatial resolution of this data largely depends on the number of flights conducted, data density is much lower compared with the virtually continuous reported VMS data. Hence, for detailed spatial coverage, it was required to monitor the fishing fleet for a longer period in the Irish Sea. Density of vessels was calculated for 1 km^2 grid cells, with a search radius of 3 km (see Mitchell 1999 for details on density calculations). For the estimation of fishing frequency as

Fig. 1. (*a*) Maps showing the locations of the two areas and the spatial distribution of sampling sites in (*b*) the North Sea (Fladen Ground) and (*c*) the Irish Sea.



times trawled·year^{-1}, the spatial data were combined with data from logbook entries. UK fishermen are by law required to report by gear type and how many hours they spent fishing within ICES rectangles. Thus, the total time reported bottom trawling over the fishing ground (ICES rectangle 37 E6) for the relevant period was divided proportionally to the vessel density information in the 1 km^2 cells. This calculation resulted in cell values of hours fished, which were converted to times trawled·year^{-1} assuming a trawling speed of 2.5 knots and a gear width of 60 m.

Sampling design

Thirteen stations were chosen in the North Sea to cover the maximum possible range of fishing intensities (Fig. 1, Table 1). Each station was designated as a box of 2.5 km × 2.5 km. Five haphazardly distributed 0.1 m^2 Day grabs were taken within each box to sample nematode communities. From each grab, a sample was taken for analysis with a cut-off syringe (1.58 cm^2, approximately 3 cm deep; De Wilde et al. 1986). The samples from the five Day grabs were pooled before analysis to integrate spatial variation in nematode distribution and preserved in 4% buffered formalin solution. Additionally, from all five grabs a sediment sample with a cut-off syringe (1.58 cm^2, ≈6 cm deep) was taken and pooled for spatial integration. Nine sampling stations, 1 km × 2 km boxes, were selected in the Irish Sea to cover the maximum possible range of fishing intensities (Fig. 1, Table 1). At three haphazardly chosen locations within each box, three 0.1 m^2 Day grabs were taken. Using a syringe corer (1.58 cm^2, ≈3 cm deep), three cores were taken at random points within each grab and pooled to integrate spatial variation of meiofaunal distribution on a centimetre scale and preserved in 4% buffered formalin solution for pending laboratory analyses. A single sediment sample was taken from each sampling site within sampling boxes using a cut-off syringe (1.58 cm^2, ≈6 cm deep).

Nematode sample processing and biomass and production estimates

For both areas, the same protocol was followed for sample processing and biomass and production estimates. Meiofauna were extracted from the samples using the method described by Somerfield and Warwick (1996). Nematodes were the dominant meiofaunal taxon (80%–95%) in the samples. Owing to the large number of replicate samples within this study, we identified only 40 randomly selected nematodes to genus level per sample to estimate genus richness for each box (Platt and Warwick 1998*a*, 1998*b*; Warwick et al. 1998). As the main focus of this study was on the broad-scale response of nematode communities to trawling disturbance, a

Table 1. Characteristics of study areas.

Station ID	Station area (km × km)	No. of samples	Trawling frequency (year^{-1})	Depth (m)	Sediment content (%)			Bed shear stress (N·m^{-2})
					Silt	Organic	Water	
North Sea								
N-1	2.5 × 2.5	5	1.59	151	95	6	48	0.08
N-2	2.5 × 2.5	5	3.81	151	96	7	47	0.08
N-3	2.5 × 2.5	5	1.74	150	95	7	47	0.08
N-4	2.5 × 2.5	5	1.17	150	93	7	47	0.08
N-5	2.5 × 2.5	5	0.45	145	93	6	41	0.10
N-6	2.5 × 2.5	5	0.21	146	95	6	44	0.09
N-7	2.5 × 2.5	5	0.79	151	95	6	44	0.09
N-8	2.5 × 2.5	5	1.74	150	95	7	45	0.08
N-9	2.5 × 2.5	5	1.52	148	95	7	48	0.08
N-10	2.5 × 2.5	5	0.26	143	94	5	40	0.11
N-11	2.5 × 2.5	5	1.09	150	95	6	45	0.09
N-12	2.5 × 2.5	5	0.86	150	93	6	43	0.09
N-13	2.5 × 2.5	5	1.80	153	97	7	47	0.08
Irish Sea								
I-1	1 × 2	3	7.52	31	56	5	39	0.22
I-2	1 × 2	3	7.35	26	54	5	40	0.24
I-3	1 × 2	3	10.16	29	70	6	42	0.21
I-4	1 × 2	3	11.81	36	86	6	44	0.21
I-5	1 × 2	3	17.09	31	82	7	42	0.19
I-6	1 × 2	3	10.34	36	61	5	38	0.19
I-7	1 × 2	3	12.06	34	71	7	40	0.17
I-8	1 × 2	3	1.85	28	74	6	46	0.18
I-9	1 × 2	3	1.66	24	77	6	41	0.23

high number of replicates over a large spatial scale was deemed more important than high taxonomic precision. Furthermore, 40 nematodes in each sample were randomly selected for the calculation of biomass (wet mass, WM) and measured under a microscope using an eyepiece graticule, according to Andrassy (1956): wet weight = (length × width^2) × 1 600 000^{-1}, where WM is in micrograms and length and width are in micrometres. If the nematodes had a long, filiform tail, the tail was not included in the measurement. Nematode production was estimated using the following equations (Vranken et al. 1986):

$$\log T_{\min} = 2.202 - 0.0461t + 0.627 \log W$$

$$\text{production:biomass ratio} = 1/T_{\min}3D$$

where $T_{\min}$ is the duration of egg to hatch development (days), t is bottom temperature, W is body weight (µg WM), and D is number of days in a year. The average yearly bottom temperature was 7.3 °C on the Fladen Ground and 10 °C on the fishing ground of the Cumbrian coast (ICES Oceanographic Database and Services: www.ices.dk/ocean/dotnet/HydChem/HydChem.aspx; North Sea data 1980–1986 and Irish Sea data 1986–2004). Nematode WM was converted to ash-free dry mass (AFDM) using the conversion factor 1g WM = 0.2 g AFDM (Heip et al. 1985). Although the $T_{\min}$ estimate is based on adult female body weight (Vranken et al. 1986), we used the equations to calculate production for individual nematodes regardless of sex and maturity stage. Nematodes mature early and as there are only small differences between male and female body weight, this seems unlikely to have caused substantial bias in our production estimates.

Sediment samples and bed shear stress

The fraction of particles <63 µm (i.e., mud (silt and clay)) was determined by weight loss following wet-sieving, while coarser fractions were determined by mechanical dry-sieving through stacked Wentworth grade sieves (Holme and McIntyre 1984). Prior to sieving sediment, percent water content of sediment samples was estimated via weight loss after drying to a constant weight at 70 °C. Organic matter content was estimated by weight loss of ≈5 g of dried sediments on ignition at 550 °C for 6 h (Holme and McIntyre 1984).

Bed shear stress was calculated from a two-dimensional hydrodynamic model of the northwest European shelf. For more detailed information on the methodology used, see Hiddink et al. (2006).

Statistical analysis

To investigate the relationship between trawling frequency (year^{-1}) and environmental parameters measured at stations (depth, silt–clay content, organic content, water content, and shear stress), a Pearson correlation analysis was performed for each area. Prior to analysis, all variables were $\log_{10}(n + 1)$-transformed so that the data approximated normality.

The relationship of trawling frequency (year^{-1}) and nematode abundance (m^{-2}), biomass (g WM·m^{-2}), production (g AFDM·m^{-2}·year^{-1}), and genus richness was investigated on the combined data from North Sea and Irish Sea using a

Table 2. Pearson's correlation coefficients (r) and p values (in parentheses) of the correlations between sediment parameters and trawling frequency for the North Sea and Irish Sea study areas.

Parameter	Silt and clay content (%)	Organic content (%)	Water content (%)	Shear stress ($N \cdot m^{-2}$)	Trawling frequency ($year^{-1}$)
North Sea					
Depth	0.51 (0.079)	0.64 (0.019)*	0.74 (0.004)*	–0.81 (0.001)*	0.73 (0.005)*
Silt and clay content		0.38 (0.204)	0.53 (0.065)	–0.47 (0.110)	0.55 (0.053)
Organic content			0.78 (0.002)*	–0.88 (0.000)*	0.75 (0.003)*
Water content				–0.95 (0.000)*	0.76 (0.003)*
Shear stress					–0.78 (0.002)*
Irish Sea					
Depth	0.16 (0.685)	0.01 (0.969)	–0.08 (0.823)	–0.58 (0.104)	0.64 (0.061)
Silt and clay content		0.83 (0.005)*	0.73 (0.025)*	–0.36 (0.348)	0.16 (0.680)
Organic content			0.56 (0.115)	–0.34 (0.375)	0.43 (0.248)
Water content				–0.27 (0.485)	–0.09 (0.819)
Shear stress					–0.32 (0.394)

*Significant at $p = 0.05$.

generalized linear model. Univariate community descriptors were assigned as dependant variables, while trawling frequency and location (North Sea, Irish Sea) were assigned as independent variables in the analysis. Both main effects and interaction terms were analysed. Prior to analysis, all variables were $\log_{10}(n + 1)$-transformed.

The response in abundance of individual nematode taxa to trawling intensities was investigated using least square regression analysis. The analysis was performed on $\log_{10}(n + 1)$-transformed abundance ($n \cdot m^{-2}$) and trawling frequency ($year^{-1}$) data. The number of genera responding in the same way in both the North Sea and Irish Sea was analysed by the Fisher exact test to establish if the number of taxa showing a similar response was significantly greater than would have been expected by chance ($p = 0.05$).

To examine the effect of trawling on community composition within the two areas, we used nonparametric multidimensional scaling (MDS) on nematode abundance data (Primer version 6). The analyses were performed on square-root transformed Bray–Curtis percent similarity matrices (Clarke and Warwick 1994). The resulting MDS plots were overlaid with bubble plots of trawling intensity to visualize possible patterns in the community ordinations. Furthermore, the data was tested for seriation to detect any directional trends in community pattern related to trawling intensity (Primer version 6 RELATE routine). The BIOENV routine was used to test which individual or combination of environmental parameters had the strongest relationship with the ordination of nematode abundance data in both areas. (Primer version 6 BIOENV routine).

Results

Trawling frequency and environmental parameters

In the Fladen Ground, trawling frequency was correlated to all but one of the measured environmental variables. Depth, organic content, and water content of the sediment were positively correlated to trawling frequency, while seabed shear stress was negatively correlated to trawling frequency (Table 2). There was no significant relationship between trawling frequency and the silt–clay content of the sediment (Table 2). In the Irish Sea, no significant correlation between trawling frequency and sediment variables existed (Table 2).

Nematode communities

In the North Sea and Irish Sea, 31 and 27 genera of nematodes were identified, respectively. The numerically most abundant nematode genera on the Fladen Ground were *Sabatieria*, *Aponema*, *Cyartonema*, and *Calomicrolaimus*. On the fishing ground in the Irish Sea, *Sabatieria*, *Aponema*, *Halalaimus*, and *Sphaerolaimus* were the most dominant genera. Nematode abundance, biomass, and production were over two times higher in the Irish Sea than in the North Sea (Fig. 2). Bottom trawling had a significant negative effect on nematode abundance, production, and genus richness in both areas (Table 3; Figs. 2*a*, 2*c*, 2*d*). Based on the results of the regression slopes in Fig. 2, a tenfold increase in trawling intensity from 1 to 10 $year^{-1}$ lead to a decrease in nematode abundance of 23.7% in the Irish Sea and 25.8% in the North Sea. Similarly, production was reduced by 25.7% and 16.3%, respectively. A tenfold increase in trawling intensity lead to a decrease in genus richness in the Irish Sea of 11.6%, while in the North Sea it decreased by 50.3%.

No significant effect of trawling frequency on nematode biomass was detected (Table 3, Fig. 2*b*). The interaction between trawling and area was significant for biomass and genus richness, indicating that the response to trawling within the two areas differed (Table 3, Fig. 2*d*).

In the North Sea, for three of the genera that were found in both areas, a significant response to trawling was detected. *Aponema* and *Sabatieria* had a positive response to increasing trawling frequency, while *Halalaimus* showed a negative response. The genera *Calomicrolaimus* and *Cyartonema*, which were not shared but were numerically important genera on the Fladen Ground, showed the following response: *Calomicrolaimus* (slope = –0.078; $r^2 = 0.66$; $p = 0.001$) and *Cyartonema* (slope = –0.002; $r^2 = 0.01$; $p = 0.906$). In the Irish Sea, three genera demonstrated a significant negative response to trawling: *Leptolaimus*, *Microlaimus*, and *Richtersia* (Table 3). Overall, 14 of the 20 showed obvious trends in response to trawling, most of

Fig. 2. The relationship between (*a*) abundance, (*b*) biomass, (*c*) production, and (*d*) genus richness with trawling frequency for nematodes. Significant regression lines are drawn (p = 0.05). Open circles indicate North Sea data; solid circles are data from the Irish Sea.

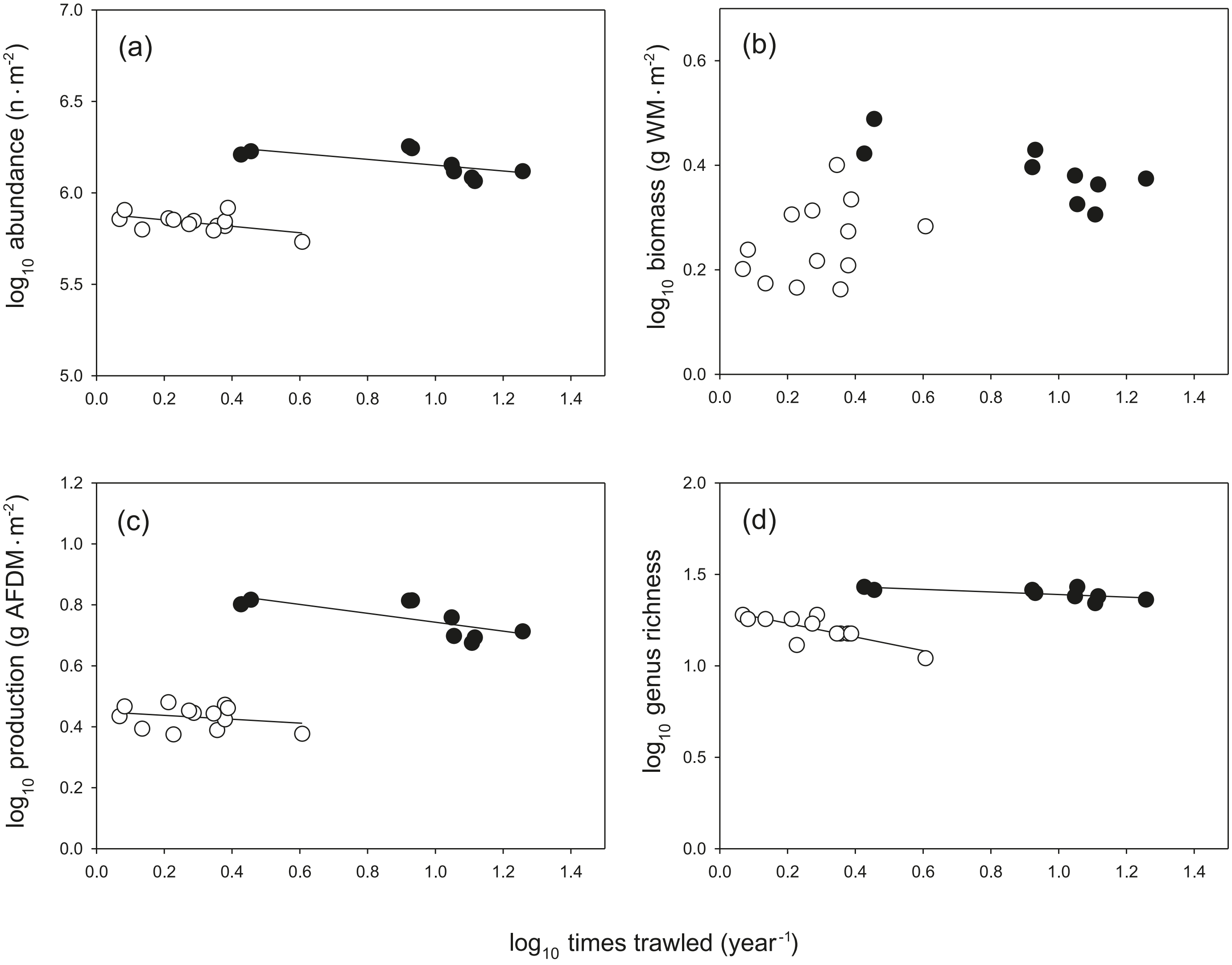


Table 3. Results of the generalized linear model analyses of the combined data from the North Sea and Irish Sea.

Dependant variable	Effect	$F_{[1,18]}$	p
$\log_{10}$ abundance ($n \cdot m^{-2}$)	Area	40.84	<0.001*
	$\log_{10}$ times trawled ($year^{-1}$)	8.89	0.008*
	Area × $\log_{10}$ times trawled ($year^{-1}$)	0.01	0.973
$\log_{10}$ biomass (g WM·m^{-2})	Area	15.28	0.001*
	$\log_{10}$ times trawled ($year^{-1}$)	0.01	0.924
	Area × $\log_{10}$ times trawled ($year^{-1}$)	5.23	0.034*
$\log_{10}$ production(g AFDM·m^{-2})	Area	66.26	<0.001*
	$\log_{10}$ times trawled ($year^{-1}$)	5.46	0.031*
	Area × $\log_{10}$ times trawled ($year^{-1}$)	1.12	0.383
$\log_{10}$ genus richness	Area	8.55	0.009*
	$\log_{10}$ times trawled ($year^{-1}$)	24.21	<0.001*
	Area × $\log_{10}$ times trawled ($year^{-1}$)	10.21	0.005*

Note: Dependant variables: univariate community descriptors (abundance, biomass, production, and genus richness). Independent variables: area (North Sea, Irish Sea) and fishing frequency (times trawled·$year^{-1}$). WM, wet mass; AFDM, ash-free dry mass; *, significant at p = 0.05.

which were in a similar direction. However, the number of genera that responded in a similar direction to trawling was not significantly higher than expected by chance (Fisher's exact test; $p = 0.17$).

The MDS plots of the North Sea and the Irish Sea overlaid with trawling intensity as bubble plots only revealed a directional pattern for the North Sea (Fig. 3), which was confirmed by the seriation test (North Sea: $\rho = 0.42$, $p < 0.001$; Irish Sea: $\rho = 0.18$, $p = 0.24$). The BIOENV analysis of the North Sea showed that the ordination of the nematode community was best explained by four variables: trawling frequency, depth, silt–clay, and organic content of the sediment ($\rho_w = 0.452$), while the single factor that best explained the observed variation was trawling frequency, with a ρ_w of 0.418. The ordination of the Irish Sea data was best explained by two factors: bed shear stress and trawling frequency ($\rho_w = 0.313$). The single factor that best explained the observed variation was shear stress, with a ρ_w of 0.253 (trawling frequency $\rho_w = 0.178$).

Discussion

Chronic bottom trawling had a significant negative effect on nematode abundance, production, and genus richness within both study areas in the North Sea and Irish Sea. However, no significant response to trawling was detected for nematode biomass. Genus richness was more strongly affected by trawling in the Fladen Ground than in the Irish Sea. The reason for this difference is not clear, but could be related to an overall different community structure of the area surveyed in the Irish Sea. The sites investigated in the Irish Sea, compared with the ones in the North Sea, are exposed to higher shear stresses and thus may have favoured nematode species already tolerant to higher natural disturbance levels. Results of the multivariate analyses indicated that the community structure on a genus level was affected by trawling frequency in the North Sea but not in the Irish Sea.

The responses of individual nematode genera to trawling were not more similar between the two areas than could be expected by chance. Nevertheless, some similarities that were detected are further supported by the findings of previous studies. The abundance of the nematodes *Sabatieria* and *Aponema* increased significantly with trawling frequency in the North Sea, and similar trends, however nonsignificant, were detected in the Irish Sea. Earlier studies also have shown that these species increase under trawling disturbance (Schratzberger and Jennings 2002; Schratzberger et al. 2002). *Halalaimus* and *Calomicrolaimus* abundance was negatively affected by trawling in the North Sea, while in the Irish Sea *Halalaimus* was found to be unaffected by trawling. The negative response of *Halalaimus* to disturbance has not been documented before; on the contrary, *Halalaimus* seemed to thrive in disturbed sediments in microcosms (Schratzberger and Warwick 1998). A plausible explanation to these opposing findings has not been found to date. *Microlaimus* and *Richtersia* showed significant negative responses to trawling in the Irish Sea, and similar trends were observed for the North Sea (although not significant). *Microlaimids* are typically found in undisturbed sediments (Schratzberger and Warwick 1998) and are vulnerable to trawling effects (Schratzberger et al. 2002). Schratzberger et al. (2000) speculated that the negative effects of fishing on *Micolaimus* might be related to limited ability to migrate upwards when buried by sediment disturbance. Schratzberger and Jennings (2002) also recorded a negative response of *Richtersia* to trawling.

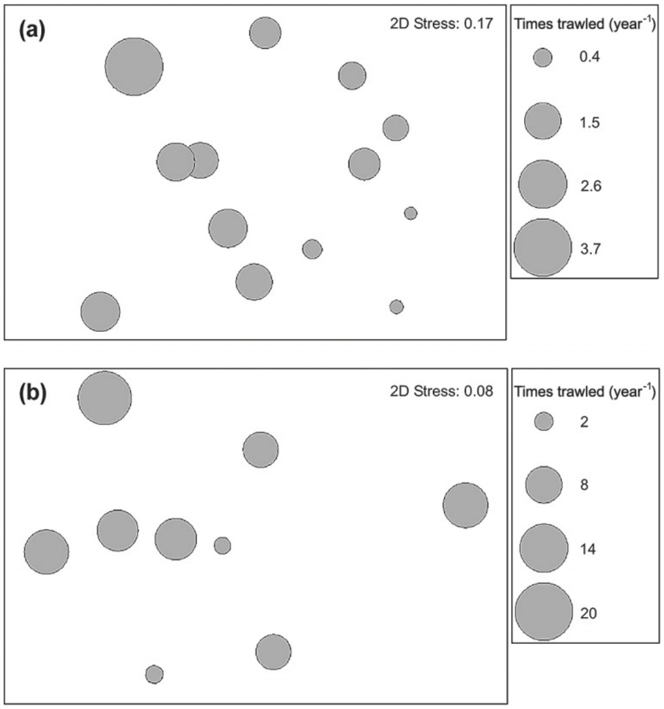


Fig. 3. Multidimensional scaling plot of nematode abundance data in (*a*) the North Sea and (*b*) the Irish Sea. Bubble sizes represent fishing intensities (times trawled·year^{-1}).

The mechanisms by which chronic trawling disturbance affects nematode communities are thus far not fully understood; however, they are most likely to be complex, and individual species can be expected to respond to different aspects of change induced by trawling. Owing to their small size, direct mortality from the physical impact of the trawling gear is unlikely to be important. Nevertheless, trawling may affect nematodes indirectly through affecting sediment composition and biological properties (e.g., biofilms on sediment particles) (Watling et al. 2001). Nematodes live in the interstitial spaces between sediment grains and therefore are thought to be susceptible to changes in sediment chemistry and composition. Trawling correlated positively with the water content of the sediment in the North Sea; this implied that the porosity of the sediment was greater under conditions of more intense trawling. These changes in sediment composition may have affected the nematode communities in the North Sea. Similar changes with increased trawling intensity were not detected in the Irish Sea, which might be related to the higher current regime within this area masking such changes. Generally, mixing of sediments and settling of resuspended matter following trawling disturbances can cause a vertical redistribution of sediment layers, which may have both positive and negative effects on nematodes (Mayer et al. 1991). Positive effects may arise from the re-release of buried organic material and nutrients from the redistribution of sedi-

Table 4. Linear relationships between nematode abundance and trawling frequency (times trawled·year^{-1}) for the genera that occurred within both areas in the North Sea and Irish Sea.

	North Sea			Irish Sea		
Taxon	Slope	r^2	p	Slope	r^2	p
Aponema	**0.065**	**0.46**	**0.006***	**0.025**	**0.05**	**0.276**
Axonolaimus	–0.009	0.00	0.555	–0.009	0.00	0.502
Daptonema	0.008	0.00	0.716	0.006	0.00	0.654
Desmoscolex	–0.011	0.00	0.335	0.008	0.00	0.567
Dorylaimopsis	0.007	0.00	0.728	–0.011	0.00	0.530
Halalaimus	**–0.042**	**0.35**	**0.019***	**0.005**	**0.00**	**0.591**
Laimella	–0.027	0.21	0.061	–0.005	0.00	0.462
Leptolaimus	**–0.021**	**0.02**	**0.288**	**–0.037**	**0.60**	**0.009***
Marylynnia	0.006	0.00	0.586	0.001	0.00	0.926
Mesacanthion	–0.006	0.00	0.727	–0.010	0.01	0.325
Microlaimus	**–0.012**	**0.14**	**0.114**	**–0.040**	**0.68**	**0.004***
Odontophora	0.026	0.06	0.208	–0.024	0.00	0.342
Paramesacanthion	0.041	0.16	0.095	–0.025	0.05	0.271
Richtersia	**–0.003**	**0.00**	**0.836**	**–0.042**	**0.56**	**0.013***
Sabatieria	**0.059**	**0.48**	**0.005***	**0.042**	**0.37**	**0.050**
Sphaerolaimus	–0.019	0.00	0.329	–0.026	0.28	0.084
Spirinia	–0.019	0.08	0.175	–0.012	0.09	0.227
Stephanolaimus	–0.018	0.11	0.146	–0.009	0.00	0.573
Terschellingia	–0.002	0.00	0.899	–0.035	0.15	0.163
Viscosia	–0.022	0.21	0.064	0.003	0.00	0.754

Note: Taxa showing a significant response in one of the two study areas are in bold type. *, significant at $p = 0.05$.

ments (Duplisea 2000), and species that are able to utilize this surplus of organic material may benefit. For example, the increase in abundance of *Sabatieria* with increasing trawling frequency, a nonselective deposit-feeder (Wieser 1953), may be explained by this. Similarly, increased organic loading of the sediment may lead to a shift towards microbial-dominated, anaerobic food chains (Brown et al. 2005), allowing only nematode species adapted to these conditions to survive. Furthermore, to understand the mechanics of chronic trawl disturbance on nematodes, the interdependence of bacteria and meio- and macro-faunal components in the benthic food web need to be acknowledged. Meiofauna and to some extend macrofauna depend on bacterial productivity, which in turn depends on the activity of the animals themselves, creating suitable conditions for bacterial growth (Gerlach 1978). Burrowing activities of meio- and macrofauna oxygenates the sediment, while their feeding activity fractionates larger organic particles in the form of faecal pellets, a substratum for bacterial growth. In addition, more sophisticated interactions exist in the form of species directly "gardening" bacterial growth (Gerlach 1978). Owing to this interdependence in benthic food webs, negative effects upon one faunal component can be expected to have an effect on the others. The direct, negative effect of trawling on macrofauna communities (Jennings and Kaiser 1998) thus may have an indirect negative effect upon nematodes by decreasing the suitability of the habitat to bacterial growth and thus ultimately food availability.

Overall nematode abundance, biomass, production, and the number of genera, as well as trawling frequency, was higher in the Irish Sea compared with the North Sea. The overall difference in the standing stock of nematodes within these two areas is most likely related to two possible factors: differences in local food supply and sampling in different seasons in the two areas. The Fladen Ground in the North Sea is characterized by relatively low primary productivity of 90–100 g C·m^{-2}·year^{-1} (De Wilde et al. 1986), while annual primary production off Cumbria is estimated at approximately 160 g C·m^{-2}·year^{-1} (K. Kennington, Scottish Environment Protection Agency, Clearwater House, Research Avenue North, Heriot Watt Research Park, Riccarton, Edinburgh EH14 4AP, United Kingdom, email: Kevin.Kennington@sepa.org.uk, personal communication). The higher primary production in the Irish Sea may at least partly explain the higher number and biomass of nematodes in the Irish Sea. On the Fladen Ground, sampling occurred during June when meiofauna abundances reach their seasonal low in this area (Faubel et al. 1983). In June, abundances are about half of those reached in December (seasonal peak). Sampling in the Irish Sea took place in November, and assuming a similar seasonal cycle for the meiofauna as for the Fladen Ground, meiofauna abundances may have been near their seasonal high, thus contributing to the differences observed between the two areas.

The results of this study clearly demonstrate that despite their small size and fast life cycle, nematodes are negatively affected by chronic trawling disturbance. Nematodes are thus not able to compensate for the loss in production by larger macrofauna as previously suggested (Jennings et al. 2001). Secondary production is thus further reduced by chronic trawling, with far-reaching consequences to the integrity of the benthic food web. Reductions within these groups may alter the pattern of energy flow through the marine ecosystem. Owing to the interdependence of bacteria and meiofauna and macrofauna production, the fate of unutilized benthic resources (such as particulate organic matter) in areas heavily defaunated by trawling remains unclear and needs further investigation.

As muddy seabeds cover over 50% of the earth's surface (Gage and Tyler 1991) and bottom trawl fisheries are expanding into ever deeper muddy habitats, the results presented in this paper are an important step towards understanding and assessing the global ecosystem effects of bottom trawling.

Acknowledgements

This study was funded by the Department for Environment, Food and Rural Affairs (DEFRA) under contract MF0731 and by the European Union as part of the project "Response", contract QLRT-2001-00787. The VMS were provided by for the North Sea by DEFRA in a raw, uninterpreted form. Overflight data for the Irish Sea was provided by DEFRA. Paul Eastwood and Craig Mills (Centre for Environment, Fisheries and Aquaculture Science (CEFAS)) are thanked for supplying the VMS data. The officers and crew of RV *Prince Madog*, Ivor Rees, Marika Galanidi, Femke van Gent, Heidi Tillin, Kathryn Barker, and Jo Gascoigne are thanked for their help in collecting samples. We also thank Andy Yule for the use of his microscope. Shear stress data for the North Sea were provided by John N. Aldridge (CEFAS) and for the Irish Sea by Alan Elliott (University of Bangor, Wales).

References

Alongi, D.M., and Robertson, A.I. 1995. Factor regulating benthic food chains in tropical river deltas and adjacent shelf areas. Geo-Mar. Lett. **15**: 145–152.

Andrassy, I. 1956. Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta. Zool. **2**: 1–14.

Bergman, M.J.N., and van Santbrink, J.W. 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. ICES J. Mar. Sci. **57**: 1321–1331.

Brown, E.J., Finney, B., Dommisse, M., and Hills, S. 2005. Effects of commercial otter trawling on the physical environment of the southeastern Bering Sea. Cont. Shelf. Res. **25**: 1281–1301.

Clarke, K.R., and Warwick, R.M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council (NERC), Plymouth Marine Laboratory, Plymouth, UK.

Coull, B.C. 1999. Role of meiofauna in estuarine soft-bottom habitats. Austral. Ecol. **24**: 327–343.

Dann, J., Millner, R., and De Clerck, R. 2002. Alternative uses of data from satellite monitoring of fishing vessel activity in fisheries management: II. Extending cover to areas fished by UK beamers. Report of EC Project 99/002.

De Wilde, P.A.W.J., Berghuis, E.M., and Kok, A. 1986. Biomass and activity of benthic fauna on the Fladen Ground (Northern North-Sea). Neth. J. Sea. Res. **20**: 313–323.

Duplisea, D.E. 2000. Benthic organism biomass size-spectra in the Baltic Sea in relation to the sediment environment. Limnol. Oceangr. **45**: 558–568.

Duplisea, D.E., Jennings, S., Warr, K.J., and Dinmore, T.A. 2002. A size-based model of the impacts of bottom trawling on benthic community structure. Can. J. Fish. Aquat. Sci. **59**: 1785–1795.

Engel, J., and Kvitek, R. 1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. Conserv. Biol. **12**: 1204–1214.

Faubel, A.E., Hartwig, E., and Thiel, H. 1983. On the ecology of the benthos of sublittoral sediments, Fladen Ground, North Sea. Meteor Forschergeb. **D36**: 105–112.

Gage, J.D., and Tyler, P.A. 1991. Deep-sea biology — a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, UK.

Gee, J.M., and Warwick, R.M. 1984. Preliminary observations on the metabolic and reproductive strategies of harpacticoid copepods from an intertidal sandflat. Hydrobiologia, **61**: 32–41.

Gerlach, S.A. 1971. On the importance of marine meiofauna for benthos communities. Oecologia, **6**: 176–190.

Gerlach, S.A. 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia, **33**: 55–69.

Heip, C., Vincx, M., and Vranken, G. 1985. The ecology of free-living nematodes. Oceanogr. Mar. Biol. Annu. Rev. **23**: 399–489.

Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E., and Piet, G.J. 2006. Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Can. J. Fish. Aquat. Sci. **63**: 721–736.

Holme, N.A., and McIntyre, A.D. 1984. Methods for the study of marine benthos. Blackwell Scientific Publications, Oxford, UK.

Jennings, S., and Kaiser, M.J. 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. **34**: 201–352.

Jennings, S., Dinmore, T.A., Duplisea, D.E., Warr, K.J., and Lancaster, J.E. 2001. Trawling disturbance can modify benthic production processes. J. Anim. Ecol. **70**: 459–475.

Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J., and Karakassis, I. 2006. Global analysis and prediction of the response of benthic biota to fishing. Mar. Ecol. Prog. Ser. **311**: 1–14.

Link, J.S. 2002. Ecological considerations in fisheries management: When does it matter? Fisheries, **27**: 10–17.

Mayer, L.M., Schick, D.F., Findlay, R.H., and Rice, D.L. 1991. Effects of commercial dragging on sedimentary organic-matter. Mar. Environ. Res. **31**: 249–261.

Mitchell, A. 1999. The Esri guide to GIS analysis. Vol. 1. Geographic patterns and relationships. Environmental Systems Research Institute, Inc., Redlands, Calif.

Palanques, A., Guillen, J., and Puig, P. 2001. Impact of bottom trawling on water turbidity and muddy sediment of an unfished continental shelf. Limnol. Oceangr. **46**: 1100–1110.

Platt, H.M., and Warwick, R.M. 1998*a*. Free living marine nematodes. Part I. British enoplids. Cambridge University Press, Cambridge, UK.

Platt, H.M., and Warwick, R.M. 1998*b*. Free living marine nematodes. Part II. British chromadorids. E.J. Brill/W. Backhuys, Leiden, The Netherlands.

Pranovi, F., Raicevich, S., Franceschini, G., Farrace, M.G., and Giovanardi, O. 2000. Rapido trawling in the northern Adriatic Sea: effects on benthic communities in an experimental area. ICES J. Mar. Sci. **57**: 517–524.

Schratzberger, M., and Jennings, S. 2002. Impacts of chronic trawling disturbance on meiofaunal communities. Mar. Biol. **141**: 991–1000.

Schratzberger, M., and Warwick, R.M. 1998. Effects of physical disturbance on nematode communities in sand and mud: a microcosm experiment. Mar. Biol. **130**: 643–650.

Schratzberger, M., Rees, H.L., and Boyd, S.E. 2000. Effects of simulated deposition of dredged material on structure of nematode assemblages — the role of contamination. Mar. Biol. **137**: 613–622.

Schratzberger, M., Dinmore, T.A., and Jennings, S. 2002. Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. Mar. Biol. **140**: 83–93.

Schwinghamer, P., Donald, C., Gordon, J., Rowell, T.W., Prena, J., McKeown, D.L., Sonnichsen, G., and Guigné, J.Y. 1998. Effects of experimental otter trawling on surficial sediment properties of a sandy-bottom ecosystem on the Grand Banks of Newfoundland. Conserv. Biol. **12**: 1215–1222.

Somerfield, P.J., and Warwick, R.M. 1996. Meiofauna in marine pollution monitoring programmes: a laboratory manual. Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, UK.

Trimmer, M., Petersen, J., Sivyer, D.B., Mills, C., Young, E., and Parker, E.R. 2005. Impact of long-term benthic trawl disturbance on sediment sorting and biogeochemistry in the southern North Sea. Mar. Ecol. Prog. Ser. **298**: 79–94.

Vranken, G., Herman, P.M.J., Vincx, M., and Heip, C. 1986. A re-evaluation of marine nematode productivity. Hydrobiologia, **135**: 193–196.

Warwick, R.M., Platt, H.M., and Somerfield, P.J. 1998. Free living marine nematodes. Part III. Monhysterids. Field Studies Council, Shrewsbury, UK.

Watling, L., Findlay, R.H., Mayer, L.M., and Schick, D.F. 2001. Impact of a scallop drag on the sediment chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic community. J. Sea Res. **46**: 309–324.

Wieser, W. 1953. Die Beziehung zwischen Mund-höhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden. Ark. Zool. **4**: 439–484.