Marine Biology (2002) 140: 83–93
DOI 10.1007/s002270100688

M. Schratzberger · T.A. Dinmore · S. Jennings

Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages

Received: 11 May 2001 / Accepted: 20 July 2001 / Published online: 21 September 2001

Abstract Disturbance due to trawling reduces the biomass and production of macro-infaunal invertebrate communities, implying that their total food-consumption rate will fall, and that production (carbon) reaching the sea floor will be processed by other animals that can withstand the effects of trawling. Meiofauna may be resistant to disturbance by trawling because they are likely to be resuspended rather than killed by trawls and because their short generation times would allow them to withstand elevated mortality. We used a BACI experimental approach to investigate the short-term effects of beam trawling on the diversity, biomass and community structure of meiofauna on real fishing grounds in the southern North Sea. Experiments at two locations 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. We assessed the power of our experiments to detect the effects of trawling and recorded a 44–85% chance of detecting a 50% change in species richness and a 65% chance of detecting an order-of-magnitude change in biomass. The power to detect changes in total abundance, however, was low (between 11% and 12% power for detecting a change of 50%). We suggest that meiofauna are more resistant to disturbance by beam trawling than are macrofauna and that they have the potential to withstand the effects of chronic trawling on real fishing grounds and to retain a key role in energy cycling.

Communicated by J.P. Thorpe, Port Erin

M. Schratzberger (✉)
The Centre for Environment,
Fisheries and Aquaculture Science,
Burnham Laboratory, Remembrance Avenue,
Burnham-on-Crouch, Essex CM0 8HA, England

E-mail: m.schratzberger@cefas.co.uk

T.A. Dinmore · S. Jennings
The Centre for Environment,
Fisheries and Aquaculture Science,
Lowestoft Laboratory, Pakefield Road,
Lowestoft, Suffolk NR33 0HT, England

Introduction

Bottom trawling is a source of chronic and widespread disturbance in shallow shelf seas and modifies the diversity, community structure, trophic structure and productivity of macrobenthic invertebrate communities (Groot and Lindeboom 1994; Dayton et al. 1995; Jennings and Kaiser 1998; Lindeboom and Groot 1998; Hall 1999; Collie et al. 2000a; Gislason et al. 2000; Kaiser and Groot 2000). Experimental and field studies have shown that the abundance of macrobenthic infaunal and epifaunal species is reduced by trawling, and that fragile species with larger body sizes and slow life histories are generally more vulnerable than those species with smaller body sizes (Kaiser and Spencer 1996; Thrush et al. 1998; Tuck et al. 1998; Bergman and Santbrink 2000a, b; Gislason and Sinclair 2000; Hall-Spencer and Moore 2000; Kaiser et al. 2000). As a result, trawled communities are increasingly dominated by small infaunal species with fast life histories (Gubbay and Knapman 1999; Kaiser et al. 2000; Jennings et al. 2001).

Since disturbance by trawling reduces the abundance of the larger macrofauna that may compete with, or predate on, smaller macrofauna, smaller species may start to proliferate. Such proliferation would require that the smaller species withstand the mortality imposed by trawling. However, a recent study of the effects of beam trawling on the biomass and production of benthic infauna in the central North Sea suggested that any increases in the biomass or production of smaller infauna were small in relation to the losses in overall community biomass and production that resulted from the depletion of larger individuals (Jennings et al. 2001).

If the biomass and production of macrofauna is reduced by trawling, the production (fixed carbon) that

arrives at the sea floor must be processed by other animals, exported or accumulated as detritus.

Previous studies of trawling effects have focused on macrofauna, because they are conspicuous, relatively easy to sample and process, killed directly by trawling gears and provide habitat structure (Currie and Parry 1996; Bradshaw et al. 2000; Collie et al. 2000a, b; Craeymeersch et al. 2000; Hall-Spencer and Moore 2000; Kaiser et al. 2000; Lindegarth et al. 2000; Piet et al. 2000; Pranovi et al. 2000; Rumohr and Kujawski 2000; Veale et al. 2000). However, meiofauna (animals that pass through a 500-μm-mesh sieve but are retained in a 63-μm-mesh sieve) can make a greater contribution to benthic production than the macrofauna, and their role in the benthic ecosystem should not be overlooked (Kuipers et al. 1981; Schwinghamer et al. 1986). Meiofauna are more productive as a result of their abundance and fast turnover times; for example, Schwinghamer et al. (1986) quote turnover times of 24 days and less for organisms $< 2.1\times10^{-7}$ g wet weight (converted from kilocalories; Brey, personal communication) an order of magnitude greater than those for most macrofauna.

Meiofauna may resist disturbance due to trawling because their small body sizes suggest they may be resuspended rather than killed by trawls (e.g. Gilkinson et al. 1998) and because their short generation times (e.g. Schwinghamer et al. 1986) would allow their populations to withstand high mortality due to trawling. If meiofauna are resistant to disturbance by trawling, then they may continue to process energy in the benthic ecosystem when the productivity of macrofauna is reduced. Moreover, they could even proliferate as a result of reduced competition and predation.

Since heavily trawled ecosystems are affected by other human activities, such as waste disposal, oil and gas drilling, transportation and recreation (Kinne 1995), it is difficult to assess the relative roles of fishing disturbance and other factors in contributing to community change (Rees and Eleftheriou 1989; Jones 1992; Dayton et al. 1995; Currie and Parry 1996; Thrush et al. 1998; Blaber et al. 2000). We therefore adopted an experimental approach to this initial study of the effects of trawling on meiofauna, working in two relatively lightly trawled muddy areas in the southern North Sea (Jennings et al. 2000).

Our aims were to: (1) describe the short- and medium-term (weeks and months) effects of beam trawling on meiofauna at two experimental locations; (2) assess the power of our experiments to detect specified changes in meiofaunal biomass, density and diversity; and (3) identify the potentially most effective biological response (biomass versus species richness).

Materials and methods

Study area

Trawling experiments were conducted at two locations in the southern North Sea: the Western Mud Hole (depth 39 m) and the Botney Cut (depth 59 m) (Fig. 1). The sediments at both experimental locations fall within the category of muddy sands (Western Mud Hole, mean particle diameter 76 μm) or muds (Botney Cut, mean particle diameter 16 μm) and were generally poorly sorted, with sorting coefficients of 2.04 and 2.27, respectively. The sediment at the Western Mud Hole consisted of 79% sand and 21% silt/clay; that at Botney Cut, of 27% sand and 73% silt/clay (D.S. Limpenny, unpublished).

We used side-scan sonar to confirm that trawl tracks were absent at the start of the experiment. This was necessary because the resolution of trawling-effort data at the study sites was too low to indicate whether 12-m-beam trawls, of the type that are most frequently deployed by trawlers in the central North Sea, had recently been towed over the small areas where we worked (Jennings et al. 2000). Meiofauna were sampled randomly at an impact site A and an untrawled control site B at both locations (Fig. 2), once before and on several occasions after experimental trawling (Before-After-Control-Impact, BACI; Faith et al. 1991; Underwood 1991, 1992).

After initial sampling, both impact sites (A) were trawled with a 4-m-beam trawl (25 parallel hauls). The trawl was fished at a speed of 5 knots (8 km h^{-1}) and was fitted with 80-mm mesh and a chain matrix (Lindeboom and Groot 1998). The presence of a physical trawling impact was confirmed using side-scan sonar, and repeat meiofauna sampling was completed at sites A and B (Fig. 2). All trawling and sampling was conducted from the CEFAS R.V. "Corystes" (LOA 53.25 m).

Since our aim was to investigate the effects of trawling on the meiofauna assemblages that are found on real beam-trawling grounds, we had to conduct our experiments at offshore locations. Logistic considerations preclude extended periods of work at these locations, and we had to make a careful cost-benefit assessment of our experimental design. Offshore sampling was possible on four to five occasions in 1999 and 2000, and we decided to sample only once before the trawling impact but on several occasions following the impact (Table 1). However, we were aware of the associated

Fig. 1 Location of experimental areas in the southern North Sea

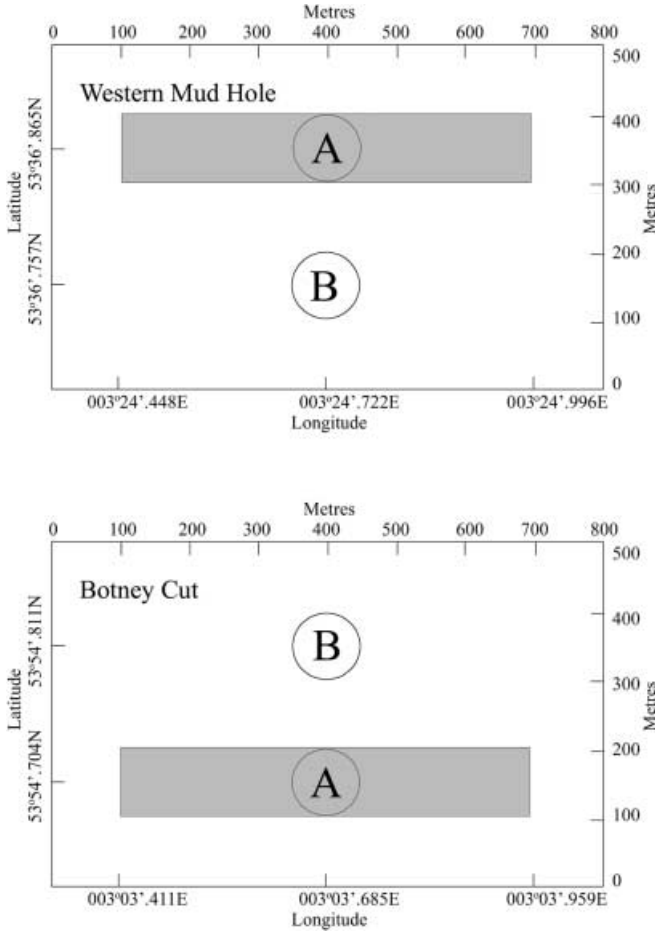

Fig. 2 Location and dimensions of control site B and impact site A in the Western Mud Hole and Botney Cut

complication in differentiating between the two potential sources of change in the meiofauna assemblages, namely that numbers of species have declined as a direct effect of trawling and that there are spatial and/or temporal differences in assemblage structure that occurred regardless of trawling impact. We addressed this problem by looking at differences in biomass, density and species richness between the control and impact site, rather than looking at absolute values. This approach assumes that the temporal impacts, other than those due to trawling, that affect the impact and control sites have the same magnitude and act in unison.

Sample collection

Meiofauna samples were collected with an NIOZ corer, a device that takes a circular core of 0.1 m^2 to a depth of >30 cm. The surface of sediment samples collected with an NIOZ corer is relatively undisturbed, and the corer retains a few centimetres of the overlying water. The corer was deployed four times at each site on each sampling occasion. On the ship, a perspex tube with a 5.5-cm internal diameter was pushed into the sediment core until the top of the tube was level with the water surface in the core. The water overlying the sediment in the core tube was carefully siphoned off into a 63-μm-mesh sieve and washed into a sample pot. A rubber bung was placed tightly in the top end of the core tube. Sediment around the core tube was excavated carefully and the core tube pulled out slowly, supporting the bottom end. The rubber bung from the top end of the core tube was removed to allow the sediment core to move down the tube until only the top 5 cm of the sediment remained in the tube. This sediment layer was transferred into the sample pot and fixed in a solution of 10% formalin in filtered sea water.

Sediment samples were also taken from the NIOZ cores with a 5.5-cm-diameter tube and frozen to a temperature of –20°C pending particle-size analysis. Sediment samples were collected at all sites in November 2000.

Meiofauna sample processing

Meiofauna samples were initially washed onto a 63-μm-mesh sieve to remove the fine silt fraction and the formalin. After decanting the samples five times onto a 63-μm-mesh sieve, the meiofauna was extracted with Ludox TM 40 with a specific gravity of 1.15 (McIntyre and Warwick 1984; Somerfield and Warwick 1996). Extraction was repeated three times.

Ninety-one to 99% of meiofauna were nematodes. Owing to their high numbers, 20% subsamples of the extract were evaporated slowly in anhydrous glycerol and evenly spread on microscope slides for identification and counting of nematodes under a compound microscope (Olympus BX 51) with Nomarski interference-contrast illumination. Nematodes were identified to genus or species level following Platt and Warwick (1983, 1988) and Warwick et al. (1998).

Five percent of all nematodes in each sample were randomly selected for the calculation of total community biomass (wet weight) according to Andrassy's (1954) formula. If the nematodes had a long, filiform tail, the tail was not included in the measurements: Wet weight = (Length × Width^2)/1,600,000, where wet weight is in micrograms and length and width are in micrometres.

Data processing

Total nematode abundance, Margalef's species richness (*d*) and total nematode wet weight (hereafter referred to as "biomass") were calculated for each sample. The data were analysed using a two-way crossed analysis of variance (ANOVA) with the factors "Site" (control site B and impact site A) and "Time" (days before/after experimental trawling). The significance of the interaction effect provides a test of experimental treatment effect. Following preliminary data exploration, biomass data were log-transformed to reduce heterogeneity of variance.

The power of the experimental design was also evaluated. Using the observed estimates of the residual variances, the power (i.e. the probability of obtaining a statistically significant response given an assumed size of experimental effect) was computed for each biological response (i.e. abundance, species richness, biomass) and

Table 1 Sampling frequency for meiofauna

Western Mud Hole		Botney Cut	
Date	Time before/after trawling	Date	Time before/after trawling
30 October 1999	5 days before	27 November 1999	8 days before
4 November 1999	1 day after	5 December 1999	1 day after
5 December 1999	31 days after		
2 May 2000	181 days after	2 May 2000	150 days after
29 November 2000	392 days after	23 November 2000	355 days after

location. The pattern of experimental effect is shown in Fig. 3. Relative to the control site, the biological response is assumed to decrease by p% at the first sampling occasion 1 day after trawling and to have recovered in equal steps by the third/fourth occasion after the impact. A change of 50% in species richness and an order of magnitude in biomass were considered ecologically significant, since these were comparable with trawling-induced changes in macro-infaunal communities in a similar area of the North Sea. Power analyses were performed using the software package S-Plus (Mathsoft International, Bagshot, Surrey, UK).

Non-metric multidimensional scaling (MDS) ordination using the Bray–Curtis similarity measure was applied to square-root-transformed species-abundance data following the procedure described by Clarke and Warwick (1994). One-way analysis of similarities (ANOSIM, Clarke 1993) was applied for each study location separately to assess the significance of differences in the composition of nematode assemblages between control and impact sites at different times of sampling. The nature of the community groupings identified in the MDS ordinations was explored further by applying the similarity percentages programme (SIMPER) to determine the contribution of individual species to the average dissimilarity between samples. All multivariate analyses were performed using the software package PRIMER (Clarke and Warwick 1994).

The most abundant nematode species, accounting for 50% of the total number of individuals, were identified, giving 16 and 9 species at the Western Mud Hole and Botney Cut, respectively. A multivariate analysis of variance (MANOVA) was performed based on the proportions of these species using an arcsine[sqrt(.)] transformation to reduce heterogeneity of variance. As with the univariate ANOVA of abundance, species richness (d) and biomass (log), evidence of an experimental effect was assessed from the interaction between "Site" and "Time". For the multivariate test there is a choice of test statistic, and here we used the Pillai Trace (Chatfield and Collins 1980).

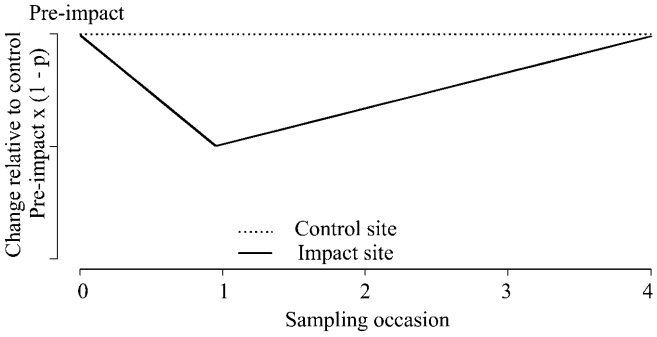

Fig. 3 The probability of obtaining a statistically significant result given an assumed size of experimental treatment effect

Results

Biomass, density and species richness

Results from the two-way crossed ANOVA for abundance, species richness (d) and total nematode biomass

Table 2 Results from two-way crossed ANOVA

Western Mud Hole					
	df	Sum of squares	Mean square	*F* value	*P* value
Total abundance					
Site	1	1,640,210	1,640,210	4.299	0.047*
Time	4	794,030	198,507	0.520	0.722
Site×Time	4	1,825,746	456,436	1.196	0.333
Residuals	30	11,447,305	381,577		
Species richness (d)					
Site	1	2.652	2.652	8.512	0.007*
Time	4	3.514	0.879	2.820	0.042*
Site×Time	4	0.166	0.042	0.134	0.969
Residuals	30	9.347	0.312		
Total biomass					
Site	1	0.000	0.000	0.000	0.995
Time	4	1.653	0.413	1.527	0.220
Site×Time	4	1.004	0.251	0.927	0.462
Residuals	30	7.850	0.271		
Botney Cut					
	df	Sum of squares	Mean square	*F* value	*P* value
Total abundance					
Site	1	86,225	86,225	0.275	0.605
Time	3	5,654,816	1,884,939	6.020	0.003*
Site×Time	3	304,526	101,509	0.324	0.808
Residuals	24	7,514,335	313,097		
Species richness (d)					
Site	1	0.500	0.500	1.202	0.284
Time	3	7.747	2.582	6.208	0.003*
Site×Time	3	0.193	0.064	0.155	0.926
Residuals	24	9.984	0.416		
Total biomass					
Site	1	0.780	0.780	3.383	0.078
Time	3	4.634	1.545	6.697	0.002*
Site×Time	3	0.501	0.167	0.723	0.548
Residuals	24	5.535	0.231		

*Significant difference at $P < 0.05$

are presented in Table 2. Although there were significant differences between control and impact site and between different sampling occasions, there were no statistically significant interactions at a significance level of 5%. At the Western Mud Hole, differences in total nematode abundance and species richness were most pronounced 1 month after the experimental trawling took place and decreased during the 1-year recovery period (Fig. 4a). At Botney Cut, the maximum difference in total nematode biomass (log) between control and impact site was observed immediately after the experimental disturbance (Fig. 4b).

Figure 5 shows for each experimental location and biological response the power of the experimental design corresponding to a hypothetical impact of p% on the first sampling occasion 1 day after trawling disturbance.

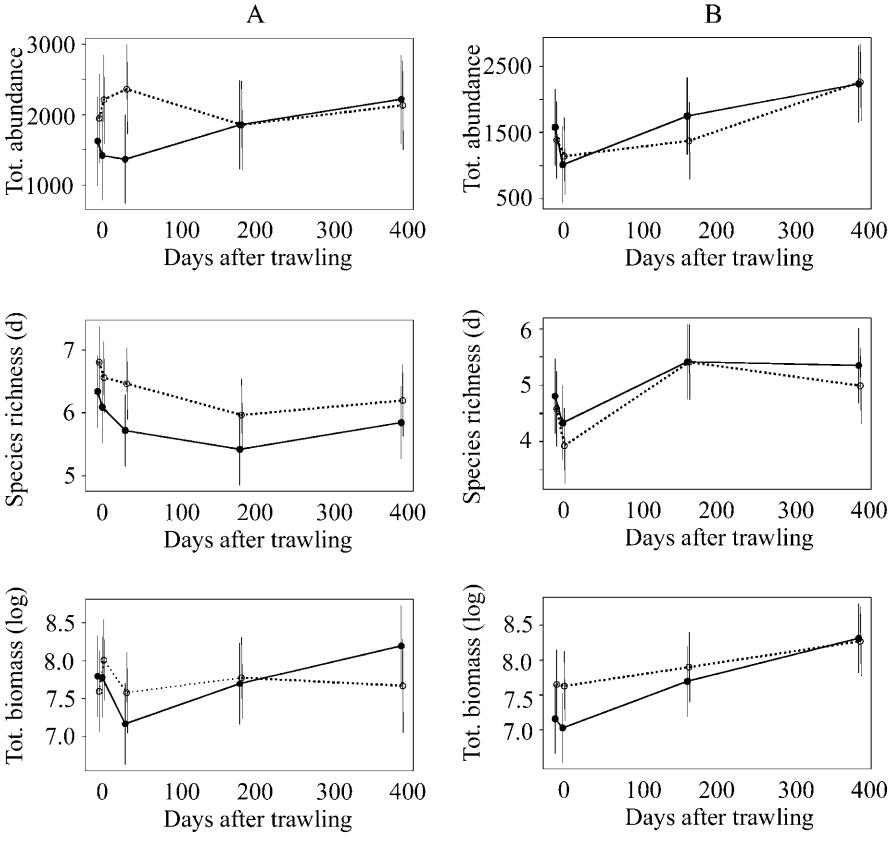

Fig. 4a, b Means of total abundance, species richness (*d*) and total biomass (log) plotted against days after disturbance for the Western Mud Hole (**a**) and Botney Cut (**b**). *Solid line* Impact site, *dotted line* control site. *Vertical lines* correspond to 95% confidence limits

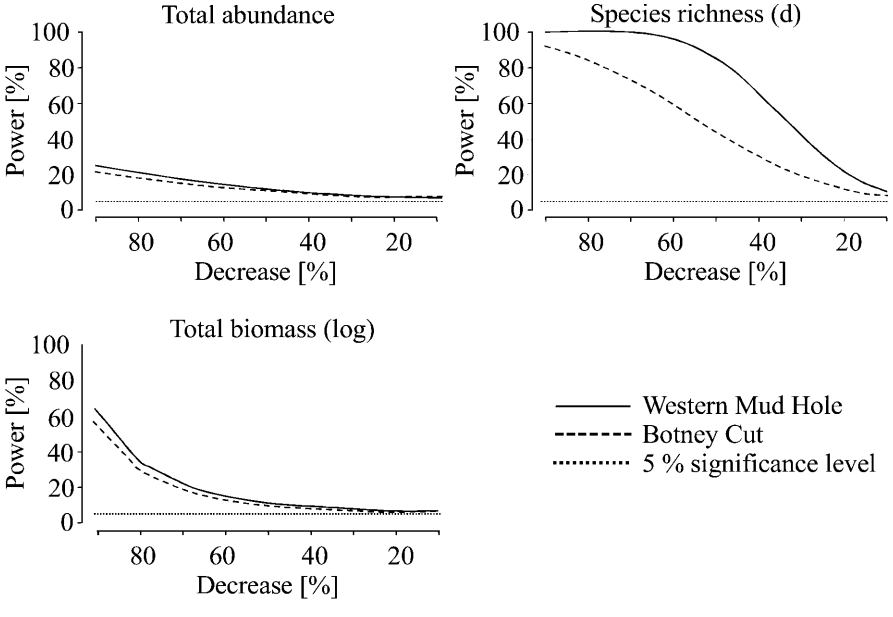

Fig. 5 Power of the experimental design corresponding to a hypothetical impact of p% on the first sampling occasion 1 day after trawling, for each experimental location and biological response

For reference, the 5% significance level (corresponding to an impact of 0%) is also shown. This indicates that potentially the most sensitive biological response was species richness. For abundance, the power rises to only approximately 10% for a relative impact of 50% immediately after trawling and to approximately 25% for a change of an order of magnitude. The probability of detecting a 50% change in species richness was 44% and 85% at Botney Cut and the Western Mud Hole, respectively. For biomass, the power of detecting an order-of-magnitude change was 65% for both experimental locations.

Table 3 gives the post hoc power of the experimental design for each experimental location and biological response, i.e. the power of the experiment to find the observed patterns of interaction significant. This provides some indication of the sensitivity of each biological response – i.e. observed signal-to-noise ratio measured by the size of the response seen in this study relative to its inherent variability. The post hoc power for all calculated indices is close or equal to the 5% significance level.

Despite the high power of the experimental design for species richness *d*, the post hoc power is low because the observed change in species richness after experimental trawling was low. Conversely, the low post hoc power for abundance and biomass is due to the high variability of abundance and biomass data with corresponding low power, and to the small observed effect.

Table 3 Post hoc power (%) of the experimental design to find observed patterns of interaction statistically significant with equivalent *p*%

Western Mud Hole		
	Post hoc power (%)	Equivalent *p*%
Total abundance	5.9	25
Species richness (*d*)	5.0	0
Total biomass	5.3	21
Botney Cut		
	Post hoc power (%)	Equivalent *p*%
Total abundance	5.0	0
Species richness (*d*)	5.0	0
Total biomass	6.2	34

Table 4 Western Mud Hole: dissimilarities (%) on different sampling occasions before (–) and after (+) trawling, based on square-root-transformed species abundance data

Impact site				
	–5 days	+1 day	+31 days	+181 days
+1 day	33			
+31 days	37	38*		
+181 days	37*	40*	40*	
+392 days	44*	46*	47*	45*
Control site				
	–5 days	+1 day	+31 days	+181 days
+1 day	31			
+31 days	31	28		
+181 days	40	40*	38*	
+392 days	48*	48*	47*	50*

*Significant differences at $P < 0.05$ based on ANOSIM test

Nematode assemblage structure

The one-way ANOSIM for each site separately (Tables 4, 5) shows that differences in nematode assemblages collected at the impact site were more pronounced than at the control site, with the highest dissimilarity between control and impact site occurring within the first 150 days after the experimental disturbance (Table 6). At both Western Mud Hole and Botney Cut, nematode assemblages became increasingly dissimilar throughout the 1-year duration of the experiment (Tables 4, 5). This indicates that possible changes in community structure due to experimental trawling were smaller than medium-term temporal changes.

The MDS plots for the control and impact sites separately show the same general trends in community structure at the Western Mud Hole (Fig. 6a) and Botney Cut (Fig. 6b) locations. Samples collected within the first 181 days of the experiment form clusters at the left-hand side of the plot, whereas samples collected 1 year after the beginning of the experiment form a cluster at the right-hand side.

In agreement with the results from the two-way crossed ANOVA (Table 2), the plots indicate that significant differences in nematode assemblage structure existed between different sampling occasions, whereas differences between control and impact site were less pronounced (i.e. the position of samples relative to each other in the plot is similar). At both experimental locations, assemblage structure appears to change in the same direction during the 12-month sampling period,

Table 5 Botney Cut: dissimilarities (%) on different sampling occasions before (–) and after (+) trawling, based on square-root-transformed species abundance data

Impact site			
	–8 days	+1 day	+150 days
+1 day	38		
+150 days	36	46*	
+355 days	38	47*	43*
Control site			
	–8 days	+1 day	+150 days
+1 day	37		
+150 days	39	40	
+355 days	42*	42*	42*

*Significant differences at $P < 0.05$ based on ANOSIM test

Table 6 Dissimilarities (%) between impact and control site on different sampling occasions before (–) and after (+) trawling, based on square-root-transformed species abundance data

Western Mud Hole		Botney Cut	
–5 days	35	–8 days	33
+1 day	32	+1 day	37
+31 days	49*		
+181 days	36	+150 days	38*
+392 days	36	+355 days	33

*Significant differences at $P < 0.05$ based on ANOSIM test

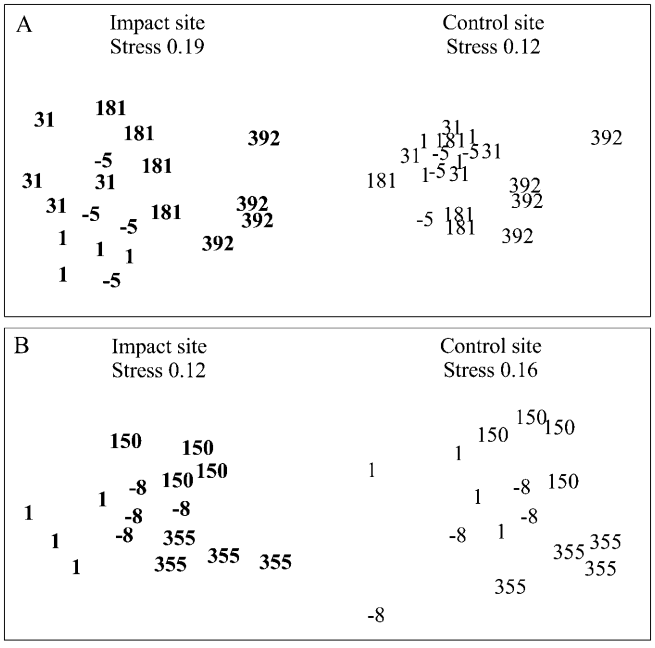

Fig. 6a, b Multi-dimensional scaling ordination based on square-root-transformed species abundance data. **a** Western Mud Hole, **b** Botney Cut. Numbers refer to days before (–) and after trawling

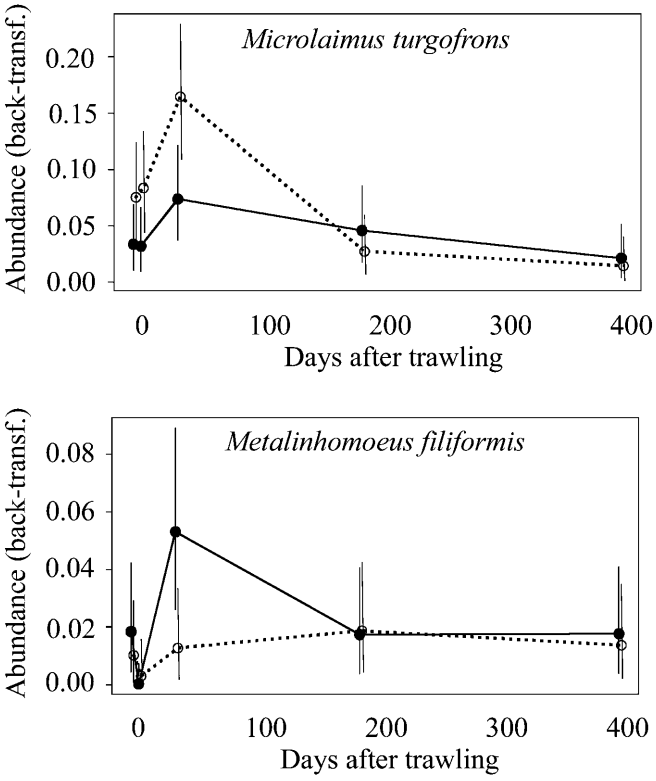

Fig. 7 *Microlaimus turgofrons* and *Metalinhomoeus filiformis*. Back-transformed mean abundance at the Western Mud Hole with individually significant interaction effects revealed by MANOVA. *Solid line* impact site, *dotted line* control site. *Vertical lines* correspond to 95% confidence limits

indicating that the same factors may have caused those changes in species composition.

From the results of the MANOVA, there is evidence that, although there were no statistically significant changes in overall abundance, species richness (*d*) or total biomass (log), there were changes in species composition. The results are given in Table 7. There was a significant interaction for the Western Mud Hole, but not for Botney Cut. The individual ANOVAs for the Western Mud Hole shows significant interaction terms for *Microlaimus turgofrons* and *Metalinohomoeus filiformis* (Fig. 7). Thirty-one days after the experimental impact, the abundance of *M. turgofrons* was considerably lower, that of *M. filiformis* significantly higher, at the impact site than at the control site.

Discussion and conclusions

The experiments at our two study locations showed that there were no short- to medium-term trawling impacts on meiofaunal diversity or biomass, but that there were mild effects on community structure at one location. Any impacts due to trawling were minor in relation to seasonal changes in the meiofaunal communities.

Table 7 Results of MANOVA

Western Mud Hole						
	df	Pillai trace	*F* value	*df* (number)	*df* (density)	*P* value
Site	1	0.59174	1.3588	16	15	0.279
Time	4	3.29976	5.3014	64	72	0.000*
Site×Time	4	2.28473	1.4985	64	72	0.048*
Residuals	30					
Botney Cut						
	df	Pillai trace	*F* value	*df* (number)	*df* (density)	*P* value
Site	1	0.26389	0.6373	9	16	0.750
Time	3	1.71387	2.6652	27	54	0.001*
Site×Time	3	0.95677	0.9365	27	54	0.563
Residuals	24					

*Significant difference at $P < 0.05$

Experimental design

The principle of a BACI design is that a disturbance at the impacted site will cause a different pattern of change from before to after it starts compared with natural change at the control location (Underwood 1992; Smith et al. 1993). BACI designs have been used in investigations of environmental impacts on the mean abundance of populations (Vose and Bell 1994; Chapman et al. 1995; Currie and Parry 1996; Hogg and Williams 1996; Korman and Higgins 1997) and community data (Faith et al. 1991; Quigley and Hall 1999).

With the sampling intensity of our experiments, the power to detect specified changes in meiofaunal density was low because of the high variance of the data. Species richness (*d*) was the least variable parameter and thus potentially most effective in detecting changes due to experimental trawling. Therefore, the risk of conducting a type II error was high for changes in abundance (approximately 88%) but lower in the case of species richness (Western Mud Hole 15%, Botney Cut 56%) and total biomass (approximately 35%; see Fig. 3).

For a given sampling intensity, the power of such BACI experiments to detect specified changes in meiofauna assemblages could be increased by reducing the mean square of the residuals or by increasing the contribution of the mean square of the Site×Time interaction term (see Table 2). This could be achieved in several ways.

1. The relatively high variability of abundance and thus biomass data might have been partly due to small-scale variability of environmental factors at the sampling sites. This could be reduced by dividing each control and impact site into separate areas. Replicate samples are then collected from each area and pooled before being analysed. Such an approach, however, would require a (time-consuming and costly) survey of the study area prior to the experiment.
2. Results from analyses of similarity indicate that possible changes in community structure caused by experimental trawling were smaller than those due to the natural variation in time. A higher number of sampling times before and after the impact would have decreased the amount of change required to produce a statistically significant impact, and thus increased the power of the test. Owing to the high cost of such offshore experiments, repeated sampling should be focused on times when the expected changes are at a maximum (i.e. immediately after the impact; see Fig. 3). An undirected increase in the number of sampling events might elevate the cost without solving the problem. Currie and Parry (1996), for example, conducted a BACI experiment at a site in south-east Australia, assessing changes to macrobenthic infauna caused by scallop dredging. Changes in macrobenthic community structure were monitored on three occasions pre-dredging and six occasions post-dredging. The authors concluded that changes in community structure caused by dredging were smaller than those that occur between seasons and years.

Effects of experimental trawling on nematode abundance, biomass and assemblage structure

To date, most fishing-impact studies have focused on changes in abundance of large macrofauna, whereas smaller animals have been largely neglected. Results from fishing-impact studies on macrofauna show that the susceptibility of species is determined by their body size and turnover rate rather than their taxonomic affiliation, with large, slowly reproducing species being more susceptible than their smaller, faster reproducing competitors (Kaiser et al. 2000; Jennings et al. 2001).

Since the meiofauna are among the smallest animals in benthic communities and have very fast turnover times, they may be expected to show little or no response to trawling, an expectation not invalidated by our experiments. Owing to the high dominance of nematodes, meiofauna in our study included only one taxon where the average individual biomass ranged from 0.44 to 3.56 μg. The macrofauna studies mentioned above, however, included many more taxa and a much wider range of size classes (six orders of magnitude). Therefore, we tried to assess an impact of trawling within a size class rather than over a range of classes. While the term ''meiofauna'' was first used by Mare (1942) to define an assemblage of mobile invertebrates distinguished from macrofauna by their smaller size, the significance of what began as a subjective size-range of benthic invertebrates has since been supported by a number of studies which infer that meiofauna constitutes a discrete, ecologically defined benthic component (e.g. Higgins and Thiel 1988; Giere 1993). As a result of their high abundance, ubiquitous distribution, rapid generation times and fast metabolic rates, this defined component may continue to play a key role in energy cycling within trawled areas.

The effects of trawling include the scraping, scouring and resuspension of the surface sediment, and the magnitude of the impact is determined by the speed of towing, physical dimensions and weight of the gear, type of substratum and strength of currents or tides in the area fished (Groot 1984; Jennings and Kaiser 1998; Gubbay and Knapman 1999; Lindeboom and Groot 1999; Hansson et al. 2000). As a result, trawling could directly affect the mortality of meiofauna or have indirect effects on their habitat. There was little evidence for high levels of direct mortality, since nematodes in all samples were of good condition and different developmental stages (juveniles, adult females and males of different sizes) were recorded, indicating that reproduction and growth of most species occurred and appeared

to have remained relatively unaffected by the experimental treatment. The high turnover rate and relatively short life spans of most nematode species may have compensated any possible short-term effects and were not notable several months after the impact. This is consistent with results obtained by Pranovi et al. (2000) who showed that experimental trawling induced a change in the meiobenthic community structure (at the taxon level) which was most obvious 1 week after the impact.

Several experiments indicate that trawling has no significant impact on the particle-size distribution of sediments (Tuck et al. 1998; Pranovi et al. 2000). However, trawling can reduce the surface roughness of a sandy seabed immediately after the impact (Schwinghamer et al. 1996) and lead to the smoothing of ripples, detrital aggregations and surface traces of bioturbation as resuspended sediments settle on the seabed. The absence of general patterns in susceptibility of nematode species to experimental trawling in our study is not surprising when the possible mechanisms contributing to mortality are considered. A number of species were probably affected by increased turbidity, high rates of sedimentation or were buried when depressions in the sediment were filled.

Univariate data analyses failed to detect changes in abundance, diversity and biomass in nematode assemblages. This suggests that the assemblages at the impact sites reached an organised structure similar to that of the control sites. The multivariate species-dependent MDS ordination was more sensitive in discriminating the assemblages collected at the trawled and control site at the Western Mud Hole, suggesting that the dominance relationships among species had changed at the trawled site compared to the undisturbed control site (Colangelo et al. 1996).

Thirty-one days after the experimental impact took place at the Western Mud Hole, the abundance of the microlaimid *Microlaimus turgofrons* was significantly lower at the impact site than at the control site. This negative response of *M. turgofrons* might have been determined by its low ability to migrate upwards when buried, a characteristic that has been described for other microlaimids (Schratzberger et al. 2000a). The abundance of *Metalinhomoeus filiformis*, however, was significantly higher at the impact site than at the control site 1 month after the trawling. A similar, though not statistically significant, response was evident for *Sabatieria punctata* at Botney Cut, a species that often persists under conditions normally restrictive for other nematodes (Tietjen 1980; Somerfield et al. 1995; Schratzberger et al. 2000b).

We have suggested that meiofauna suffer low direct mortality due to trawling disturbance because they are resuspended rather than crushed by the trawl. This would be consistent with the effects of trawl doors on the smallest bivalves (Gilkinson et al. 1998). Results from multivariate analyses might point to indirect effects of disturbance on nematode species mediated through reworking and disturbance of the sediment being more important than direct effects of experimental trawling.

Short-term experiments on small scales offer a number of advantages when attempting to identify the acute effects of trawling, but the acute impact does not reflect the chronic disturbance caused by trawls in real fisheries (Collie et al. 1997; Thrush et al. 1998; Kaiser et al. 2000). Recovery from disturbance in small experimental areas may be a result of immigration, a form of recovery that may not be possible in large and repeatedly trawled areas. To describe the effects of trawling at the level of the fishery, it is necessary to study real fisheries where disturbance occurs on large scales over long time periods. The next step is to assess the resilience of meiobenthic communities at this scale, although considerable replication is likely to be needed to gain sufficient power to detect any statistically significant effects.

Acknowledgements We thank Brian Edwards, Chris Firmin, Roger Flatt, Alison Hewer, Paul Hudson, Steve Lovewell, Tracy Mead, Dave Palmer, Alison Reeve, Dave Sivyer, Christie Steward, Peter Walker, Karema Warr and the officers and crew of R.V. "Corystes" for practical assistance in the sample collection. David Limpenny and Claire Mason conducted the particle-size analyses. John Pilkington wrote the macro for the image-analysis programme used in this study. We are grateful to Caroline Wall for assistance in the sample processing and to Mike Nicholson for advice on statistical analysis of the data. Dan Duplesea made constructive comments on the manuscript. The work was supported by the Department for Environment, Food and Rural Affairs.

References

Andrassy I (1954) Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool 2:1–14

Bergman MJN, Santbrink JW van (2000a) Fishing mortality of populations of megafauna in sandy sediments. In: Kaiser MJ, Groot SJ de (eds) Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell, Oxford, pp 49–68

Bergman MJN, Santbrink JW van (2000b) 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

Blaber SJM, Cyrus DP, Albaret JJ, Chong Ving Ching, Day JW, Elliott M, Fonseca MS, Hoss DE, Orensanz J, Potter IC, Silvert W (2000) Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. ICES J Mar Sci 57:590–602

Bradshaw C, Veale LO, Hill AS, Brand AR (2000) The effects of scallop dredging on gravelly seabed communities. In: Kaiser MJ, Groot SJ de (eds) Effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell, Oxford, pp 83–104

Chapman MG, Underwood AJ, Skilleter GA (1995) Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two control assemblages. J Exp Mar Biol Ecol 189:103–122

Chatfield C, Collins AJ (1980) Introduction to multivariate analysis. Chapman and Hall, London

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth

Colangelo MA, Macri T, Ceccherelli VU (1996) A field experiment on the effect of two types of sediment disturbance on the rate of recovery of a meiobenthic community in an eutrophicated lagoon. Hydrobiologia 329:57–67

Collie JS, Escanero GA, Valentine PC (1997) Effects of bottom fishing on the benthic megafauna of Georges Bank. Mar Ecol Prog Ser 155:159–172

Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000a) A quantitative analysis of fishing impacts on shelf sea benthos. J Anim Ecol 69:785–798

Collie JS, Escanero GA, Valentine PC (2000b) Photographic evaluation of the impacts of bottom fishing on benthic epifauna. ICES J Mar Sci 57:987–1001

Craeymeersch JA, Piet GJ, Rijnsdorp AD, Buijs J (2000) Distribution of macrofauna in relation to the micro-distribution of trawling effort. In: Kaiser MJ, Groot SJ de (eds) Effects of fishing on non-target species and habitats, Blackwell Science, Oxford pp 187–197

Currie DR, Parry GD (1996) Effects of scallop dredging on a soft sediment community: a large-scale experimental study. Mar Ecol Prog Ser 134:131–150

Dayton PK, Thrush SF, Agardy MT, Hofman RJ (1995) Environmental effects of marine fishing. Aquatic Conservation: Mar Freshw Ecosyst 5:205–232

Faith DP, Humphrey CL, Dostine PL (1991) Statistical power and BACI designs in biological monitoring: comparative evaluation of measures of community dissimilarity based on benthic macroinvertebrate communities in Rockhole Mine Creek, Northern Territory, Australia. Aust J Mar Freshw Res 42:589–602

Giere O (1993) Meiobenthology – the microscopic fauna in aquatic sediments. Springer, Berlin Heidelberg New York

Gilkinson K, Paulin M, Hurley S, Schwinghamer P (1998) Impacts of trawl door scouring on infaunal bivalves: results of a physical trawl door model/dense sand interaction. J Exp Mar Biol Ecol 224:291–312

Gislason H, Sinclair MM (2000) Ecosystem effects of fishing. ICES J Mar Sci 57:465–791

Gislason H, Sinclair M, Sainsbury K, O'Boyle R (2000) Symposium overview: incorporating ecosystem objectives within fisheries management. ICES J Mar Sci 57:468–475

Groot SJ de (1984) The impact of bottom trawling on benthic fauna of the North Sea. Ocean Manage 9:177–190

Groot SJ de, Lindeboom HJ (1994) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Sea Research, Texel

Gubbay S, Knapman PA (1999) A review of the effects of fishing within UK European marine sites. UK Marine SAC's Project, English Nature, ISBN 1857164822

Hall SJ (1999) The effects of fishing on marine ecosystems and communities. Blackwell, Oxford

Hall-Spencer JM, Moore PG (2000) Scallop dredging has profound, long-term impacts on maerl habitats. ICES J Mar Sci 57:1407–1415

Hansson M, Lindegardth M, Valentinsson D, Ulmestrand M (2000) Effects of shrimp-trawling on abundance of benthic macrofauna in Gullmarsfjorden, Sweden. Mar Ecol Prog Ser 198:191–201

Higgins RP, Thiel H (1988) Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC

Hogg ID, Williams DD (1996) Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. Ecology 77:395–407

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. Adv Mar Biol 34:201–352

Jennings S, Warr KJ, Greenstreet SPR, Cotter AJ (2000) Spatial and temporal patterns in North Sea fishing effort. In: Kaiser MJ, Groot SJ de (eds) Effects of fishing on non-target species and habitats: biological conservation and socio-economic issues. Blackwell, Oxford, pp 3–14

Jennings S, Dinmore TA, Duplesea DE, Warr KJ, Lancaster JE (2001) Trawling disturbance can modify benthic production processes. J Anim Ecol 70:459–475

Jones JB (1992) Environmental impact of trawling on the seabed: a review. N Z J Mar Freshw Res 26:59–67

Kaiser MJ, Groot SJ de (2000) The effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell, Oxford

Kaiser MJ, Spencer BE (1996) The effects of beam-trawl disturbance on infaunal communities in different habitats. J Anim Ecol 65:348–358

Kaiser MJ, Ramsay K, Richardson CA, Spence FE, Brand AR (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. J Anim Ecol 69:494–503

Kinne O (1995) Ecology of the North Sea: problems, successes, failures, future needs. Helgol Wiss Meeresunters 49:303–312

Korman J, Higgins PS (1997) Utility of escapement time series data for monitoring the response of salmon populations to habitat alterations. Can J Fish Aquat Sci 54:2058–2067

Kuipers BR, Wilde PAW de, Creutzberg F (1981) Energy flow in a tidal flat ecosystem. Mar Ecol Prog Ser 5:215–221

Lindeboom HJ, Groot SJ de (1998) The effects of different types of fisheries on the North Sea and Irsh Sea benthic ecosystems. Netherlands Institute of Sea Research, Texel

Lindeboom HJ, Groot SJ de (1999) The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. Mar Environ Manage Rev 1998 Future Trends 6:87–94

Lindegarth M, Valentinsson D, Hansson M, Ulmestrand M (2000) Interpreting large-scale experiments on effects of trawling on benthic fauna: an empirical test of the potential effects of spatial confounding in experiments without replicated control and trawled areas. J Exp Mar Biol Ecol 245:155–169

Mare MF (1942) A study of a marine benthic community with special reference to the micro-organisms. J Mar Biol Assoc UK 25:517–554

McIntyre AD, Warwick RM (1984) Meiofauna techniques. In: Holme NA, McIntyre AD (eds) Methods for the study of marine benthos. IBH Handbook No. 16, 2nd edn. Blackwell, Oxford, pp 217–244

Piet GJ, Rijnsdorp AD, Bergman MJN, Santbrink JW van, Craeymeersch J, Bujis J (2000) A quantitative evaluation of the impact of beam trawling on benthic fauna in the southern North Sea. ICES J Mar Sci 57:1332–1339

Platt HM, Warwick RM (1983) Free-living marine nematodes. Part I. British enoploids. Cambridge University Press, Cambridge

Platt HM, Warwick RM (1988) Free-living marine nematodes. Part II. British chromadorids. Cambridge University Press, Cambridge

Pranovi F, Raicevich S, Franceschini G, Farrace MG, 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

Quigley MP, Hall JA (1999) Recovery of macrobenthic communities after maintenance dredging in the Blyth Estuary, north-east England. Aquatic conservation. Mar Freshw Ecosyst 9:63–73

Rees HL, Eleftheriou A (1989) North Sea benthos: a review of field investigations into the biological effects of man's activities. J Cons Int Explor Mer 45:284–305

Rumohr H, Kujawski T (2000) The impact of trawl fishery on the epifauna of the southern North Sea. ICES J Mar Sci 57:1389–1394

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

Schratzberger M, Rees HL, Boyd SE (2000b) Effects of simulated deposition of dredged material on structure of nematode assemblages – the role of burial. Mar Biol 136:519–530

Schwinghamer P, Hargrave B, Peer D, Hawkins CM (1986) Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. Mar Ecol Prog Ser 31:131–142

Schwinghamer P, Guigné JY, Sui WC (1996) Quantifying the impact of trawling on benthic habitat structure using high resolution acoustics and chaos theory. Can J Fish Aquat Sci 53:288–296

Smith EP, Orvos DR, Cairns J (1993) Impact assessment using the Before-After-Control-Impact (BACI) model: concerns and comments. Can J Fish Aquat Sci 50:627–637

Somerfield PJ, Warwick RM (1996) Meiofauna in marine pollution monitoring programmes. A laboratory manual. Ministry of Agriculture, Fisheries 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 disposals. Mar Ecol Prog Ser 127:103–112

Thrush SF, Hewitt JE, Cummings VJ, Dayton PK, Cryer M, Turner SJ, Funnell GA, Budd RG, Milburn CJ, Wilkinson MR (1998) Disturbance of marine benthic habitat by commercial fishing: impacts at the scale of the fishery. Ecol Appl 8:866–879

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

Tuck I, Hall SJ, Roberston M, Armstrong E, Basford D (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. Mar Ecol Prog Ser 162:227–242

Underwood AJ (1991) Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural communities. Aust J Mar Freshw Res 42:569–587

Underwood AJ (1992) Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J Exp Mar Biol Ecol 161:145–178

Veale LO, Hill AS, Hawkins SJ, Brand AR (2000) Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats. Mar Biol 137:325–337

Vose FE, Bell SS (1994) Resident fishes and macrobenthos in mangrove-rimmed habitats: evaluation of habitat restoration by hydrologic modification. Estuaries 17:585–596

Warwick RM, Platt HM, Somerfield PJ (1998) Free-living marine nematodes. Part III. British monhysterids. Field Studies Council, Shrewsbury