

# Effects of chronic bottom trawling disturbance on benthic biomass, production and size spectra in different habitats

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## Abstract

Bottom trawling has widespread impacts on benthic communities and habitats. It is argued that the impact of chronic bottom trawling on benthic infauna depends on the natural disturbance levels to which benthic communities are adapted. We analysed biomass, production and size structure of two communities from a muddy and a sandy habitat, in relation to quantified gradients of trawling disturbance on real fishing grounds. We used an allometric relationship between body mass and individual production to biomass ratio to estimate community production. Chronic trawling had a negative impact on the biomass and production of benthic communities in the muddy habitat, while no impact was identified on benthic communities from the sandy habitat. These differences are the result of differences in size structure within the two communities that occur in response to increasing trawling disturbance.

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## 1. Introduction

Bottom trawling has global impacts on benthic communities and habitats and is relatively non-selective (Kaiser and Spencer, 1996; Rijnsdorp et al., 1998; Bergman and van Santbrink, 2000). Benthic invertebrate bycatches can account for up to 90% of commercial catches that include undersized target species and non-marketable species (Bergmann and Moore, 2001; Bergmann et al., 2002; Lindeboom and de Groot, 1998). This disturbance affects the diversity, abundance,

size structure and the production of benthic communities (Bergman and Hup, 1992; Kaiser and Spencer, 1996; Ball et al., 2000a,b; Bergman and van Santbrink, 2000; Collie et al., 2000; Frid et al., 2000; Bergmann and Moore, 2001; Jennings et al., 2001, 2002; Duplisea et al., 2002; Hermsen et al., 2003). With the increasing recognition of the need to adopt an ecosystem-based approach to fisheries management (Pikitch et al., 2004), it is imperative that the impact of bottom trawling on benthic communities is evaluated at the scale of commercial fisheries, to test the findings of small-scale manipulative studies (Jennings et al., 1999; Kaiser et al., 2000; Collie et al., 2000).

The mortality of benthic invertebrates that are removed as trawl bycatch is high (Kaiser and Spencer, 1995; Ramsay et al., 1997) but the mortality rates caused

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by bottom trawling are significantly higher for animals that remain on the seabed (Lindeboom and de Groot, 1998). The greatest damage occurs when animals come into contact with the hard parts of the fishing gear. Larger body-sized infauna are more susceptible to damage, particularly shallow burrowing species (Bergman and Hup, 1992). Gilkinson et al. (1998) demonstrated that smaller body-sized fauna are less susceptible to physical damage, as they are pushed aside with fluidized sediments generated by the pressure wave that occurs in front of the moving trawl. Many ecological processes, such as production, are functions of body mass (Dickie et al., 1987). The smaller organisms that are less vulnerable to trawl disturbance generally have a higher annual reproductive output (Brey, 2001) and higher intrinsic rates of natural increase, both of which decrease with body-size within a population (Brey, 1999; Collie et al., 2000; Duplisea et al., 2002). Bottom trawling could therefore lead to changes in community composition and size structure through removal of large body-sized species and the largest individuals within populations (Ball et al., 2000a).

Within the body-size spectrum, a small individual of a large species is equivalent to a large individual of a small species (Jennings et al., 2002). Hence, a size-based analytical approach is advantageous when assessing the impacts of trawling on complex marine communities that comprise numerous interactions among different trophic levels (Benoit and Rochet, 2004). Body mass is negatively correlated to the individual production to biomass ratio ( $P/B$ ) (Banse and Mosher, 1980; Dickie et al., 1987), so a shift to dominance by small-sized species could increase benthic productivity, as biomass would be reduced to a greater extent than production (Jennings et al., 2001; Hermsen et al., 2003; Hiddink et al., in press). However, overall reductions in benthic invertebrate production have been reported from areas of intense bottom trawling (Jennings et al., 2001). A size-based model developed by Duplisea et al. (2002) was used to assess the trawling impacts on the benthos and indicated that smaller animals are unlikely to have the capacity to utilize all the resources that become available when the abundance of large body-sized competitors is reduced. This suggests that under these conditions resources may be redirected to other components of the system that are not of direct use to fish and other predators that feed on benthos.

Habitat characteristics may be strong determinants of the relative impact of bottom trawling activity on benthic size structure and production. Hydrodynamics will affect the species composition of benthic communities by, for example, physical erosion of body structures and limi-

tation of larval settlement and survival (Warwick and Uncles, 1980; Wiekling and Kröncke, 2003). Stable environments, such as sheltered, fine sediment depositional areas, can support rich and diverse communities, including large body-sized, long-lived species, such as large bivalves and sea-urchins (Duineveld et al., 1991; Ball et al., 2000b). Coarser sediments that are subjected to storms and wave erosion are characterized by small-sized, fast growing, highly productive species, and the communities are characterized by low species diversity and abundances (Kaiser and Spencer, 1996). The degree of natural disturbance in which a community develops may therefore determine the degree to which it is affected by trawling disturbance (Kaiser and Spencer, 1996; Collie et al., 2000; Hiddink et al., in press). It is expected that, in the long-term, communities found in areas with high levels of natural disturbance will be more resilient to the increased mortality rates generated by bottom trawling activity, while communities from areas with low levels of natural disturbance may be susceptible to irreversible change.

We compared the effects of chronic disturbance by bottom trawling on two infaunal communities under different regimes of natural disturbance (sandy and muddy sediments). We analysed the impact of trawling in these communities by relating quantified gradients of trawling intensity to variations in biomass, production and community biomass size spectra. We hypothesised that stronger variation in biomass, production and size spectra in response to trawling would occur in the community from the more stable muddy environment.

## 2. Methods

### 2.1. Study sites

We chose a muddy-sand area in the Irish Sea (off Sellafield) and a sandy area in the Dogger Bank (central North Sea) as study sites (Fig. 1). Both areas show strong gradients in the intensity of exploitation by bottom trawlers (Lindeboom and de Groot, 1998), but are relatively homogeneous in terms of environmental conditions and benthic communities within each area. The Dogger Bank is mostly fished by beam trawlers that target plaice (*Pleuronectes platessa* Linnaeus) (Rijnsdorp et al., 1998). It is characterised by moderate hydrodynamic conditions, with wind driven waves and high currents that make sand transport sudden and unpredictable near the seabed (Molen, 2002). As a result, the accumulation of particulate organic material and other sources of food for the benthos is low (Wiekling and Kröncke, 2003). These conditions lead to the

presence of a highly variable benthic community with low species abundances and no apparent species dominance (Wiekling and Kröncke, 2003). The study area in the Irish Sea is intensively exploited by otter trawlers that target the Norway lobster (*Nephrops norvegicus* Linnaeus). The area is characterised by mild hydrodynamic conditions, with large tidal ranges that allow for mud–sand belts to accumulate (Jones et al., 2004). The benthic community is characterized by the abundant presence of fragile species, such as gastropods and sea urchins, and is dominated by the brittlestar *Amphiura filiformis* (Müller) (Mackie, 1990; Jones et al., 2004). Beam trawls and otter trawls are expected to have different effects on the sea bed. In general, these two types of gear are expected to be used in different types of sediment — otter trawls are generally used over soft-sediment beds, while beam trawls are more common in coarser sediment. Additionally, otters (doors) can be very heavy, scarring the seabed with marks that can be up to 20 cm deep, and that can last for more than a year under sheltered

conditions (Lindeboom and de Groot, 1998). Scarring of the seabed by beam trawlers is generally more ephemeral due to the physically dynamic nature of the relevant habitats.

Sampling took place in May and September of 2003, in the Irish Sea and the Dogger Bank, respectively. Within each area 7 stations were sampled for infaunal macro-invertebrates and environmental parameters. Sampling stations were chosen to cover the whole trawling intensity range that was available within each area while keeping environmental conditions within an area as homogeneous as possible. Stations were defined as  $1 \times 1$  km boxes on the Dogger Bank and  $1 \times 2$  km boxes in the Irish Sea. On the Dogger Bank, five Hamon grab samples ( $0.1 \text{ m}^2$ ) were taken at haphazard locations at each station. In the Irish Sea, four Jonasson Olausson box-corer samples ( $0.09 \text{ m}^2$ ) were taken at haphazard locations at each station. The maximum distance between stations within an area was 19 km on the Dogger Bank and 32 km in the Irish Sea. The experimental design is summarised in Table 1.

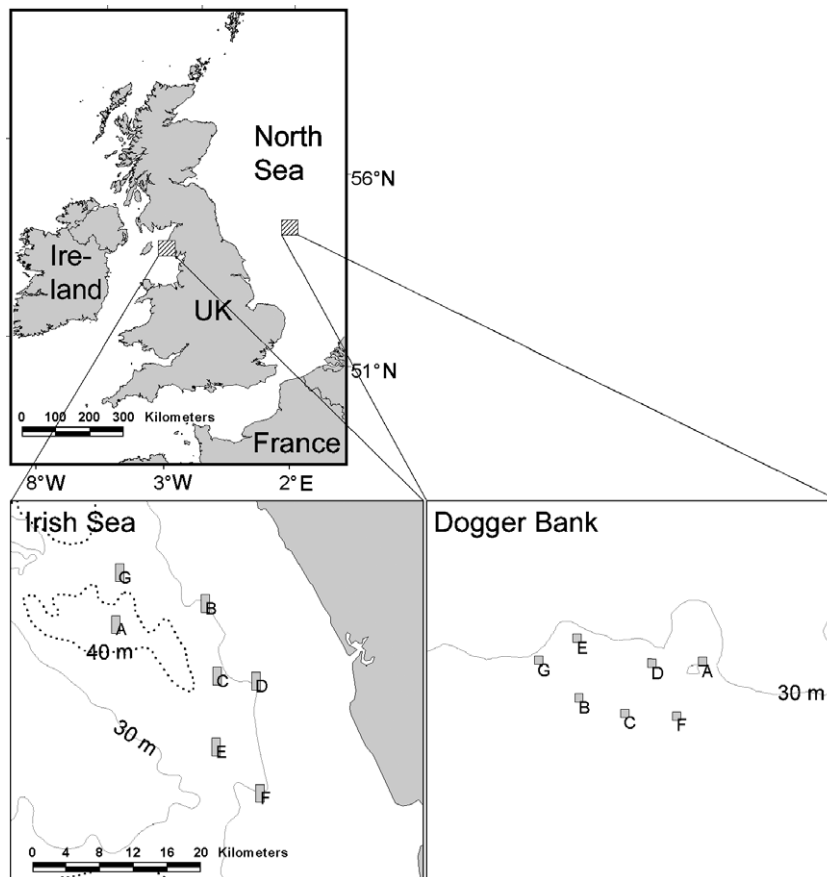


Fig. 1. Overview of the study areas and sampling stations in the Irish Sea and the Dogger Bank. The 30 and 40 m depth contours are shown.

Table 1  
Environmental characteristics and sampling procedure applied in study areas

Study area	Station	Station area (km $\times$ km)	Nr samples	Depth (m)	Trawling effort (yr $^{-1}$ )	Sediment type	MPD (mm)	Silt-clay%
DB	A	1.0NS $\times$ 1.0EW	5	30	0.390	Sand	0.141	2.5
DB	B	1.0NS $\times$ 1.0EW	5	25	1.550	Sand	0.137	1.8
DB	C	1.0NS $\times$ 1.0EW	5	25	0.770	Sand	0.227	0.6
DB	D	1.0NS $\times$ 1.0EW	5	29	0.000	Sand	0.126	2.5
DB	E	1.0NS $\times$ 1.0EW	5	28	0.970	Sand	0.221	2.0
DB	F	1.0NS $\times$ 1.0EW	5	26	0.000	Sand	0.189	0.7
DB	G	1.0NS $\times$ 1.0EW	5	28	0.000	Sand	0.173	2.9
IS	A	1.0NS $\times$ 2.0EW	4	40	3.330	Muddy-sand	0.079	45.0
IS	B	1.0NS $\times$ 2.0EW	4	30	1.410	Muddy-sand	0.086	57.9
IS	C	1.0NS $\times$ 2.0EW	4	33	3.530	Muddy-sand	0.083	74.7
IS	D	1.0NS $\times$ 2.0EW	4	27	0.400	Muddy-sand	0.099	28.7
IS	E	1.0NS $\times$ 2.0EW	4	33	2.320	Muddy-sand	0.086	71.4
IS	F	1.0NS $\times$ 2.0EW	4	30	0.400	Muddy-sand	0.108	33.9
IS	G	1.0NS $\times$ 2.0EW	4	38	0.100	Muddy-sand	0.103	15.9

“DB”: Dogger Bank; “IS”: Irish Sea; “MPD”: mean particle diameter (excludes the fraction <63  $\mu$ m); Silt-clay%: (percentage of the sediment <63  $\mu$ m in sample dry-mass).

## 2.2. Estimation of trawling disturbance

Trawling effort was expressed as the average trawling disturbance at each station over the period between 1995 and 2004, which includes the times of sample collection. Trawling effort was estimated from British Fisheries Protection (BFP) overflight data according to Jennings et al. (2002). The use of a relatively long period of overflight data was necessary to get a representative estimate of small scale patterns in chronic trawling intensity because the frequency of overflights is low. However, the number of overflights does not provide sufficient resolution to permit a good estimate of the time since an area was last trawled. We assumed that the relatively large area over which the collected samples were spaced (Table 1) overlapped both recent and old trawl-tracks and hence the average trawling intensity since 1995 was the most appropriate descriptor of the trawling disturbance experienced by the sampled community. Sightings of fishing vessels during BFP flights at stations were expressed as the number of sightings per unit of aircraft search effort (SPUE). The total area swept by one fishing vessel in a year (km $^2$ ) was then estimated by multiplying the number of fishing hours in a day fished by the average trawler, days in a year, average net width and trawling speed. These values vary between study sites, as different types of trawling activity take place at each location. Hence, we assumed that at the Dogger Bank the average trawler fishes at 6 kn with two 12 m wide beam trawls, for 24 h a day (Jennings et al., 2002). In the Irish Sea the average trawler fishes at 2.5 kn with a 60 m wide net, for 12 h a day, as most of the vessels are day-boats (H. Hinz, unpublished data). We estimated trawling effort at a scale of 6.25 km $^2$  to ensure

that the trawling intensity estimates were not affected by small scale patchiness in the distribution of effort (Rijnsdorp et al., 1998; Dinmore et al., 2003). A SPUE of 1 means that one trawler was always present and that therefore an area of 2336 km $^2$  was trawled on the Dogger Bank or 1217 km $^2$  was trawled in the Irish Sea. Trawling intensity (fraction of the area covered by trawls per year, yr $^{-1}$ ) was therefore calculated by multiplying SPUE with the area that is trawled by one vessel in a year, divided by 6.25 to correct for the area over which effort was estimated. Trawling effort distribution patterns may partly represent the suitability of the seabed for trawling (Rijnsdorp et al., 1998). Therefore we compared trawling effort with sediment characteristics and depth within each of the study areas to see if any relationship existed between these parameters and trawling activity.

Since 2001, detailed satellite observations (Vessel Monitoring System, VMS) have become available for all fishing vessels >24 m. These observations can be used to calculate an independent estimate of trawling effort to check the reliability of effort estimates from overflight observations (Dinmore et al., 2003). The veracity of the BFP data for the Irish Sea could not be related to VMS observations as its coverage has not been extended to the small otter trawlers that fish in the Irish Sea study area.

## 2.3. Sampling of the macro-infauna communities

Different types of sediment in the two study areas necessitated the use of different types of sampling gear. In the Dogger Bank area, macro-infauna samples were collected with a 0.1 m $^2$  Hamon grab, which has a maximum penetration of 10 cm (Eleftheriou and Holme, 1984). This penetration depth is considered effective for

quantitative analysis in coarse sediment, as most animals are expected to be found within the top 10 cm (Dauwe et al., 1998; Lindeboom and de Groot, 1998). In the Irish Sea, a 0.09 m<sup>2</sup> Jonasson Olausson box-corer was used. This corer has a maximum penetration depth of 50 cm, but only the top 10 cm layer of the cores was used, to make the biological data comparable between study areas. The samples were sieved through a 1 mm mesh at both sites, and preserved in buffered 4% formalin and seawater.

All animals from the samples were identified in the laboratory and individual wet mass (WM) determined after blotting. The following protocols were applied: tubiculous animals were removed from their tubes prior to weighing; body parts were assembled to complete animals whenever possible, but were discarded when <30% of the organism remained. All individuals from the phylum Phoronida were excluded from analysis due to the absence of an efficient method of removing animals from their sediment tubes. The abundance of the ophiuroid *Amphiura filiformis* (Müller) was found to be higher than 100 individuals per sample in many of the Irish Sea samples. Whenever total abundance exceeded 50 individuals of this species, 20% sub-samples were taken prior to weighing and corrections applied to all calculations.

We limited the analysed body-size range of sampled individuals used for calculations. All individual wet-weights were assigned to log<sub>2</sub> size-classes to exclude classes for which sampling was considered too low for quantitative analysis. The lower body-size limit was defined at 0.001 g (WM) as this was the lowest size-class that was sampled in all stations and at both study sites. Since infaunal samples were sieved through a 1.0 mm mesh, it is considered that this lower limit only included macro-infauna. Size structure is considered to be a conservative feature of marine communities (Benoit and Rochet, 2004), so different body-size range upper limits were accepted between study sites, covering up to 95% of the observed size-class frequencies in each case. 0.5 g was set as the upper limit for the Dogger Bank samples, while for the Irish Sea it was set at 0.25 g.

Sediment samples (200 g) were collected with a Day Grab (Eleftheriou and Holme, 1984) at each station, for Particle Size Analysis.

#### 2.4. Community biomass and production estimates

Subsequent conversions between wet mass and ash-free dry mass (AFDM) were made, using conversion factors provided by Brey (2001). Secondary production was estimated from individual weights (AFDM) based on the allometric relationship between weight and  $P/B$  (Banse and Mosher, 1980; Dickie et al., 1987). The

relationship was described using the equation given by Jennings et al. (2002):

$$\log_{10}P/B = -0.431 - (\log_{10}B^{0.236})$$

which is adequate for the analysed body-size range. We considered this relationship to be valid in our analysis as we did not account for trophic positions within the community (Thiebaut and Dickie, 1993). Community biomass and production were calculated per station as the mean of the sums of all individual weights, and production values, per replicate grab/core.

Both community biomass and production estimates were analysed using Mixed Effects Models (MEM). We used two main factors: trawling effort, and the abiotic variable that showed the greatest variation within study areas, and showed strong correlation with trawling effort. Habitat (i.e., study area) was considered as grouping variable (Pinheiro and Bates, 2000). The use of MEM was intended to: (1) incorporate in the model random factors that related to habitat uniqueness, i.e., to include the possible effect of unknown variables that were not considered in the model and that, additionally to the ones that were, contribute to the distinctness of the study areas (Pinheiro and Bates, 2000); (2) observe how the two main factors affected community biomass and production between and within habitats. The procedure for building the MEM was the same for biomass and production analysis, and consisted of the following. In step one, a linear model was fitted to the data ignoring grouping structure, and fits were compared between different fixed effects structures using  $F$ -statistic,  $R^2$ , and diagnostic plots. In step 2, random structure was built, starting with random effects for all factors, and using restricted maximum-likelihood estimation of coefficients. In this stage, random effects were removed from the model sequentially, and different models were compared using Akaike's and Bayesian information criteria (AIC and BIC). After the random structure of the model was set, a third step involved maximum-likelihood estimation of model coefficients and comparison of the latter model with the linear model (from step 1), using the log-Likelihood ratio test. Additionally, separate linear models were fit to each subset of data to make inferences about the individual effects of the considered factors within each of the habitats.

We then analysed the contribution of different taxonomical classes to community biomass and production. We attempted to model the variations of classes that were considered to best explain the observed variations of community biomass and production, and that were identified in at least half of the stations. Biomass and production of these classes were compared

to trawling effort and another relevant variable (see above), within each study area.

A less detailed analysis of the effect of trawling on benthic invertebrate communities in the Dogger Bank area is presented elsewhere (Hiddink et al., in press).

### 2.5. Construction of biomass size spectra

Individual weights (AFDM) were assigned to  $\log_2$  size-classes; the classes were reported as the upper end of the class interval. Total biomass per  $\log_2$  size-class per station was calculated as the mean of the sums of all individual weights (AFDM) per size-class of all replicate grabs/cores. Biomass values were normalised between size-classes, relative to the width of narrowest size class. We subsequently determined which of the measured environmental parameters was best related to the observed local variations in community size spectra using a BIOENV analysis (Clarke and Warwick, 1994). This procedure calculates the maximum rank correlation that occurs between the environmental and community (size spectra) similarity matrices. For the calculation of the environmental variable similarity matrix, we included mean particle diameter (MPD) in the analysis because size spectra are thought to be related to particle size distribution within the sediment (Schwinghamer, 1981; Duplisea and Drgas, 1999). We also included the silt-clay percentage as an indicator of organic content in the sediment, which is known to influence the presence of bacteria. Microbial activity within the sediment may affect production of the ecosystem (Duplisea et al., 2001). Mean water depth was also included as it is considered to have a major influence on community structure (Duineveld et al., 1991; Frid et al., 2000).

## 3. Results

### 3.1. Trawling effort estimates

Trawling intensity varied between 0.00 and  $1.55 \text{ yr}^{-1}$  in the Dogger Bank and between 0.10 and  $3.53 \text{ yr}^{-1}$  in the Irish Sea (Table 1). The trawling intensity as estimated using overflight observations correlated significantly with the trawling intensity as estimated using VMS observations (Pearson correlation  $\rho=0.898$ ,  $p=0.003$ , Fig. 2), although the absolute values deviated by about a factor 3. Trawling intensity correlated significantly with MPD ( $\rho=-0.480$ ,  $p=0.041$ ), the silt-clay fraction ( $\rho=0.746$ ,  $p=0.001$ ), and depth ( $\rho=0.490$ ,  $p=0.038$ ). The silt-clay fraction was therefore incorporated in the mixed effects models for biomass and production because this was found to have the strongest correlation

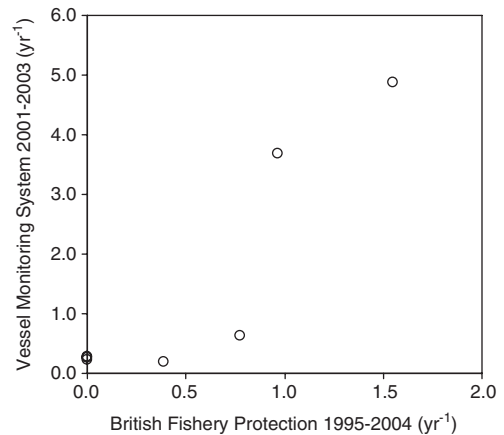


Fig. 2. Comparison of trawling effort estimates for the Dogger Bank using British Fisheries Protection and Vessel Monitoring System data.

with trawling intensity, and had greater variation among sites ( $cv_{\text{silt-clay}}=1.13$ ,  $cv_{\text{MPD}}=0.40$ ,  $cv_{\text{depth}}=0.16$ ).

### 3.2. Biomass and production estimates

In total, 1555 and 375 individuals were identified in the Irish Sea and the Dogger Bank respectively, belonging to 71 and 56 taxa. 90.4% of all individuals in the Irish Sea samples (within the analysed size range) were collected from the top 10 cm sediment layer of the cores. Biomass and production levels of the Irish Sea community were always higher than in the Dogger Bank, when trawling intensities overlapped (Fig. 3a and c).

Community biomass and production varied with trawling intensity and the silt-clay fraction in the two study areas (Fig. 3). The best linear models estimated for biomass and production included the silt-clay fraction in sediment and the interaction between this factor and trawling intensity as independent variables (biomass:  $\log[\text{biomass}]=0.563+0.014(\text{silt-clay}\%) - 0.038(\text{silt-clay}\% \times \log[\text{trawling intensity}])$ ,  $R^2=0.460$ ,  $F_{2, 11}=4.683$ ,  $p=0.034$ ,  $\log\text{-Likelihood}=-8.497$ ; production:  $\log[\text{production}]=-0.308+0.016(\text{silt-clay}\%) - 0.039(\text{silt-clay}\% \times \log[\text{trawling intensity}])$ ,  $R^2=0.499$ ,  $F_{2, 11}=5.408$ ,  $p=0.023$ ,  $\log\text{-Likelihood}=-7.428$ ). The best mixed effects models (MEM) estimated for biomass and production, and the same independent variables, included only one random effect, for the interaction of the two factors in both cases (biomass:  $\log\text{-Likelihood}=-8.497$ ; production:  $\log\text{-Likelihood}=-7.428$ ). The log-Likelihood ratio test showed that, for both biomass and production, the MEM did not explain the data significantly better than the linear model (biomass:  $\log\text{-Likelihood ratio}=0.001$ ,  $p=0.980$ ; production:  $\log\text{-Likelihood ratio}=0.001$ ,  $p=0.980$ ). These results indicate that sediment composition and the interaction of

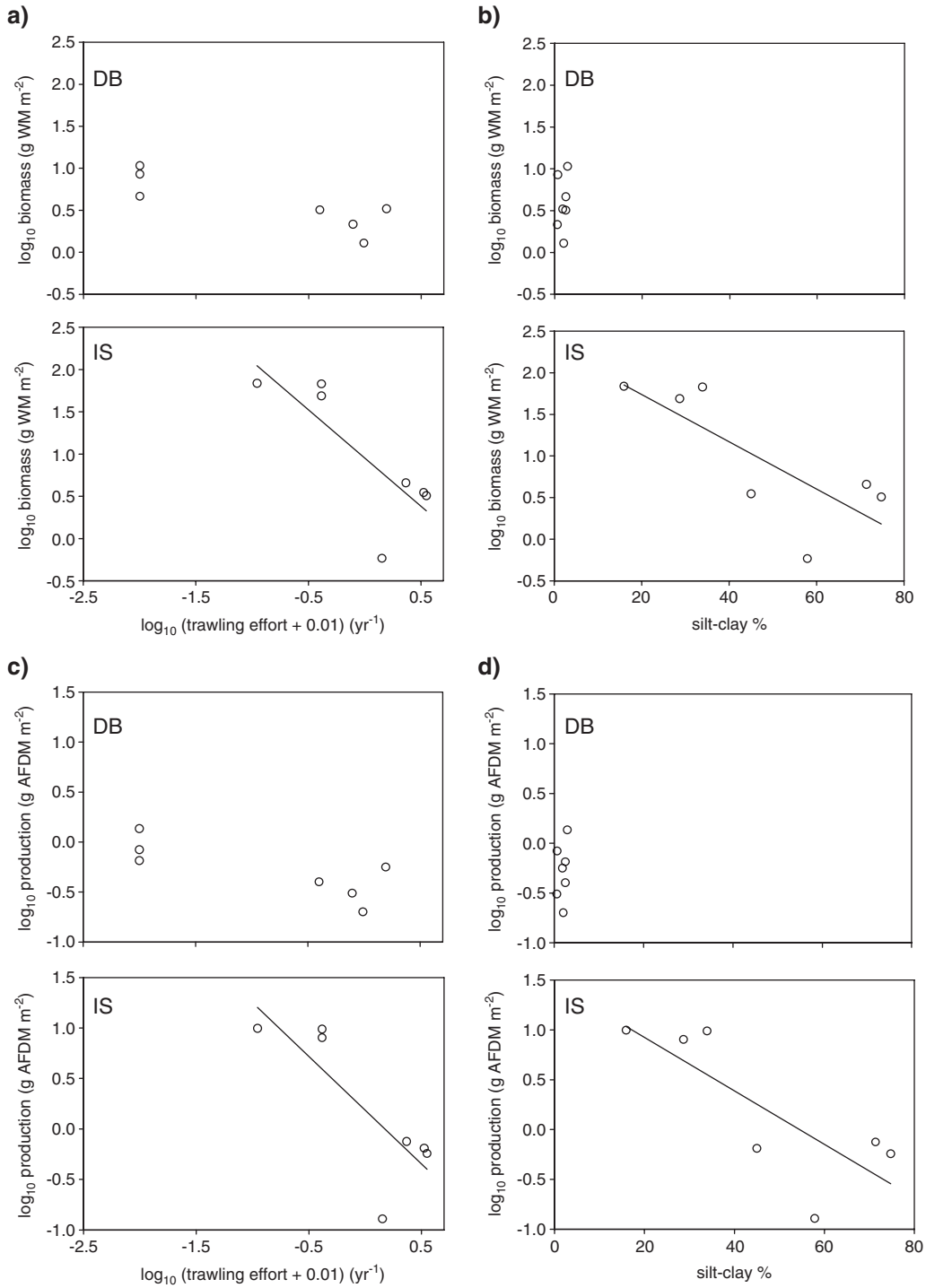


Fig. 3. Biomass and production estimates. (a) The relationship between biomass and trawling effort; (b) the relationship between biomass and the silt-clay fraction in the sediment; (c) the relationship between production and trawling intensity; (d) the relationship production and the silt-clay fraction in the sediment. “IS”: Irish Sea; “DB”: Dogger Bank.

sediment composition with trawling intensity best explained the observed variation in the variables considered. The separate linear models fitted to the biomass and

production data with trawling and the silt-clay fraction (Irish Sea), had marginally significant effects in all cases (Tables 2 and 3). The coefficients for the separate models

calculated for the Dogger Bank were not significant (Tables 2 and 3). Thus, sediment composition only had an effect on benthic biomass and production in the Irish Sea. The significant interaction of sediment composition and trawling intensity show that the observed variations in community biomass and production are not solely due to differences in habitat characteristics, but that trawling intensity does affect biomass and production of the analysed communities when the effect of sediment alone is taken into account.

Community composition in the Irish Sea appears to change considerably in response to trawling intensity. Biomass and production are dominated by brittlestars in less intensively trawled stations (Fig. 4a and c), while in the most intensively disturbed areas there was no consistent dominance of community composition. Only the biomass and production of *Stelleroidea*, which were solely represented by the species *Amphiura filiformis*, decreased significantly with increasing trawling intensity and the silt-clay fraction in the sediment (biomass:  $\log[\text{biomass}] = 2.796 - 0.604 (\log[\text{trawling intensity}]) - 0.065 (\text{silt-clay}\%)$ ,  $R^2 = 0.876$ ,  $F_{2,4} = 14.181$ ,  $p = 0.015$ ; production:  $\log[\text{production}] = 1.034 - 1.032 (\log[\text{trawling intensity}]) - 0.037 (\text{silt-clay}\%)$ ,  $R^2 = 0.864$ ,  $F_{2,4} = 12.751$ ,  $p = 0.018$ ). *A. filiformis* accounted for an average of 64.13% of community biomass and 62.0% of community production when present. In the Dogger Bank, there was no dominant taxonomical group (Fig. 4b), but polychaetes contributed most to community production (Fig. 4d). There were no significant effects of trawling intensity and/or the silt-clay fraction on biomass or production of the major taxonomical groups for the Dogger Bank community.

### 3.3. Community size spectra

Different size structure patterns emerged between the two study areas, when compared with trawling effort. In the Irish Sea, biomass distribution through size classes changed with increasing trawling intensity (Fig. 5a). In the less intensively trawled stations, there was a bimodal

Table 3

Linear models fit to the Dogger Bank (DB) and Irish Sea (IS) production data subsets

Study area	Model factor	Coefficient estimate	<i>t</i> -value	<i>p</i> -value
DB	$\log_{10}$ trawling effort	-0.210	-1.445	0.179
IS	$\log_{10}$ trawling effort	-1.066	-4.008	0.002
DB	Silt-clay%	0.082	0.446	0.665
IS	Silt-clay%	-0.027	-3.530	0.005

distribution of biomass through size range that peaked in both large and small size classes. This biomass maximum was higher for larger size classes. With increasing trawling intensity, biomass levels decreased across the entire size range. In the Dogger Bank, biomass distribution across size-classes did not appear to change as a direct result of increasing trawling intensity (Fig. 5b). Community size structure seemed to vary across the entire trawling intensity range, but it appeared that the biomass maximum shifted to smaller size-classes as trawling disturbance increased. BIOENV analysis performed with size spectra data revealed that trawling intensity was the variable that best correlated with size structure variations at both study sites. In the Irish Sea, the calculated ranked Spearman coefficient was high ( $\rho_s = 0.645$ ) and confirmed that size structure varied in the same manner as the trawling effort. In the Dogger Bank, calculated ranked Spearman coefficient was low ( $\rho_s = -0.208$ ), indicating an absence of a biological relationship between community size structure and trawling effort. However, this may partly be explained by the limited range of relative trawling intensity recorded for the Dogger Bank cf. the Irish Sea. This is supported further by the cluster analysis performed on size spectra (Fig. 6). For the Irish Sea, size spectra (Fig. 6a) were clearly grouped according to trawling intensity, indicating that, within this study area, communities that have similar levels of trawling disturbance also had similar size structures, whereas for the Dogger Bank, no such relationship was apparent (Fig. 6b).

## 4. Discussion

To date, this is the first study to analyse the effects of chronic trawling disturbance on the size structure of infaunal communities that occur in different habitats. Recent site-specific studies have focused on the impact of trawling on community size structure, but no comparison has been made between communities that are adapted to different types of natural disturbance. Our

Table 2

Linear models fit to the Dogger Bank (DB) and Irish Sea (IS) biomass data subsets

Study area	Model factor	Coefficient estimate	<i>t</i> -value	<i>p</i> -value
DB	$\log_{10}$ trawling effort	-0.261	-1.656	0.129
IS	$\log_{10}$ trawling effort	-1.139	-3.950	0.003
DB	Silt-clay%	0.062	0.300	0.770
IS	Silt-clay%	-0.028	-3.318	0.008

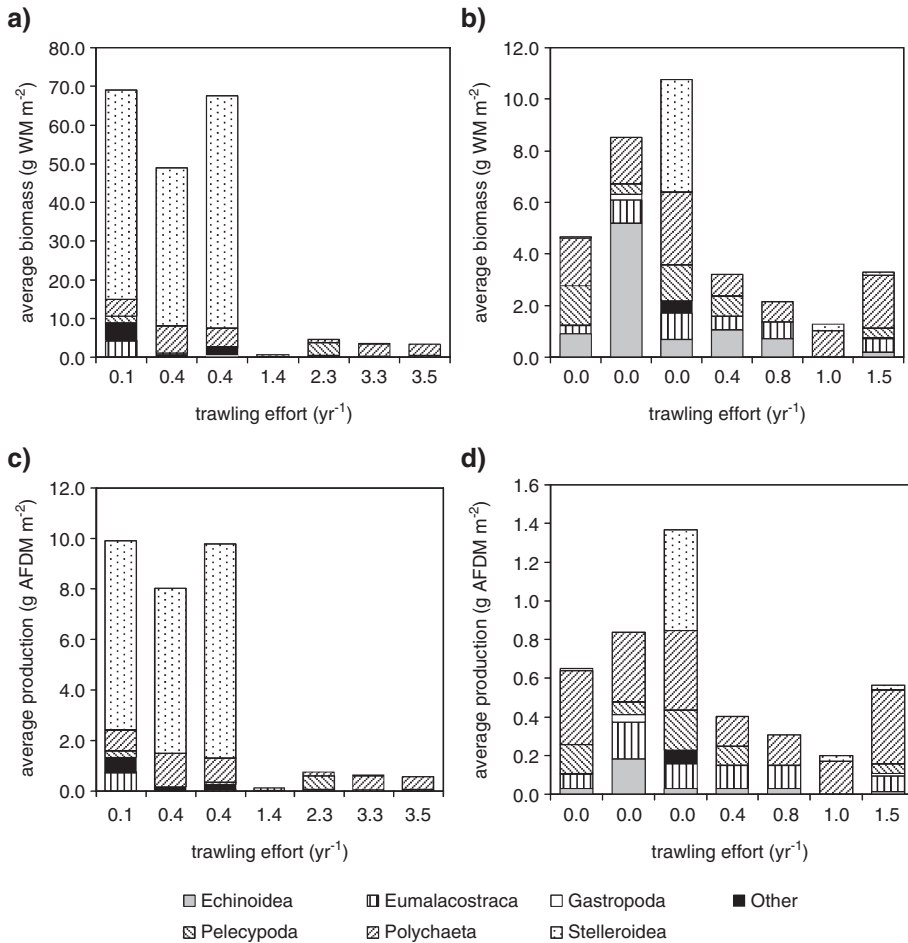


Fig. 4. Contribution of taxonomical groups (at the Class level) to community biomass and production. (a): Irish Sea biomass; (b): Dogger Bank biomass; (c) Irish Sea production; (d): Dogger Bank production.

results demonstrate that although trawling has a ubiquitous negative impact on infaunal macro-invertebrate communities, the manner in which size structure is affected differs distinctly between different habitats.

The mixed-effects modelling (MEM) approach used to explore the response of biomass and production to fishing disturbance, was chosen to eliminate the influence of variables that were not considered, since we compared data from two different habitats. However, after accounting for silt content and trawling, no additional variables would have improved the model fit. When analysed together, biomass and production levels of the two communities were found to be related to trawling intensity and sediment characteristics. Although significant, the two linear models were found to have low coefficients of determination. We believe that this is the result of the very different responses that were observed for the two communities in response to the analysed factors.

Community biomass and production in the Irish Sea decreased simultaneously with increasing trawling intensity and the proportion of the sediment silt-clay fraction. Therefore, the present experimental design could not disentangle the impact of trawling and sediment composition on the composition of the Irish Sea community, since the two factors act in the same direction. Because sediment composition generally correlated with the hydrodynamic conditions, the stations within the Irish Sea may in fact have represented infaunal communities adapted to different levels of natural disturbance, which could have compromised our experimental design. However, trawling increases the fraction of fine sediment on superficial layers of the seabed. [Trimmer et al. \(2005\)](#) found significant correlations between trawling intensity and sediment silt content. It is believed that this is the results of continual resuspension of sediment by trawling, which in the absence of significant advective transport can lead to the accumulation

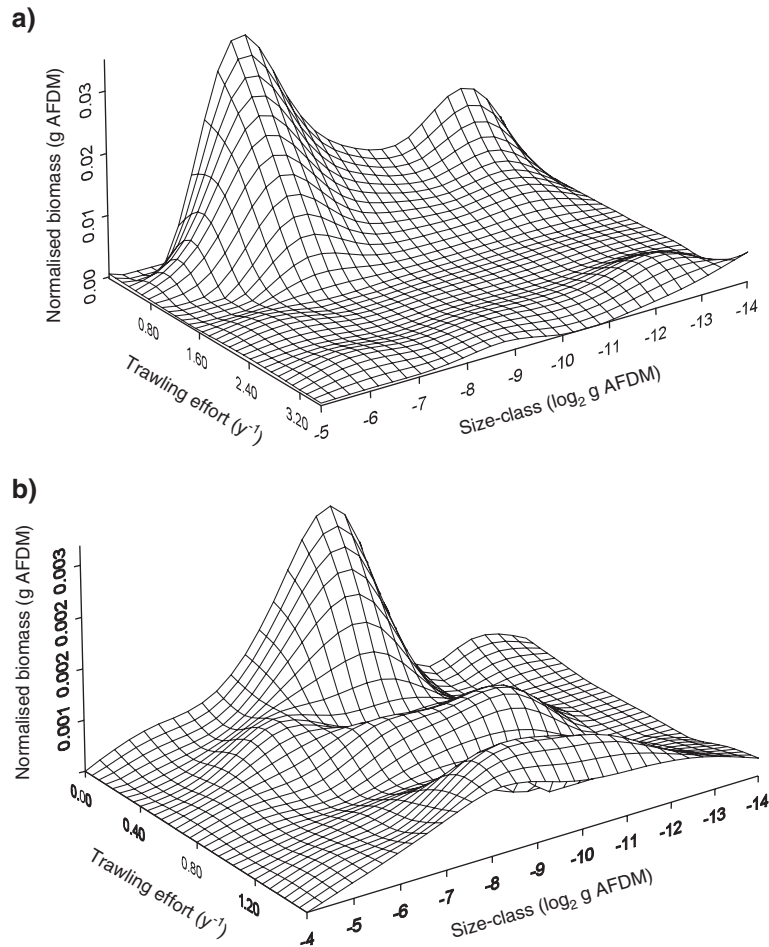


Fig. 5. Normalised size spectra in relation to trawling intensity of the Irish Sea (a) and the Dogger Bank (b).

of fine sediments in the superficial layers of trawling grounds (Trimmer et al., 2005; Jennings and Kaiser, 1998). We suggest, therefore, that the identified correlation between sediment composition and biomass and production in the Irish Sea is in fact a consequence of trawling activity.

The loss of community production in the Irish Sea, and apparent resilience of the Dogger Bank benthos, may be explained by the observed variation in patterns of size structure in the two communities, in response to trawling disturbance. As biomass decreased across the entire body-size range of the Irish Sea community, production levels were not sustained. The analysis of the Irish Sea community size spectra agrees with the results found by Duplisea et al. (2002), in which community size structure was shown to be strongly influenced by trawling disturbance. This finding therefore suggests that the small body-sized fauna are incapable of utilizing the resources that become available as larger fauna are

removed from this community, and demonstrates that trawling disturbance does not always lead to dominance by small sized species.

Conversely, the analysis of the Dogger Bank data demonstrated that the size spectra of infauna did not clearly vary as a function of increasing trawling intensity. It is possible that the apparent redirection of the biomass maximum to smaller sized fauna may in part explain the absence of an effect of trawling on production levels in this community. Therefore, the apparent absence of a clear effect of trawling on the Dogger Bank community can be explained by its adaptation to natural disturbance by the general dominance of small-bodied polychaetes, which do not seem to be greatly affected by trawling.

In the Irish Sea biomass and production is dominated by a single species, the brittlestar *Amphiura filiformis*. The abundance of *A. filiformis* seems to explain most of the effect of trawling in the Irish Sea. A problem in the

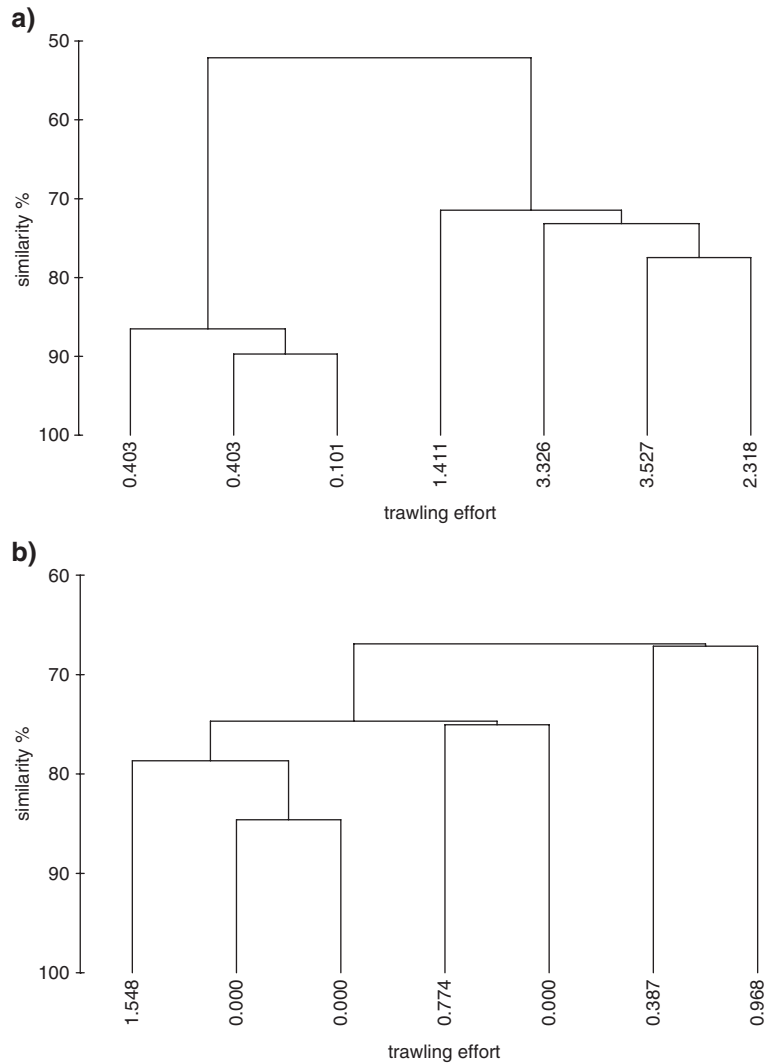


Fig. 6. Cluster analysis of size spectra from the Irish Sea (a) and the Dogger Bank (b). Vertical axis show Bray–Curtis similarity index. Stations are labelled by trawling effort (Table 1).

interpretation of the abundance of *A. filiformis* is that its abundance decreased simultaneously with trawling intensity, increasing mud content and increasing depth. *A. filiformis* is known to occur in abundance at depths up to 100 m (Hagberg et al., 2003) and therefore depth is unlikely to explain the observed decrease in abundance. It is well established that *A. filiformis* only occurs in muddy sediments, but the upper limit of the mud content of the sediment it tolerates is unknown. We can therefore not exclude entirely the possibility that the heavily trawled areas were unsuitable for *A. filiformis* due to environmental constraints. Nevertheless, trawling remains the most likely mechanism for the observed trend between *A. filiformis* and fishing intensity. Trawling resuspends sediment in large quantities (Durrieu de

Madron et al., 2005) which can inhibit the growth of *A. filiformis* (Amaro, 2005). Amaro (2005) suggested that the benthic community in a frontal area switched from a situation with relatively low sediment loads, many *A. filiformis* and few burrowing mud shrimps (*Callinassa subterranea* and *Upogebia deltaura*), to a situation where resuspension of sediments by the mud shrimps caused *A. filiformis* populations to collapse. The pattern was also observed in the Irish Sea, with more mud shrimps (in this case *Jaxea nocturna*) in the heavily trawled areas and more *A. filiformis* in the lightly trawled area. As deep burrowing shrimps are less vulnerable to trawling than *A. filiformis* they may come to dominate heavily trawled areas and their bioturbatory activities may exclude *A. filiformis*. In addition, the latter is highly

vulnerable to physical disturbance and may be killed or injured directly by trawls. Increased predation due to exposure after trawling might also be a substantial cause of death (Kaiser and Ramsay, 1997). In an experimental trawl impact study the number of *Amphiura filiformis* that occurred in a trawling lane was much lower than in an adjacent control area, while the sediments were similar (Smith et al., 2000). *A. filiformis* is sensitive to O<sub>2</sub> deprivation (Skold et al., 2001) which occurs as trawling activity reworks reduced substrata into the water column (Trimmer et al., 2005).

It is clear that across the trawling intensity range both the biomass and production of the Dogger Bank community was lower than for the Irish Sea community. So although no evidence was found for a significant negative impact of bottom-trawling at the Dogger Bank, it may be the case that these effects were not detected because biomass and production levels are inherently low, even at low intensities of disturbance which concurs with current model predictions (Hiddink et al., in press).

Within the most fragile habitat were found small areas where the infauna community was still well preserved, while in areas of more intense trawling disturbance it had already been strongly adulterated. This could only be the case because spatial distribution of trawling effort is patchy even, as shown, within similar habitat conditions. The results here presented corroborate the idea that any management policy that would increase the homogeneity of fishing effort distribution within one fishing ground could have severe consequences on marine communities (Dinmore et al., 2003). As the initial effects of fishing benthic communities are known to be stronger (Jennings and Kaiser, 1998; Hiddink et al., in press), the redistribution of fishing effort to areas that were previously not fished would have greater damage than maintaining effort distributions and preserving small, lightly disturbed areas within one fishing ground (Dinmore et al., 2003). The redistribution of fishing effort within one fishing ground will have an even stronger impact if fragile habitats, and communities, become disturbed.

Our study showed that bottom trawling affects the lower levels of the food-web that are an important energy source to higher trophic levels, especially to many commercially-important demersal species (Rijnsdorp et al., 1998; Hermsen et al., 2003). It is imperative that fishery management begins to incorporate all the levels that are affected by fisheries within the ecosystem, beyond target-species. The results of the present study emphasise that management policy that increased the homogeneity of fishing effort distribution within current fishing grounds could have severe consequences for benthic community structure (Dinmore et al., 2003;

Jennings and Kaiser, 1998; Hiddink et al., in press). It is clear that while certain habitats and their associated communities are relatively resilient to fishing disturbance, others are far less resilient. The use of size-structure based responses enables the results of the present study to inform predictions about likely effects of trawling in soft-sediment communities elsewhere.

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