

Effects of chronic trawling disturbance on the production of infaunal communities

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ABSTRACT: Trawling causes widespread physical disturbance in shallow shelf seas. While the impacts of trawling on the biomass and community structure of benthic fauna are well known, no existing studies have quantified the effects of trawling disturbance on the absolute production of small benthic infauna. We investigated the effects of beam trawling disturbance on the production of small benthic infauna (AFDM > 0.78 to 62.5 mg) at 9 sites that were subject to a 17.5-fold range in annual trawling disturbance, using a size-based approach that could be applied to other soft-bottom systems. We developed a generalised additive model to test for relationships between trawling disturbance and infaunal production and size structure, after accounting for differences in sediment characteristics and depth. The statistical power of our analyses to detect linear and non-linear relationships between production and disturbance, including increased production at intermediate levels of disturbance, was high (>90% probability of detecting a 50% change in production across the range of disturbance). The analyses showed that trawling frequencies of 0.35 to 6.14 times yr⁻¹ did not have a significant effect on the production of small infauna or polychaetes. This result contrasts with order of magnitude decreases in the production of large infauna, and shows that small polychaetes with fast life histories are less vulnerable to trawling disturbance. Since small infaunal polychaetes are a key source of food for flatfishes, we conclude that beam trawling disturbance does not have a positive or negative effect on their food supply.

KEY WORDS: Fishing effects · Size spectra · Production · Infauna · Disturbance · Power analysis

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INTRODUCTION

Bottom trawling causes chronic and widespread disturbance to soft-sediment communities in shelf seas (De Groot & Lindeboom 1994, Jennings & Kaiser 1998, Lindeboom & de Groot 1998, Hall 1999, Collie et al. 2000b, Kaiser & De Groot 2000). The relative impacts of this disturbance depend on the frequency of trawling and levels of natural disturbance. In general, studies of trawling impacts have compared community structure at sites subject to different intensities of trawling disturbance; usually based on multivariate analysis of transformed species abundance data. Such

studies have focused on impacts on larger macrofauna and habitat forming species, primarily because reductions in their abundance and diversity are an important conservation issue, and because they provide habitat for bottom-dwelling fishes (Auster & Langton 1999, Collie et al. 2000a,b, Koslow et al. 2001). Few studies have considered the implications of trawling disturbance on ecosystem processes (Duplisea et al. 2001). Such processes include the production of the benthic community and its role in supporting the production of fished species which, from a human perspective, is an important function of the marine ecosystem.

Infauna are an important link in the food chains supporting fish production. Commercially important flatfishes such as plaice *Pleuronectes platessa* and sole *Solea solea*, that live on open sand and mud-sand sea

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beds (Kaiser et al. 1999), feed predominantly on infaunal polychaetes (Braber & De Groot 1973, De Clerck & Buseyne 1989). Since the advent of beam trawling in parts of the NE Atlantic, there have been increases in the growth rates of flatfishes, and these have been linked to improved feeding conditions (Rijnsdorp & Vingerhoed 2001, Rijnsdorp & Van Leeuwen 1996). This implies that there may have been absolute increases in the abundance of small polychaetes in trawled areas (Rijnsdorp & Van Leeuwen 1996), although the analysis is complicated by increases in primary production over the same period (Kroncke et al. 1998, Reid et al. 1998). Small infauna could proliferate in response to trawling disturbance because trawling significantly reduces the biomass of larger benthic fauna (Bergman & Van Santbrink 2000a,b, Kaiser et al. 2000, Jennings et al. 2001a), and other organisms that can withstand trawling disturbance may benefit from reduced competition. The only organisms likely to do this will have small body sizes and high intrinsic rates of increase, characteristics that reduce their vulnerability to trawling (Gilkinson et al. 1998, Bergman & Van Santbrink 2000a,b).

The only existing study of trawling impacts on infaunal production showed that there were 6-fold reductions in total community production across a gradient of trawling disturbance (Jennings et al. 2001a). This study focused on an assessment of the relative production of larger infauna, and the reductions in production were largely due to reductions in the biomass of large bivalves and spatangoids, species that are very vulnerable to trawling (Rumohr & Krost 1991, Bergman & Van Santbrink 2000a,b, Rumohr & Kujawski 2000). Multivariate analyses (Clarke & Ainsworth 1993) showed that the reduction in biomass and production of larger animals was due to trawling effects rather than sediment type or depth (Duplisea et al. in press). The results were clear for the large bivalves and spatangoids that play a key role in bioturbation and community production; however, for the small polychaetes and bivalves that support flatfish production, the sampling design and analysis provided little power to determine the effects of trawling.

Size-based analyses provide a useful approach for studying the impacts of trawling disturbance on production processes because mortality rates and the capacity to sustain elevated mortality are functions of body size (Brey 1990, 1999). Marine soft-sediment communities have characteristic distributions of biomass among body mass classes, and analyses of these size spectra have been used to describe structure and energy flux in ecosystems (Schwinghamer et al. 1986, Duplisea 2000). Within a size spectrum, ecological processes such as production are treated solely as a function of body mass and thus, a small individual of a large

species is equivalent to a large individual of a small species in the same body mass class. Changes in the slopes and intercepts of the size spectra reflect changes in body-size distribution in the community and can indicate whether the depletion of larger individuals leads to increased biomass or production in smaller size classes.

Most studies of trawling effects have relied on experiments. These experiments are often short-term and do not reflect the chronic disturbance caused by trawls in real fisheries. To assess the impacts of trawling disturbance at the scale of the fishery requires knowledge of temporal and spatial variation in trawling intensity, data that are rarely available on appropriate scales (Collie et al. 1997, Thrush et al. 1998, Kaiser et al. 2000, Jennings et al. 2001a,b). If quantified levels of trawling disturbance in real fisheries could be linked to quantifiable changes in the production of benthic communities, this would be a first step towards predicting and mitigating any undesirable and indirect effects of fishing on the ecosystem processes that lead to fish production.

The aim of this study is to investigate the effects of beam trawling disturbance on the production of the smaller size classes of benthic infauna that support flatfish production. We use a size-based approach that could be applied to other soft-bottom systems. Our study was conducted on real fishing grounds with a quantified history of trawling disturbance. We used a generalised additive model (Hastie & Tibshirani 1990) to test for the effect of trawling disturbance, and to account for differences in sediment type and depth that could also affect infaunal production. Because the variation in these predictor variables was not controlled, it is important to quantify how effective the statistical analyses of these data are likely to be. This is particularly important when interpreting statistical non-significance under a precautionary regime (Peterman & M'Gonigle 1992). We have therefore assessed the statistical power of all our analyses to detect (1) linear increases and decreases in infaunal production; and (2) increased production at intermediate levels of disturbance.

MATERIALS AND METHODS

Study site. The Silver Pit region of the central North Sea (Fig. 1a) is a relatively homogeneous area of sand and mud sediment that is regularly fished by beam trawlers targeting sole and plaice. The Silver Pit is 50 to 75 m deep, with mean winter and summer temperatures of 5 and 13.5°C, respectively. The production of benthic communities was studied at 9 sites in the Silver Pit (Fig. 1b). Sites were 5 n miles (9.3 km) north-south

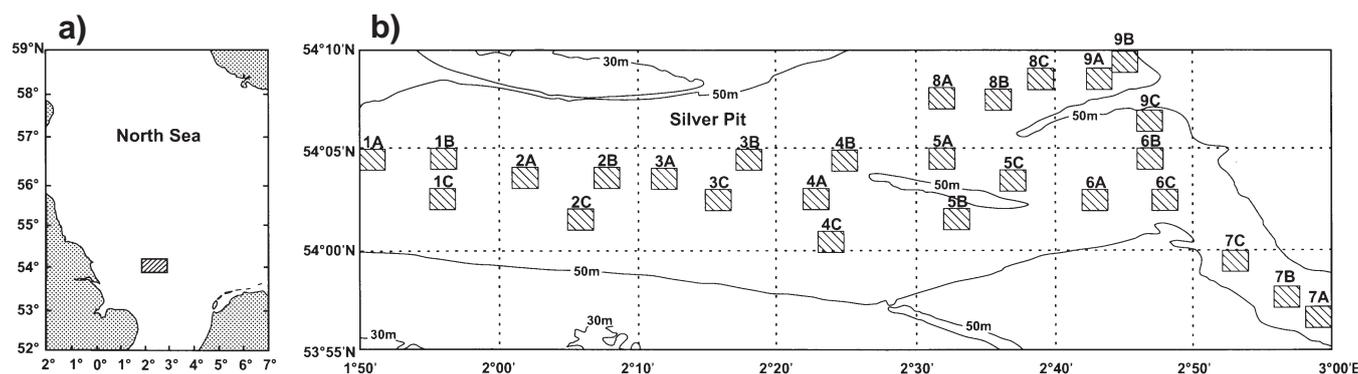


Fig. 1. The Silver Pit region in (a) the central North Sea and (b) the location of Sites 1 to 9 and Boxes A, B and C within the Silver Pit. The 30 and 50 m depth contours are shown

by 6 n miles east-west (11.1 km), and were selected haphazardly in an area where there were known to be spatial variations in the frequency of trawling disturbance (Jennings et al 2000). Within each site, we sampled the infaunal community in 3 boxes of 1 n mile north-south by 1 n mile east-west (1 n mile = 1.85 km). Boxes were haphazardly located within sites.

Sample collection and processing. Benthic infauna were sampled with a NIOZ (Netherlands Institute for Sea Research) corer. This device takes a circular sediment core of 35.7 cm internal diameter (area of 0.1 m²) to a depth of 40 cm. Ten cores were taken from each of the 27 boxes, 5 from 21 November to 4 December 2000 and 5 from 5 to 18 April 2001, to account for the variations in size structure that result from 'pulses' of recruits growing up the size spectrum. Core samples were sieved through 1 mm² mesh. All infaunal species retained by the mesh were removed for processing and preserved in 4% formalin diluted with seawater and buffered with 3 g l⁻¹ sodium acetate. A sediment sample was also taken from each core for particle size analysis (Dyer 1986). This was removed with a 5.5 cm diameter perspex tube and frozen to -20°C pending analysis. After thawing, sediment samples were wet-sieved through a 500 µm sieve and the fraction greater than 500 µm was oven-dried at 90°C for 24 h. This fraction was then dry-sieved at 0.5 phi intervals, down to 1 phi (500 µm) and weighed on a top pan balance (precision = 0.01 g). The fraction smaller than 500 µm was freeze-dried and analysed on a Coulter LS 130 laser sizer. The laser sizer results were combined with the dry-sieve results to give the full particle size distribution. The mean particle size diameter and sorting coefficient were calculated from these results (Dyer 1986).

In the laboratory, infaunal samples were sorted to higher taxonomic categories (from genus to phylum) and individual animals were weighed (blotted wet weight) to the nearest 0.001 g. Tube-forming polychaetes were removed from tubes before weighing. We did not apply shrinkage factors to account for

weight changes following preservation as these were not available for the very wide range of species included in our samples. As this study dealt with the production of benthic animals that would be available to support production at higher trophic levels, we converted wet weight to ash-free dry mass (AFDM) using conversion factors kindly provided by Thomas Brey (pers. comm.). All individuals with a calculated AFDM of ≤62.5 mg were included as they were small infauna in the size classes eaten by many fishes and effectively sampled with the NIOZ corer. Inevitably, a proportion of the animals in our samples were damaged or incomplete. We applied the following rules to damaged specimens. First, we tried to assemble 'complete' animals from the fragments in the sample, and recorded these as a single individual. Second, if fragments of an animal constituted less than 30% of the expected mass of a complete animal, we discarded them.

Trawling disturbance. Mean levels of trawling disturbance at the study sites were determined from records of beam trawler sightings by fishery protection aircraft. These aircraft patrol the fishing grounds around the United Kingdom and record a description and location for all vessels they observe fishing. Trawling disturbance can therefore be estimated as the number of beam trawler sightings per unit of aircraft search effort (SPUE). Within each site, we calculated beam trawler SPUE on an annual basis from 1994 to 2000. Sightings were the number of times that a beam trawler was recorded at each site and search effort was the number of times that an aircraft visited the site (Jennings et al. 2000). We assumed that beam trawler SPUE was directly and linearly proportional to trawling effort and trawling disturbance (Jennings et al. 2001a).

The SPUE data were converted to a mean frequency of beam trawling at each site. We assumed that the average beam trawler fishing in the Silver Pit will tow two 12 m wide beams at a speed of 6 knots (11.1 km h⁻¹), and that 267 264 m² of seabed will be disturbed

each hour. Therefore, an annual SPUE of 1 (beam trawler always sighted at the site) should equate to the entire area of the site being trawled, on average, 22.73 times yr^{-1} . In reality, trawling effort within the site will be patchy and some areas will be trawled more frequently than others. However, the mean frequency of trawling provides a useful comparative index of disturbance, and side-scan observations of trawl tracks within the Silver Pit study sites (where the sediment is sufficiently soft for trawl tracks to persist for a few days after trawling) suggest that tracks cross the more heavily fished sites in many directions (T. A. Dinmore & S. Jennings unpubl. data).

Data analyses. Body size spectra were produced for the infaunal communities at each site. Biomass by size class (\log_2 AFDM classes for all animals of AFDM ≤ 62.5 mg) was calculated for each box in each site as the means for the 10 replicates cores from 2 seasons. Biomass size spectra were normalised by dividing the biomass in a given body mass class interval by the width of that class interval. The relationship between size (as classes) and total normalised biomass was described using least-squares linear regression.

Production was calculated from biomass using an allometric relationship between P:B and mean AFDM. This was calculated using the subset of Brey's (1999) data set described in Jennings et al. (2001a). The relationship for the same species, but parameterised for AFDM, was $\log_{10} \text{P:B} = -0.431 - (0.236 \times \log_{10} \text{B})$. Total production of animals > 0.78 to 62.5 mg AFDM (boundaries of the size range were selected to correspond with the boundaries of the \log_2 AFDM classes) was calculated as the sum of production estimates in the appropriate \log_2 AFDM classes.

Following a preliminary assessment of the data, each effect variable was analysed using a generalised additive model of the form:

$$y_i = a_0 + a_1x_{1i} + a_2x_{1i}^2 + a_3x_{2i} + a_4x_{3i} + lo(x_{4i}) + \varepsilon_i$$

for observation i , where x_{1i} = mean particle diameter, x_{2i} = sorting coefficient, x_{3i} = depth, x_{4i} = trawling disturbance, $lo(\cdot)$ indicates a loess smoother and ε_i is normally distributed with constant variance.

The smoother was given approximately 3 degrees of freedom, corresponding to a span of 0.66, and each term was fitted and tested sequentially at the 5% significance level.

Post hoc power analyses were used to assess the power of our analysis to detect a linear trend in the production of all small animals or small polychaetes (> 0.78 to 62.5 mg AFDM).

Power was calculated as a function of the percentage change from the mean response to mean response $\pm 50\%$ over the range from the minimum to the maximum frequency of trawl disturbance. Post hoc power analyses were also used to assess the power of our analysis to detect a linear trend in the slope and intercept of the biomass size spectra.

Since non-linear responses to trawl disturbance may arise, we also tested the power of our analyses to detect non-linear trends in the production of small animals or small polychaetes. The most likely forms of non-linear response are those that reflect increased production at some intermediate level of disturbance where, for example, small animals would benefit from reduced competition or predation, but where the rates of population growth would be sufficiently high to tolerate mortality due to trawling. To incorporate a range of possible response scenarios, a family of hypothetical responses were generated using a function of the form:

$$\text{response}_i = \text{constant} \times x_i^a (1 - x_i)^a$$

where $x_i = x_{4i} - \min(x_{4i}) / [\max(x_{4i}) - \min(x_{4i})]$ is the i th proportion of trawl disturbance, and the constant scales the maximum of the response curve to be constant for different values of a shape parameter, a . When $a = 0$, the function describes a negative linear response and when $a = 1$, a positive linear response. For intermediate values of a , the function describes higher levels of production at intermediate levels of disturbance.

RESULTS

All the study sites were trawled. There was a 17.5-fold range in the mean frequency of beam trawling disturbance among the Silver Pit study sites (maximum frequency 6.14, minimum frequency 0.35; Table 1). The

Table 1. Mean annual sightings per unit searching effort (SPUE) of beam trawlers by fishery protection flights at the Silver Pit study sites, and the mean number of times the sites are beam-trawled each year. Data are based on 1517 sightings of beam trawlers from 1 January 1994 to 31 December 2000

Site code	Mean SPUE (number visit ⁻¹)	95% CI	Mean frequency (times trawled yr ⁻¹)	95% CI
1	0.04	0.015	0.98	0.346
2	0.10	0.044	2.29	1.019
3	0.18	0.044	4.11	1.013
4	0.22	0.103	4.94	2.354
5	0.27	0.101	6.14	2.311
6	0.22	0.099	5.10	2.263
7	0.02	0.010	0.35	0.229
8	0.15	0.063	3.44	1.452
9	0.10	0.040	2.37	0.924

Table 2. Depth and sediment characteristics at the Silver Pit sites; except Phi, data are mean ± 95 % CI

Site/ box code	Depth (m)	Sediment diameter (mm)	Phi	Sediment sorting coefficient	Sand (% by weight)	Mud/silt (% by weight)
1A	74.1 ± 1.7	0.053 ± 0.007	4.26	2.432 ± 0.060	63.1 ± 2.8	36.9 ± 2.8
1B	69.1 ± 0.5	0.056 ± 0.009	4.19	2.263 ± 0.083	67.4 ± 4.2	32.6 ± 4.2
1C	74.8 ± 1.3	0.081 ± 0.013	3.65	2.364 ± 0.091	74.9 ± 2.0	25.1 ± 2.0
2A	69.3 ± 1.3	0.058 ± 0.019	4.20	2.378 ± 0.076	65.4 ± 8.2	34.6 ± 8.2
2B	69.9 ± 0.6	0.047 ± 0.006	4.42	2.484 ± 0.060	59.8 ± 5.0	40.2 ± 5.0
2C	70.0 ± 1.8	0.085 ± 0.020	3.60	2.349 ± 0.087	75.9 ± 5.7	24.1 ± 5.7
3A	71.7 ± 0.5	0.052 ± 0.028	4.43	2.382 ± 0.128	62.9 ± 9.5	37.1 ± 9.5
3B	64.7 ± 1.1	0.053 ± 0.009	4.27	2.439 ± 0.106	64.6 ± 4.8	35.4 ± 4.8
3C	69.7 ± 1.5	0.048 ± 0.007	4.39	2.318 ± 0.078	63.1 ± 3.0	36.4 ± 3.3
4A	64.3 ± 1.3	0.063 ± 0.018	4.04	2.322 ± 0.117	69.7 ± 6.3	30.3 ± 6.3
4B	68.3 ± 0.3	0.044 ± 0.003	4.50	2.263 ± 0.038	64.3 ± 3.2	35.7 ± 3.2
4C	66.5 ± 0.5	0.062 ± 0.014	4.03	2.143 ± 0.188	74.8 ± 6.9	25.1 ± 6.9
5A	64.8 ± 0.3	0.039 ± 0.010	4.74	2.369 ± 0.172	63.9 ± 3.4	38.7 ± 5.8
5B	63.4 ± 2.0	0.036 ± 0.003	4.81	2.316 ± 0.077	57.8 ± 2.9	42.2 ± 2.9
5C	60.2 ± 0.6	0.078 ± 0.022	3.73	2.386 ± 0.113	73.3 ± 5.7	26.7 ± 5.7
6A	60.7 ± 0.4	0.027 ± 0.002	5.24	2.339 ± 0.041	47.6 ± 2.0	52.4 ± 2.0
6B	68.8 ± 3.9	0.016 ± 0.003	5.99	2.247 ± 0.095	25.3 ± 8.0	74.7 ± 8.0
6C	61.1 ± 0.6	0.033 ± 0.001	4.92	2.301 ± 0.046	54.7 ± 0.7	45.3 ± 0.7
7A	59.8 ± 0.7	0.015 ± 0.002	6.03	2.299 ± 0.031	25.9 ± 2.8	74.1 ± 2.8
7B	60.4 ± 0.5	0.018 ± 0.002	5.87	2.366 ± 0.024	31.8 ± 4.5	68.2 ± 4.5
7C	58.9 ± 0.6	0.018 ± 0.003	5.83	2.382 ± 0.085	32.2 ± 4.0	67.6 ± 4.2
8A	62.9 ± 0.2	0.039 ± 0.004	4.69	2.203 ± 0.054	61.2 ± 3.2	38.8 ± 3.2
8B	59.1 ± 0.3	0.037 ± 0.005	4.76	2.295 ± 0.057	55.9 ± 4.4	44.1 ± 4.4
8C	61.3 ± 0.6	0.034 ± 0.003	4.88	2.217 ± 0.034	55.3 ± 4.5	44.7 ± 4.5
9A	48.3 ± 0.6	0.035 ± 0.004	4.83	2.271 ± 0.055	58.0 ± 4.2	42.0 ± 4.2
9B	59.7 ± 0.4	0.034 ± 0.004	4.91	2.289 ± 0.051	56.0 ± 4.8	44.0 ± 4.8
9C	58.1 ± 4.1	0.056 ± 0.018	4.21	2.275 ± 0.230	68.6 ± 7.7	31.4 ± 7.7

95% confidence intervals for trawling frequency showed that there was considerable inter-annual variation in the frequency of trawling at some sites. The trawled sites and boxes ranged from 48.3 to 74.8 m deep and were predominantly sandy or muddy-sand with mean particle size diameters ranging from 0.015 to 0.081 mm. The variance in sediment particle diameter within boxes was low (Table 2).

Biomass size spectra

The slopes of the infaunal biomass size spectra were all significant and negative, and ranged from -0.10 to -0.25 (Table 3). The relationships between the slopes and intercepts of the biomass size spectra and the environmental variables and trawling disturbance (Table 4a) showed that the slopes were significantly related to mean particle diameter (MPD) and MPD², and that after the model had been fitted, there was no evidence for a change in the slopes of the biomass size spectra with trawling disturbance (Fig. 2a). The post hoc power analysis showed that the power to detect a change of ±20% in slope due to disturbance would have been high (Fig. 3) The intercepts were significantly related to the sorting coefficient (SC) and depth,

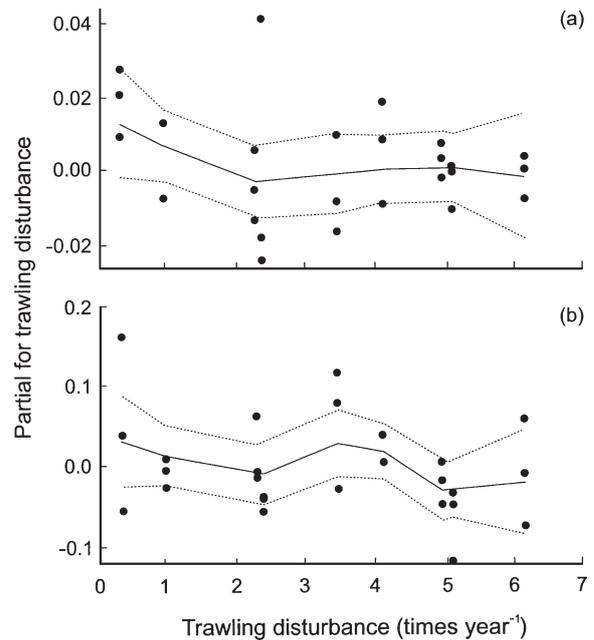


Fig. 2. Partial regressions of (a) the slopes and (b) intercepts of the biomass size spectra having fitted the mean particle diameter (MPD), MPD², sorting coefficient and depth. The solid line is a fitted loess smoother with approximately 3 df and a span of 0.66, the broken lines show the lower and upper 95% confidence limits for this line

and after the model had been fitted, there was no evidence for a significant change in the intercepts of the biomass size spectra with trawling disturbance (Fig 2b, Table 4b). The power to detect a change of $\pm 50\%$ in the intercepts with disturbance was also high (Fig. 3).

Production

The production ($\text{g AFDM m}^{-2} \text{ yr}^{-1}$) of all small animals ($\text{AFDM} > 0.78$ to 62.5 mg) in the community (Table 5) was significantly related to MPD, MPD^2 , SC and depth, and after these effects were accounted for in the generalised additive model, there was no evidence for a significant effect of trawling on production (Fig. 4a). The production ($\text{g AFDM m}^{-2} \text{ yr}^{-1}$) of small polychaetes ($\text{AFDM} > 0.78$ to 62.5 mg) in the community (Table 5) was significantly related to MPD, MPD^2 and depth ($p = 0.06$) (Table 4c). After these effects were accounted for in the model, there was no evidence for a significant linear effect of trawling on production (Fig. 4b). The power to detect linear and non-linear responses (as defined by parameter a , Fig. 5) of small animals and polychaetes was high. Thus, the post hoc power analysis showed that there was a minimum 90%

Table 3. Slopes, intercepts and significance of linear regressions used to describe infaunal size spectra (plots of \log_{10} normalised ash-free dry mass per sample by \log_2 size class vs \log_2 size class for all individuals $\leq 62.5 \text{ mg AFDM}$)

Site/ box code	a	b	r^2	$F_{1,8}$	p
1A	0.30	-0.23	0.90	70.5	<0.001
1B	0.20	-0.24	0.90	74.4	<0.001
1C	0.25	-0.22	0.87	52.3	<0.001
2A	0.23	-0.25	0.89	64.4	<0.001
2B	0.29	-0.24	0.86	49.8	<0.001
2C	0.32	-0.20	0.87	55	<0.001
3A	0.27	-0.25	0.93	106.4	<0.001
3B	0.29	-0.21	0.94	114.6	<0.001
3C	0.27	-0.22	0.95	155.9	<0.001
4A	0.18	-0.23	0.92	97.5	<0.001
4B	0.17	-0.21	0.88	60.3	<0.001
4C	0.15	-0.22	0.86	49.6	<0.001
5A	0.31	-0.22	0.88	52.8	<0.001
5B	0.22	-0.20	0.90	68.5	<0.001
5C	0.14	-0.22	0.88	57.9	<0.001
6A	0.22	-0.19	0.94	135.4	<0.001
6B	0.18	-0.14	0.82	35.2	<0.001
6C	0.18	-0.20	0.84	43.2	<0.001
7A	0.45	-0.10	0.73	21.8	<0.001
7B	0.24	-0.14	0.74	23	<0.001
7C	0.33	-0.13	0.79	31.4	<0.001
8A	0.15	-0.22	0.85	45.7	<0.001
8B	0.28	-0.22	0.94	117.2	<0.001
8C	0.31	-0.19	0.81	34.9	<0.001
9A	0.11	-0.22	0.86	48	<0.001
9B	0.17	-0.22	0.91	79.1	<0.001
9C	0.10	-0.18	0.76	25.6	<0.001

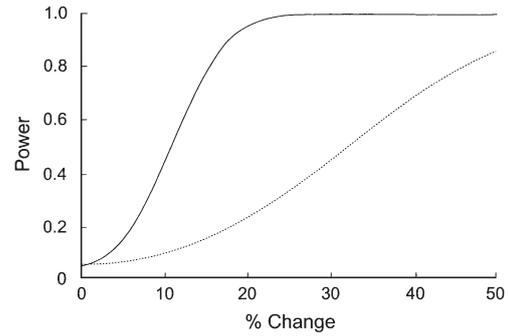


Fig. 3. The power of detecting significant linear relationships between the slopes (continuous line) and intercepts (broken line) of the biomass size spectra and trawling disturbance

probability of detecting a 50% change in the production of small animals, whether that change was positive, negative or resulted in increased production at intermediate levels of disturbance (Fig. 6).

DISCUSSION

Our results suggest that chronic beam trawling disturbance has minimal effects on the production and size structure of small benthic infauna. This conclusion is likely to be robust because the power of our analyses to detect small negative or positive changes in produc-

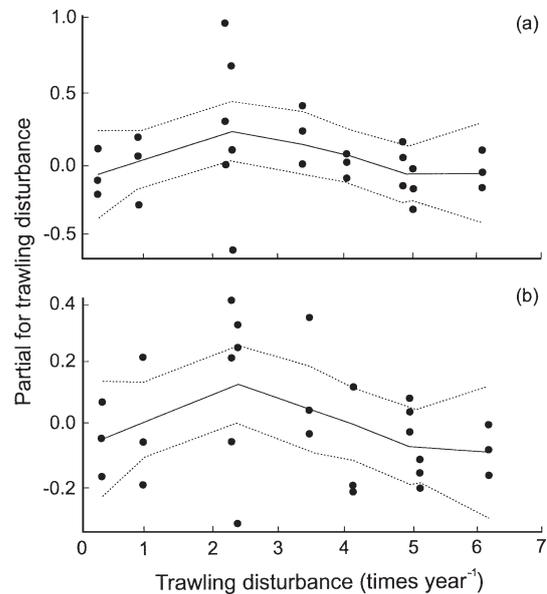


Fig. 4. Partial regressions of production of (a) small animals and (b) polychaetes having fitted the mean particle diameter (MPD), MPD^2 , sorting coefficient and depth. The solid line is a fitted loess smoother with approximately 3 df and a span of 0.66, the broken lines show the lower and upper 95% confidence limits for this line

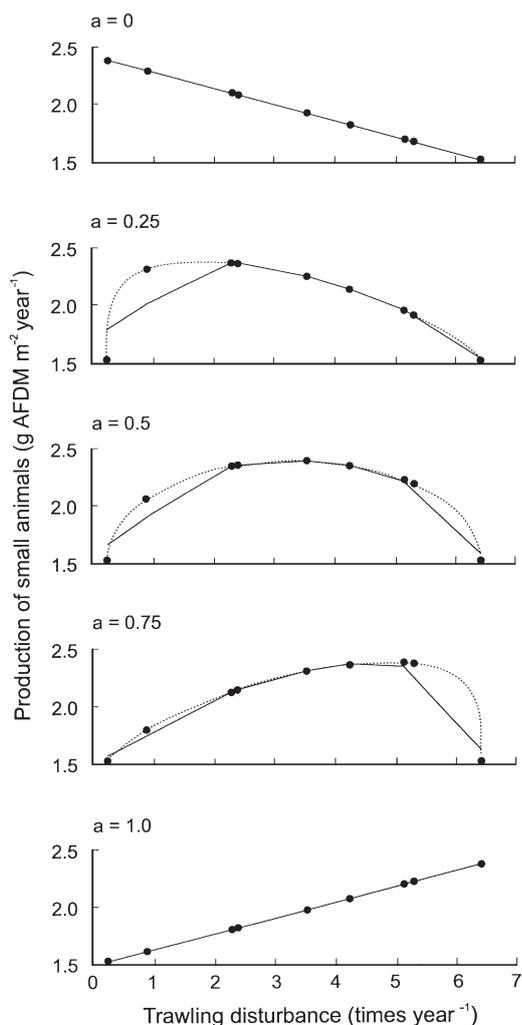


Fig. 5. Hypothetical responses of small animal or polychaete production to trawling disturbance for different values of the shape parameter a . Values corresponding to the observed trawl disturbances are shown as filled circles, and the solid lines show the degree to which the loess smoother is able to track the response curve

tion, or increased production at intermediate levels of disturbance, is high. Our results can probably be generalised to other shallow, trawled, sand and mud habitats dominated by free-living species. We would expect, however, very different results in areas where the habitat is more complex, especially where there are many biogenic species and where there was no previous history of fishing activity (e.g. Collie et al. 1997, 2000a,b, Auster & Langton 1999). The small infauna we studied are among the few groups of benthic invertebrates for which biomass and production do not appear to be reduced by trawling disturbance. Since small infaunal polychaetes are a key source of food for flatfishes (Rijnsdorp & Vingerhoed 2001), we conclude that beam trawling disturbance has a relatively minor

impact on the food chains that support the production of the primary target species (plaice and sole). Our results also suggest that beam trawling is not 'farming the sea' by boosting production at intermediate levels of disturbance, even though trawling may expose small infauna and increase their availability to fishes and other predators (Ramsay et al. 1997). Moreover, our results show that the size distribution of small infauna is not markedly affected by trawling, even though the power of our analyses to detect an effect is high.

Our results contrast with the results of studies that have focused on trawling impacts on larger infauna or biogenic epifauna (e.g. Kenchington et al. 2001, Thrush et al. 2001). For example, studies of the impacts of trawling on the production of larger infauna in the central North Sea showed that there were 6-fold reductions in production, and order of magnitude reductions in the biomass of bivalves and spatangoids across trawling frequencies of 0.2 to 6.5 times yr^{-1} (Jennings et al. 2001b). If there had been comparable changes in the relative production of the smaller animals that we considered in this study, then the design of our experiment and power of our analyses would have ensured that the changes were detected. For example, the power analysis showed that we had a minimum 90% probability of detecting a 50% change in the mean production of small animals, whether that change was a positive, negative or resulted in increased production at intermediate levels of disturbance. Our results suggest that only the smaller animals have sufficient rates

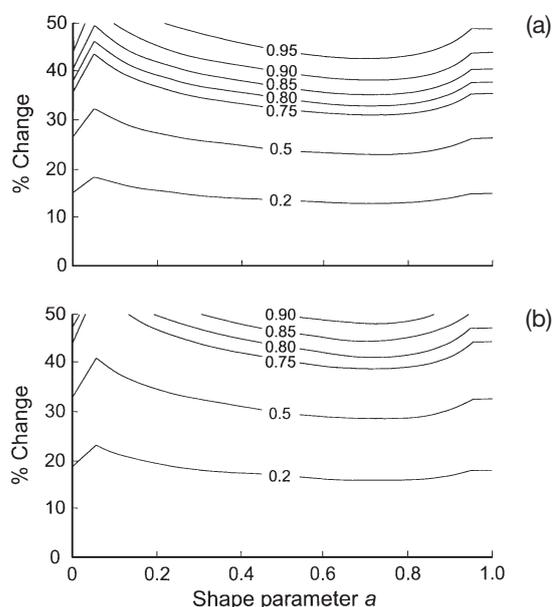


Fig. 6. The power of our analyses for (a) small animals and (b) polychaetes to detect a significant impact of trawling disturbance as a function of % change in production and the type of response (as defined by shape parameter a)

of recruitment and growth, and suffer sufficiently low levels of mortality, to tolerate regular trawling disturbance. Since the range of disturbances recorded at our study sites span the range recorded on most beam trawling grounds in the North Sea (e.g. Rijnsdorp et al. 1998), our results suggest that the production and biomass of smaller infauna are largely unaffected by trawling disturbance on sand-mud sediments. Most of the diet of 11 to 25 cm sole, 11 to 30 cm dab and 11 to 35 cm plaice consists of polychaetes (Braber & De Groot 1973, Rijnsdorp & Vingerhoed 2001). Siphons of bivalve molluscs are important in the diet of larger plaice (Braber & De Groot 1973), but these fish are an increasingly small component of the fishery following intensive exploitation of the plaice stock (Rijnsdorp & Millner 1996). In general, beam trawling appears to have created a system where small fish feed on small food items. This may have minimal effects on the growth and production of flatfishes, but the size structure, biomass and total production of the infaunal and fish communities are fundamentally different from those in the unfished state.

While the production of small animals that support commercial fish species was not reduced by trawling disturbance, the role of the infaunal community will change following chronic trawling disturbance. Polychaetes and small infauna dominate the benthic fauna in heavily trawled areas, because populations of larger species are greatly depleted (Frid et al. 1999, Kaiser et al. 2000, Jennings et al. 2001a), and yet the smaller infauna are much less significant as bioturbators (Swift 1993). As a result, sediment community function, carbon mineralisation and biogeochemical fluxes are likely to be strongly affected by trawling activity because the physical effects of trawling are equivalent to those of an extreme bioturbator, and yet, unlike bioturbating macrofauna, trawling does not directly contribute to community metabolism (Duplisea et al. 2001).

There are 2 principal concerns about our method of assessing infaunal production. First, we could not consider the effects of differential fish predation in the areas subject to different levels of trawling disturbance. We might expect that fish are more abundant in areas where trawlers operate, and that our

Table 4. Analysis of variance for the generalised additive model fitted to relationships between (a) the production of small animals (AFDM > 0.78 to 62.5 mg), (b) the production of small polychaetes (AFDM > 0.78 to 62.5 mg), (c) the slopes of biomass size spectra (see Table 3), (d) the intercepts of biomass size spectra (see Table 3), environmental variables (see Table 2) and trawling disturbance (see Table 1).

Terms were added sequentially, first to last. AFDM = ash-free dry mass

	df	SS	MS	F	p
(a) Production of small animals					
Mean particle diameter	1	3.527	3.527	31.94	0.000
Mean particle diameter ²	1	3.102	3.102	28.09	0.000
Sorting coefficient	1	1.344	1.344	12.17	0.002
Depth	1	0.515	0.515	4.66	0.042
Residuals	22	2.430	0.110		
Loess (trawling disturbance)	3.32	0.370	0.111	1.010	0.417
Residuals	18.68	2.060	0.108		
(b) Production of polychaetes					
Mean particle diameter	1	0.413	0.413	8.64	0.008
Mean particle diameter ²	1	0.250	0.250	5.22	0.032
Sorting coefficient	1	0.104	0.104	2.17	0.155
Depth	1	0.181	0.181	3.78	0.065
Residuals	22	1.051	0.048		
Loess (trawling disturbance)	3.32	0.181	0.055	1.17	0.350
Residuals	18.68	0.870	0.047		
(c) Slope of biomass size spectra					
Mean particle diameter	1	0.014	0.014	46.93	0.000
Mean particle diameter ²	1	0.014	0.014	45.51	0.000
Sorting coefficient	1	0.000	0.000	0.91	0.349
Depth	1	0.000	0.000	0.09	0.769
Residuals	22	0.007	0.000		
Loess (trawling disturbance)	3.32	0.000	0.000	0.687	0.585
Residuals	18.68	0.006	0.000		
(d) Intercept of biomass size spectra					
Mean particle diameter	1	0.005	0.005	1.21	0.283
Mean particle diameter ²	1	0.014	0.014	3.13	0.091
Sorting coefficient	1	0.034	0.034	7.73	0.011
Depth	1	0.016	0.016	3.66	0.069
Residuals	22	0.097	0.004		
Loess (trawling disturbance)	3.32	0.025	0.007	1.94	0.154
Residuals	18.68	0.072	0.004		

production estimates will be biased down in those areas. Equally, fishing may deplete the abundance of fish in the trawled areas and therefore release infauna from predation. Long-term estimates of changes in the abundance of fishes at small spatial scales are not available and we cannot therefore determine whether they biased our results. Second, our production estimates may underestimate decreases in production as mortality rates rise. This is because the P:B ratio will reflect recruitment and growth. We assumed that the P:B ratio increased continuously as body size fell, but if the mean size of a population tends below the size at maturity, recruitment will be impaired. As a result, larger species that are present in the community at low mean body size may only have the capacity for individual rather than population growth.

Table 5. Calculated production of infauna and polychaetes (ash-free dry mass [AFDM] > 0.78 to 62.5 mg)

Site/ box code	Infauna production (AFDM g m ⁻² yr ⁻¹)	Polychaete production (AFDM g m ⁻² yr ⁻¹)	Polychaete production as % infauna production
1A	2.16	0.91	0.42
1B	1.93	0.88	0.46
1C	2.00	1.19	0.59
2A	3.15	1.43	0.45
2B	2.68	1.28	0.48
2C	1.45	0.76	0.52
3A	2.31	1.18	0.51
3B	2.16	0.73	0.34
3C	1.89	0.74	0.39
4A	1.85	0.95	0.51
4B	1.58	0.88	0.56
4C	1.60	0.86	0.54
5A	1.87	0.86	0.46
5B	1.36	0.61	0.45
5C	1.43	0.62	0.44
6A	0.98	0.50	0.51
6B	0.60	0.53	0.88
6C	0.98	0.49	0.50
7A	0.52	0.42	0.82
7B	0.57	0.38	0.67
7C	0.64	0.61	0.95
8A	1.53	0.79	0.51
8B	1.77	1.07	0.61
8C	1.15	0.65	0.57
9A	1.55	0.71	0.46
9B	1.37	1.03	0.75
9C	0.91	0.38	0.41

The production of smaller infauna in heavily trawled areas may be sustained by the settlement and growth of recruits from adjacent undisturbed habitats. Our analysis does not allow us to identify the relative role of recruitment in mitigating the effects of trawling, but for practical purposes, consistent patchiness in trawling effort will help to limit the overall impacts of trawling. In the absence of changes to management strategies that result in the relocation of effort, the spatial distribution of trawling effort is quite consistent from year to year because trawlers will tend to return to tows that are stored on their navigation systems and known to be clear of obstructions (Rijnsdorp et al. 1998). In the North Sea and at the scale of the ICES rectangle (211 rectangles of 0.5° latitude by 1° longitude: area of rectangle 3720 km² at 53°N), 50% of rectangles are beam-trawled for less than 2000 h yr⁻¹. Since a typical beam trawler will impact 534.5 km² of seabed in 2000 h (Jennings et al. 2001b), it will take at least 7 yr to trawl an entire rectangle if it is fished for less than 2000 h yr⁻¹. Such infrequent trawling would have a small effect on most benthic fauna. We suggest that fishery management strategies that lead to patchy but temporally stable patterns of trawling will often have lower total impacts on benthic communities than strategies that lead to more homogeneous and temporally unstable distribution of the same effort.

If the patchiness of trawling effort is maintained at present levels, our study suggests that the production of fish food on flatfish trawling grounds is unlikely to be compromised by trawling disturbance. However, trawling disturbance will reduce the biomass of many larger species and affect biogeochemical processes. Given the power of our analyses and the lack of evidence for the increased production of small infauna at intermediate levels of disturbance, recent increases in the production of small benthic infauna in the North Sea are more likely to reflect increases in primary production following climate change (Kroncke et al. 1998, Reid et al. 1998), and the tolerance of the small polychaetes and bivalves to trawling disturbance. This conclusion could only have been reached by comparing the spatial impacts of trawling with existing analyses of temporal trends in the abundance

of North Sea infauna and shows why both spatial and temporal analyses should be considered when making any assessment of the impacts of fishing.

Acknowledgements. We thank Nic Denney, Chris Firmin, Alison Hewer, Paul Hudson, Steve Lovewell, Tracy Mead, Dave Palmer, Michaela Schratzberger, Christie Stewart, Chris Sweeting, Peter Walker, Karema Warr and the officers and crew of RV 'Corystes' for practical assistance with sample collection. Claire Mason conducted the particle size analyses, Karema Warr maintained the fishing effort database and Thomas Brey provided unpublished data on mass conversions for benthic invertebrates. The work was funded by the Department for Environment, Food and Rural Affairs, UK, through the MF07 'Impacts of fishing' programme (Projects MF0716 and MF0731).

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