

Trawling disturbance can modify benthic production processes

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Summary

1. Trawling disturbance has wide-ranging impacts on the marine environment and is well known to modify benthic habitat and community structure. This has led to speculation about the positive and negative impacts of trawling on ecosystem processes such as production.

2. Existing theory suggests that frequent trawling disturbance may lead to the proliferation of smaller benthic species, with faster life histories, because they can withstand the mortality imposed by trawling and benefit from reduced competition or predation as populations of larger species are depleted. Since smaller species are more productive, trawling disturbance may 'farm the sea', with knock-on benefits for consumers, including fish populations.

3. We conducted the first large-scale studies of trawling effects on benthic production across quantified gradients of trawling disturbance on real fishing grounds in two regions (Silver Pit and Hills) of the North Sea. There were 27- and 10-fold differences in levels of beam trawl disturbance among the Silver Pit and Hills sites, respectively.

4. Size structure was described using normalized size-spectra, and the slopes and intercepts of these spectra were related to levels of trawling disturbance. Production was estimated from the size spectra, using a new allometric relationship between body mass and the production to biomass (P:B) ratio of marine invertebrates. The general validity of the relationship was confirmed using a phylogenetic comparative approach.

5. In the Silver Pit region, trawling led to significant decreases in infaunal biomass and production. The abundance of larger individuals was depleted more than smaller ones, as reflected by the positive relationship between the slope of the normalized size spectra and trawling disturbance. The effects of trawling disturbance were not significant in the epifaunal community. In the Hills region, where the range of trawling disturbance was lower, trawling disturbance did not have significant effects on biomass or production.

6. In the Silver Pit, relative infaunal production (production per unit biomass) rose with increased trawling disturbance. This was attributable largely to the dominance of smaller animals in the disturbed communities. The increase in relative production did not compensate for the loss of total production that resulted from the depletion of large individuals. There was some evidence for the proliferation of small polychaetes at moderate levels of disturbance, but at higher levels of disturbance their biomass and production fell.

7. We conclude that reported increases in the biomass and production of small infaunal invertebrates in the North Sea are attributable largely to recent increases in primary production that were driven by climate change, and not to the effects of trawling disturbance.

Key-words: allometry, beam trawling, fishing effects, P:B ratios, phylogeny, size spectra.

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Introduction

Trawling disturbance is well known to affect the species composition and structure of marine benthic communities, but virtually nothing is known of the effects of trawling disturbance on size structure and production (Dayton *et al.* 1995; Jennings & Kaiser 1998; Lindeboom & de Groot 1998; Hall 1999; Collie *et al.* 2000; Kaiser & de Groot 2000). We might reasonably expect trawling disturbance to affect size structure and production, because mortality due to trawling disturbance is positively correlated with body size (Lindeboom & de Groot 1998; Bergman & van Santbrink 2000) and because there are close relationships between body size distributions and production (Brey 1999). Changes in size structure and production would have wide-ranging significance in the marine ecosystem, since they affect the amount of food available to predators at higher trophic levels (Jennings & Kaiser 1998).

Body size distributions have fundamental significance in determining the function of communities since body sizes determine potential predators and prey, and are correlated with many aspects of life history (Peters 1983). The distribution of biomass by body size classes in aquatic ecosystems follows regular patterns that can be described with size spectra (Sheldon, Prakash & Sutcliffe 1972; Sheldon, Sutcliffe & Prakash 1973) and the patterns can be predicted from models of energy flow from prey to predators (Kerr 1974; Platt & Denman 1977, 1978; Dickie, Kerr & Boudreau 1987; Boudreau, Dickie & Kerr 1991; Thiebaut & Dickie 1992, 1993). Size spectra have been used to describe the structure of fish (Pope *et al.* 1988; Duplisea & Kerr 1995; Rice & Gislason 1996) and benthic communities (Schwingamer 1981; Duplisea & Drgas 1999) and the slope of the spectrum can provide a broad indication of the intensity of exploitation (Pope *et al.* 1988; Rice & Gislason 1996).

There are consistent links between body size and life history. Increased body size is correlated with lower natural mortality, slower growth, lower annual reproductive output, increased longevity and lower intrinsic rates of natural increase (Charnov 1993; Brey 1999). As a result, production to biomass ratios (P:B) are inversely related to body size (Banse & Moser 1980; Schwingamer *et al.* 1986; Brey 1999). Cross-species relationships between body mass and P:B are used widely to estimate production for marine communities, but the errors associated with individual predictions can be large because of the problems with accounting for phylogeny, environment and measurement errors in the individual studies used to compile the data set (Tumbiolo & Downing 1994; Brey 1999). However, the advantage of cross-species relationships is that they allow large-scale comparisons of production in systems where it would be impractical or impossible to measure actual production (Schwingamer *et al.* 1986).

Trawling causes mortality of many benthic species because they are crushed directly by the trawl or become caught and have died by the time they are taken on deck and returned to the sea. Within and

among species, mortality is generally size dependent. Thus larger bivalves suffer very high mortality while smaller bivalves and polychaetes suffer lower mortality (Lindeboom & de Groot 1998; Bergman & van Santbrink 2000), often because lighter animals are pushed aside by the pressure wave in front of the net (Gilkinson *et al.* 1998). Not only are larger individuals likely to suffer higher mortality, but the mortality rates they can withstand will be lower. This suggests that intensive trawling may favour smaller species and, since these have higher P:B ratios, they may be more productive and compensate for the loss of production among larger species.

Long-term studies of the benthos in the southern and central North Sea suggest that biomass and production have increased (Kröncke 1992; Kröncke *et al.* 1998). This could be a response to trawling disturbance, climate change or eutrophication (Rijnsdorp & van Leeuwen 1996; Kröncke *et al.* 1998). Increases in benthic production have been linked to increases in the growth of flatfishes (Rijnsdorp & van Beek 1991; Rijnsdorp & van Leeuwen 1996). To some, these studies have suggested that trawling disturbance is 'farming the sea'; ploughing the seabed to boost production. To others, trawling is assumed to damage key functional processes (Jennings & Kaiser 1998). Remarkably, there have been no attempts to look at the effects of trawling on production. One impediment to such research has been a lack of data on the spatial distribution of trawling disturbance (Kaiser *et al.* 2000).

Studies of the effects of trawling have often relied on experiments, where small areas of seabed are deliberately trawled by the investigator. Many experiments of this type have shown that trawling disturbance alters benthic community structure (Bergman & Hup 1992; Eleftheriou & Robertson 1992; Thrush *et al.* 1995; Currie & Parry 1996; Kaiser & Spencer 1996; Pitcher *et al.* 1997; Tuck *et al.* 1998; Bradshaw *et al.* 2000). However, these experiments are usually short-term and their acute nature 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 may be rapid (Collie *et al.* 1997; Kaiser *et al.* 1997), but recovery at small experimental scales is simply immigration, a form of recovery that may not be possible in large and repeatedly trawled areas. Indeed, a comparison of recovery rates (Collie *et al.* 2000), with reported population growth rates for benthic communities (e.g. Warwick, George & Davis 1978; George & Warwick 1985; Brey 1999), shows that some of the fast recovery times reported for mobile infauna and epifauna cannot be achieved by recruitment and growth. To describe the effects of trawling disturbance at the level of the fishery, it is necessary to study real fisheries where disturbance occurs on large scales over long time periods. Only in a very few studies have trawling effects been examined in real fisheries across quantifiable gradients of disturbance (Collie *et al.* 1997; Thrush *et al.* 1998; Kaiser *et al.* 2000), and these have addressed changes in structure rather than function.

In the north-east Atlantic, trawling effort data are usually recorded in very large areas such as ICES statistical rectangles (area of one rectangle 3720 km² at 53°N). These trawling effort data do not provide enough resolution to determine the frequency of trawling disturbance on the smaller scales at which biological samples are collected. Biological indicators of trawling disturbance may improve the resolution of disturbance estimates (Gaspar, Richardson & Monteiro 1994; Witbaard & Klein 1994; Mensink *et al.* 2000), but many of these long-lived species have been extirpated in heavily trawled areas (e.g. Rumohr & Krost 1991). An alternative method for quantifying trawling disturbance on a scale that approaches that of biological sampling is to use records of trawlers sighted by fishery enforcement aircraft that patrol fishing grounds. These aircraft record locations, types and registration numbers of all vessels of all nationalities that are seen fishing. Relative trawling disturbance can be estimated as the number of trawlers sighted per unit of search effort per unit area (Jennings *et al.* 2000).

In this study we compare the size composition and production of benthic invertebrate communities across quantified gradients of trawling disturbance. Changes in size composition are described using size spectra, and production is predicted from the size spectra using allometric relationships between body size and the P:B ratio. Since allometric relationships do not account for evolutionary relatedness among species, we also examine the relationship between body size and the P:B ratio using a phylogenetic comparative approach (Felsenstein 1985; Harvey & Pagel 1991). We test the hypothesis that larger organisms decline in response to trawling disturbance while smaller ones proliferate. If this hypothesis is correct, then both the slope and intercept of the size spectra would be positively correlated with trawling disturbance and total production of the community will rise if the increased production of smaller animals exceeds the loss of production in depleted populations of larger animals. If the hypothesis is invalid, then trawling disturbance would be positively correlated with the slope of the size spectra but not with the intercept, and the overall production of the community will fall.

Methods

STUDY SITES

We investigated the impacts of trawling in the Silver Pit and Hills regions of the central North Sea (Fig. 1). These regions are likely to have been fished with beam trawls since these gears were first widely used in the 1970s (Jennings *et al.* 1999a). The regions were chosen because a preliminary analysis showed that there were large spatial variations in trawling effort, because infaunal and epifaunal biomass was dominated by free-living species typical of beam trawl grounds, and because the sediment types, depths, bottom temperatures and tidal currents within each region were similar (Lee & Ramster

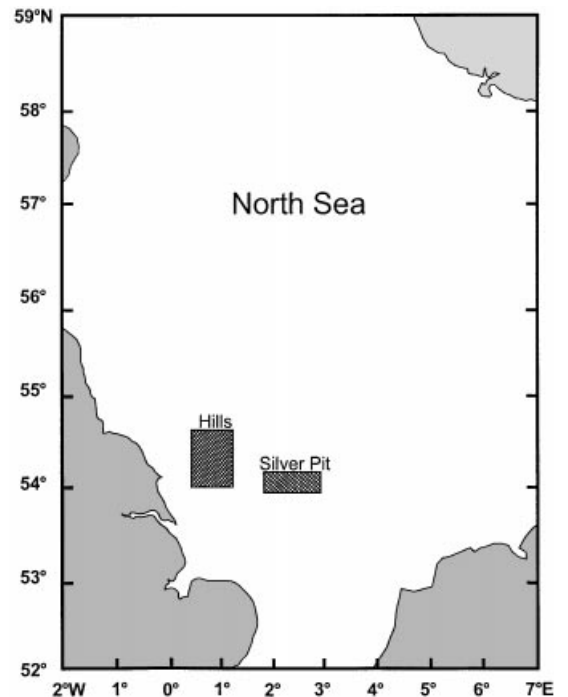


Fig. 1. The Silver Pit and Hills regions in the North Sea. The boundaries of the shaded boxes correspond with the boundaries of the maps in Fig. 2.

1981; Jennings *et al.* 2001; British Geological Survey, unpublished). The Silver Pit region (at the sample sites) is 55–75 m deep, with muddy sand sediment and mean winter and summer temperatures of 5 °C and 13.5 °C, respectively. The Hills region is 40–65 m deep and the sediment is sandy. Mean winter and summer temperatures are 5.5 °C and 13.0 °C (CEFAS, unpublished). Seven sites subject to different levels of trawling disturbance were studied in the Silver Pit and 13 sites in the Hills (Fig. 2). Sites were chosen to cover the range of fishing intensities from the maximum to the minimum in each region. Each site was a square of 1 nautical mile North–south (1 nm = 1853 m) × 1 nm East–west.

ESTIMATION OF TRAWLING DISTURBANCE

Trawling disturbance was determined from records of vessel sightings by fishery protection aircraft as described by Jennings *et al.* (2001). The Silver Pit and Hills regions (Fig. 1) were divided into 5-nm (North–south) × 6-nm (East–west) boxes; working South from the northern limit of the maps in Fig. 2. Within each box, the mean number of beam or otter trawl SPUE (effort measured as number of visits) by fishery protection aircraft was calculated. We assumed that SPUE was directly and linearly proportional to trawling effort and trawling disturbance. Trawling effort in the 1-nm² study sites within the 30-nm² boxes was taken as 1/30th of that in the box. Our approach assumes that trawling and aircraft search patterns within the boxes are random, because existing data do not allow us to quantify the bias that trawling and aircraft search patterns introduce. Since

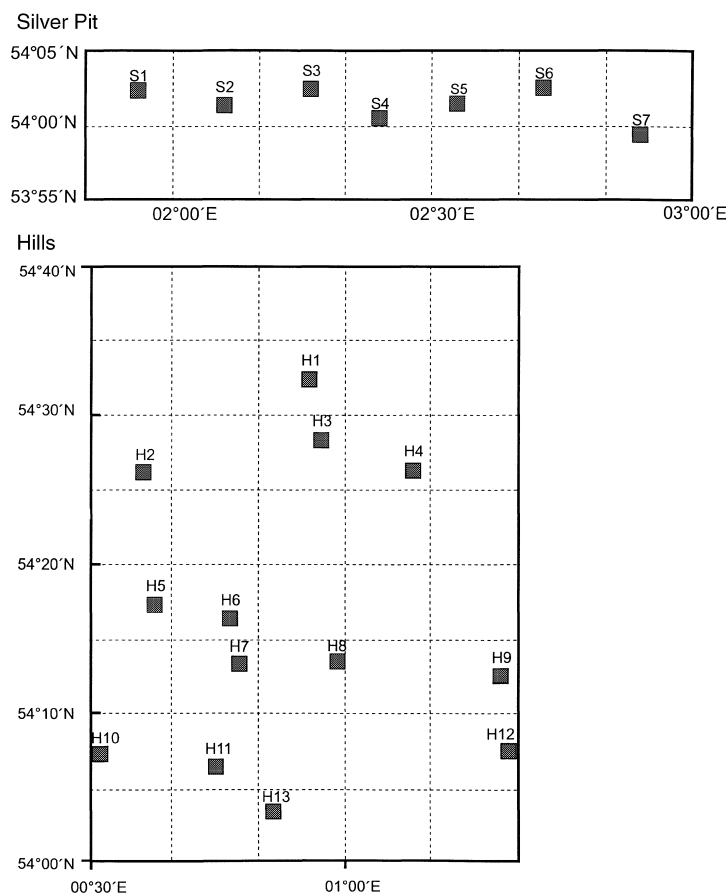


Fig. 2. Study sites in the Silver Pit and Hills regions. The boundaries of the 6 × 5-nm areas within which trawling disturbance was assessed are shown by broken lines.

the relative impacts of beam trawls on the structure of the benthic community of the southern North Sea are greater than those of otter trawls (Lindeboom & de Groot 1998), we related changes in production to differences in beam trawling effort.

SAMPLING OF BENTHIC INVERTEBRATE COMMUNITY

We sampled the infaunal and epifaunal invertebrate communities in both regions in winter and summer, to account for the variations in size structure that result from 'pulses' of recruits growing up the size spectrum. Epibenthic invertebrates were sampled with a 2-m beam trawl fitted with a 1-mm mesh liner and infaunal invertebrates with an anchor dredge (Kaiser, Rogers & McCandless 1994; Jennings *et al.* 1999b; Kaiser *et al.* 2000). We deliberately chose gears that sampled relatively large areas of seabed, even though the samples they take reflect relative rather than absolute abundance. Both gears sample on an appropriate scale for the study of fishing effects (over areas of m² to 10s m²) and integrate small-scale patchiness of the larger macrofauna (individual body mass > 0.0625 g) that were the focus of this study. We assumed that the catchability of different species did not change from site to site, so bias in abundance estimates was consistent.

Three randomly located replicate tows with each gear were completed at each site in each season. The beam trawl was towed for 5 min at 1 knot and the anchor dredge was towed for 1 min while drifting. The towing period was timed from the moment that the net contacted the seabed until the moment of hauling and the distance trawled was confirmed retrospectively, using Sextant software linked to the ship's Differential Global Positioning System (DGPS). All sampling was carried out from the research vessel *Corystes*. Winter samples were collected from 22 November to 8 December 1999 and summer samples from 1 to 13 May 2000.

All organisms taken in the beam trawl sample were sorted and free-living epifauna were removed for processing. A subsample of 0.2 m³ of sediment was taken from each anchor dredge sample and sieved through 1-mm square mesh. All free-living infaunal species retained by the mesh were removed for processing. Free-living epifauna were defined as those species that live on the seabed or burrow in it temporarily while infauna were defined as those for which parts of the body remains more or less permanently in the substrate.

All individuals were weighed, either fresh using heave-compensated balances, or after preservation in 4% seawater formalin buffered with 3 g L⁻¹ sodium acetate. Most individuals estimated to weigh less than 0.5 g were preserved. 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, and blotted weight was recorded in each case. After weighing, all infauna and epifauna were assigned to \log_2 body size categories. Subsequent conversions between dry mass, ash-free dry mass (AFDM), kcal, kJ and wet mass were made using conversion factors kindly provided by Thomas Brey (personal communication).

RELATIONSHIPS BETWEEN P:B AND BODY MASS

Allometric (cross-species) relationships were used to estimate P:B ratios and production from individual body mass. We calculated the cross-species relationship between P:B and body mass using a subset of the data compiled by Brey (1990, 1999). We restricted the species and studies included in the analysis to marine invertebrates living at depths of 1–100 m and water temperatures of 0°–15 °C. Within the subset of data, the relationship between mean production and P:B could not be improved by the addition of other variables such as temperature and depth. Some changes were made to the subset of data before analysis. *Nucula nitidosa* and *N. turgida* as they appear in the original compilation are synonyms, so mean production and P:B were calculated and assigned to *N. nitidosa*. *Magelona mirabilis* and *M. papillicornis* are also synonyms and mean production and P:B were assigned to *M. mirabilis*. The species *Gyraulius acronicus* and *Mesidothea entomon* were removed from the data subset as these were not recognized. All other generic and specific names were updated to follow current forms, based primarily on Howson & Picton (1997). The final subset of data included 25 annelid, 15 crustacean, 30 mollusc and seven echinoderm species (total $n = 77$). Due to the paucity of data for parameterizing P:B and body mass relationships, we pooled across phyla. The costs of reduced replication within phyla exceeded the gains of trying to control for taxonomic differences. Where necessary, conversions between mass and energy content were made using the factors provided by Brey (personal communication).

Since allometric relationships do not account for evolutionary relatedness among species, we also analysed the Brey (1990, 1999) data set using a phylogenetic comparative approach. Phylogenetically based analyses overcome the fact that related taxa may share traits due to common ancestry and that data on the life histories of different taxa are not statistically independent (Felsenstein 1985; Harvey & Pagel 1991). These analyses have been applied to a range of problems linking body size and life histories (Reynolds, Jennings & Dulvy 2001). Phylogenetically independent differences (contrasts) in life history traits within pairs of related species were calculated by subtracting the \log_{10} body mass of the smaller species from the larger one. Contrasts in \log_{10} P:B were then calculated in the same sequence for the same species pair. In the cases where phylogenetic relationships among species could not be resolved, we

calculated all $(n^2 - n)/2$ contrasts for each group and presented mean values. The significance of the relationship between the contrast in mass and contrast in P:B was determined using a binomial test (Harvey & Pagel 1991). Phylogenetic relationships among taxa were determined from published taxonomic evidence (primarily Hayward & Ryland 1990a,b; Howson & Picton 1997), because an appropriate molecular phylogeny was not available.

SIZE SPECTRA AND PRODUCTION ESTIMATES

Body size spectra were calculated for the infaunal and epifaunal communities at each site. Biomass by size class and production by size were calculated as means for the six replicates from two seasons. Biomass size spectra were normalized 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 normalized biomass was described using least squares linear regression. Production was calculated from biomass using the allometric relationship determined from studies of P:B and mean body mass. Total production for the community was given as the sum of production estimates by size class.

Results

All the study sites were trawled. There was a 27-fold range in beam trawl disturbance (SPUE) among the Silver Pit sites and 10-fold among the Hills sites (Table 1). We expressed the level of trawling disturbance as an index,

Table 1. Mean sightings per unit searching effort (SPUE) of beam trawlers by fishery protection flights in the Silver Pit and Hills areas of the North Sea, and an index of relative beam trawl disturbance where disturbance is expressed relative to the lowest beam trawl SPUE

Site	Beam trawl disturbance (lowest SPUE = 1)	Index of beam trawl disturbance
Silver Pit		
S1	1.57	5.12
S2	3.87	12.53
S3	6.86	22.18
S4	6.08	19.65
S5	9.51	30.82
S6	6.72	21.82
S7	0.34	1.12
Hills		
H1	1.47	4.76
H2	0.29	1.00
H3	0.64	2.06
H4	0.98	3.24
H5	3.14	10.12
H6	3.38	10.88
H7	2.60	8.47
H8	1.86	6.06
H9	1.67	5.35
H10	2.25	7.29
H11	3.33	10.82
H12	1.42	4.53
H13	1.13	3.59

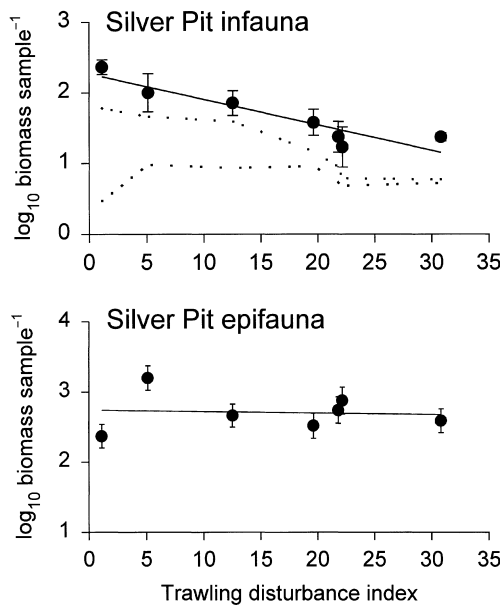


Fig. 3. The relationship between trawling disturbance and the biomass of infauna and epifauna in the Silver Pit region. The continuous lines are the fitted linear regression between biomass and trawling disturbance. In the upper panel, the upper broken line shows the biomass of spatangoids/bivalves, and the lower broken line the biomass of polychaetes.

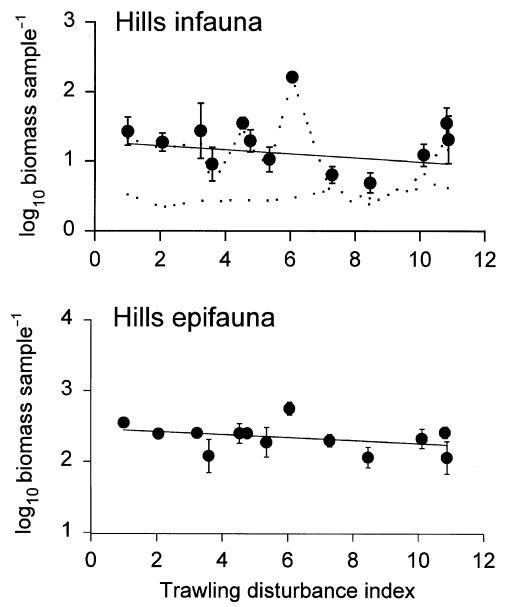


Fig. 4. The relationship between trawling disturbance and the biomass of infauna and epifauna in the Hills region. The continuous lines are the fitted linear regression between biomass and trawling disturbance. In the upper panel, the upper broken line shows the biomass of spatangoids/bivalves, and the lower broken line the biomass of polychaetes.

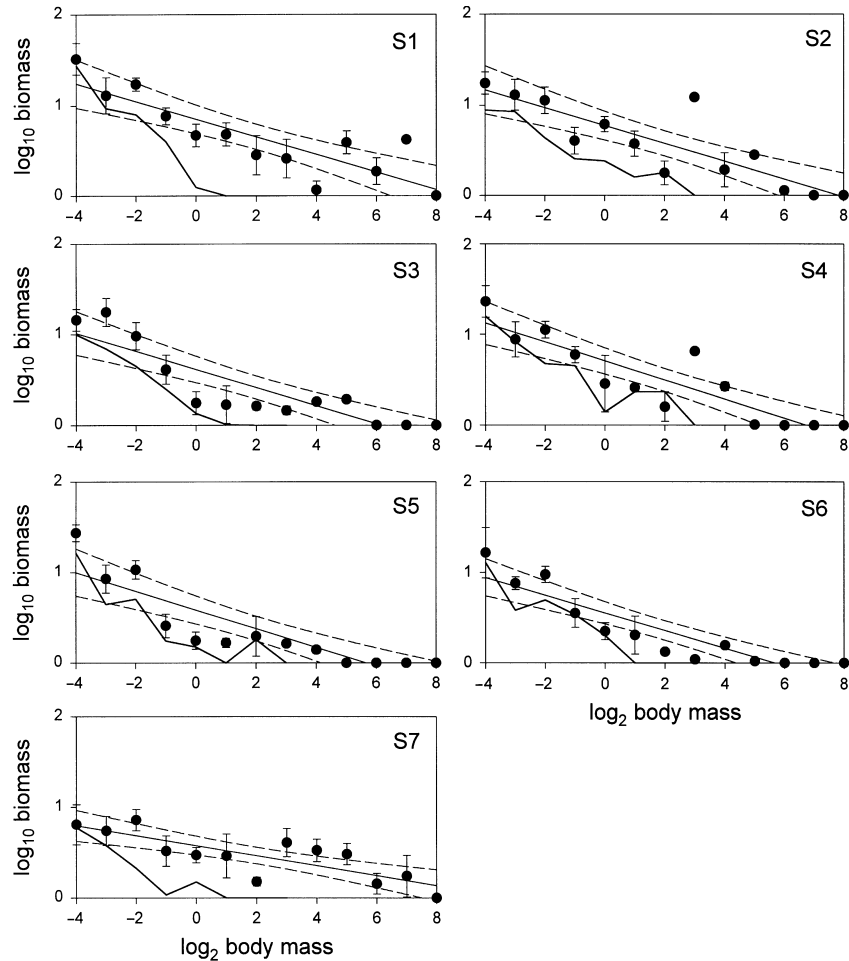


Fig. 5. Normalized size spectra for infaunal communities at the Silver Pit sites. Normalized biomass data are means \pm SD. Straight continuous lines are linear regressions fitted to these data, and broken lines are the 95% confidence limits for the regression. The lower continuous lines on each panel show the normalized spectrum for polychaetes.

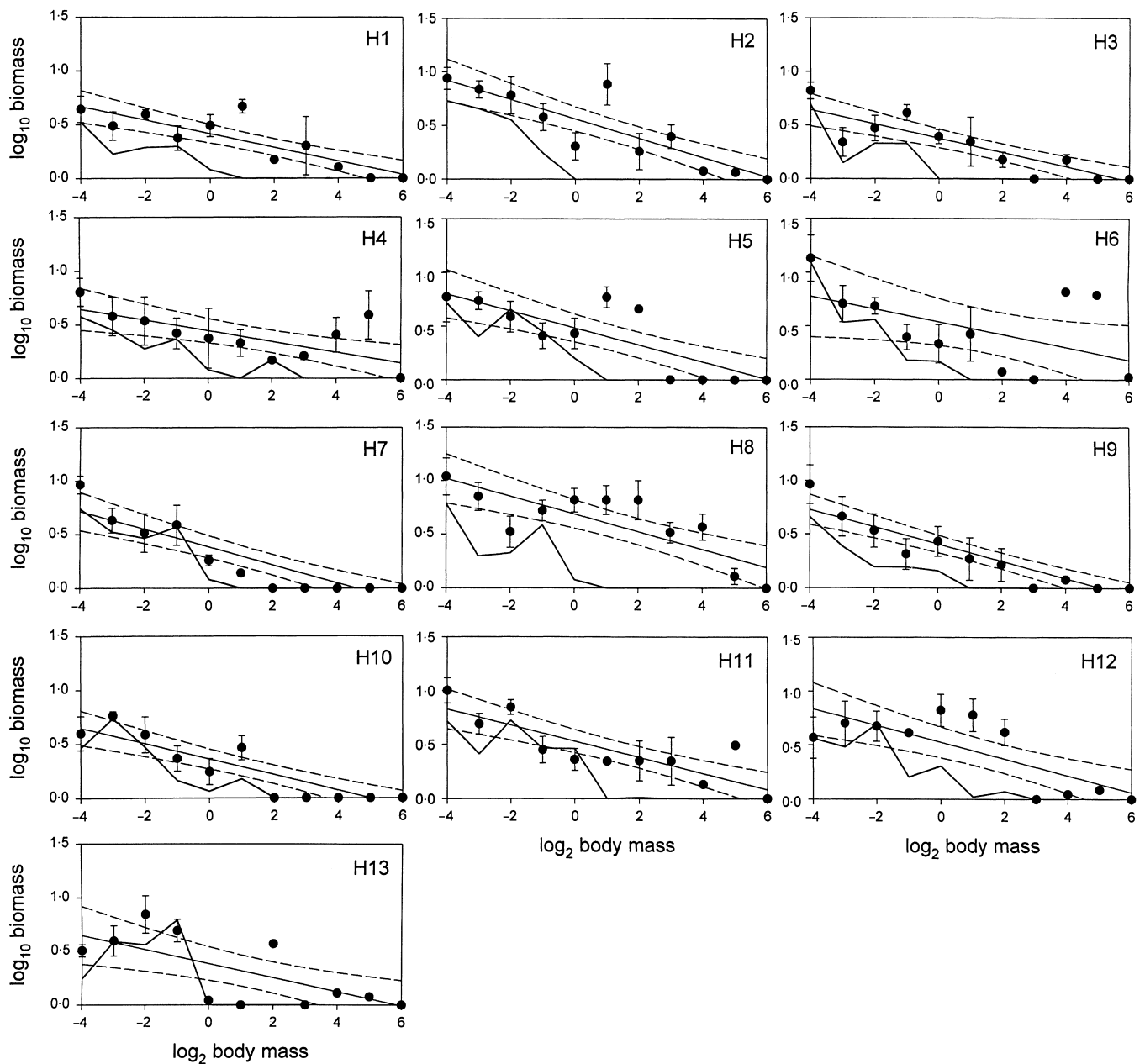


Fig. 6. Normalized size spectra for infaunal communities at the Hills sites. Normalized biomass data are means \pm SD. Straight continuous lines are linear regressions fitted to these data, and broken lines are the 95% confidence limits for the regression. The lower continuous lines on each panel show the normalized spectrum for polychaetes.

where the lowest level of disturbance was given a value of 1 on a linear scale (Table 1). The most intensively trawled site in the Silver Pit was trawled almost three times more often than the most frequently trawled site in the Hills.

In the Silver Pit region, there was a significant negative relationship between the total biomass of infauna and trawling disturbance (Fig. 3; $F_{1,5} = 30.42$, $P = 0.003$). When relationships between trawling disturbance and polychaete biomass or bivalve/spatangoid biomass were tested separately, that between disturbance and polychaete biomass was not significant ($F_{1,5} = 0.02$, $P = 0.883$), while that between disturbance and bivalve/spatangoid biomass was ($F_{1,5} = 43.37$, $P = 0.001$). However, polychaete biomass at the least disturbed site was lower than at the sites subject to more frequent disturbance.

For epifauna, there was no significant relationship between trawling disturbance and biomass in the Silver Pit region (Fig. 3; $F_{1,5} = 0.35$, $P = 0.581$).

In the Hills region, the total biomass of infauna was not significantly related to levels of trawling disturbance ($F_{1,11} = 0.00$, $P = 0.946$) and was very variable among sites (Fig. 4). Polychaete biomass was significantly and positively related to disturbance ($F_{1,11} = 10.90$, $P = 0.003$) but there was no relationship between bivalve/spatangoid biomass and disturbance ($F_{1,11} = 0.00$, $P = 0.972$). There was no significant relationship between trawling disturbance and biomass of epifauna in the Hills region (Fig. 4; $F_{1,11} = 0.55$, $P = 0.475$).

Normalized size spectra for the infaunal communities at the Silver Pit (Fig. 5) and Hills (Fig. 6) sites showed

Table 2. Slopes, intercepts and significance of linear regressions used to describe infaunal size spectra (plots of \log_{10} normalized biomass per sample by \log_2 size class vs. \log_2 size class)

Site	Slope	Intercept	r^2	$F_{1,11}$	P
S1	-0.098	0.851	0.73	30.02	< 0.001
S2	-0.099	0.775	0.74	30.85	< 0.001
S3	-0.100	0.614	0.78	37.97	< 0.001
S4	-0.105	0.704	0.80	42.56	< 0.001
S5	-0.103	0.586	0.76	35.34	< 0.001
S6	-0.098	0.554	0.82	50.45	< 0.001
S7	-0.055	0.574	0.67	22.43	< 0.001
H1	-0.063	0.415	0.77	33.86	< 0.001
H2	-0.090	0.562	0.80	36.67	< 0.001
H3	-0.066	0.378	0.79	36.88	< 0.001
H4	-0.050	0.443	0.56	12.48	0.005
H5	-0.080	0.484	0.70	23.81	< 0.001
H6	-0.060	0.538	0.32	4.750	0.054
H7	-0.083	0.382	0.80	40.99	< 0.001
H8	-0.083	0.689	0.71	24.68	< 0.001
H9	-0.080	0.409	0.86	61.52	< 0.001
H10	-0.072	0.360	0.80	38.76	< 0.001
H11	-0.075	0.529	0.76	30.75	< 0.001
H12	-0.077	0.524	0.65	18.88	0.001
H13	-0.066	0.386	0.53	11.26	0.007

Table 3. Slopes, intercepts and significance of linear regressions used to describe polychaete size spectra (plots of \log_{10} normalized biomass per sample by \log_2 size class vs. \log_2 size class)

Site	Slope	Intercept	r^2	$F_{1,6}$	P
S1	-0.216	0.394	0.90	51.14	< 0.001
S2	-0.135	0.403	0.94	87.40	< 0.001
S3	-0.159	0.298	0.92	71.28	< 0.001
S4	-0.150	0.465	0.85	32.73	0.001
S5	-0.151	0.331	0.77	20.12	0.004
S6	-0.155	0.326	0.89	48.29	< 0.001
S7	-0.109	0.181	0.80	23.31	0.003
H1	-0.070	0.142	0.82	26.26	0.002
H2	-0.122	0.211	0.86	36.74	0.001
H3	-0.082	0.147	0.65	11.06	0.016
H4	-0.078	0.200	0.80	23.41	0.003
H5	-0.110	0.249	0.83	29.19	0.002
H6	-0.143	0.245	0.82	27.07	0.002
H7	-0.115	0.239	0.84	32.23	0.001
H8	-0.101	0.209	0.68	12.95	0.011
H9	-0.086	0.157	0.83	29.55	0.002
H10	-0.094	0.212	0.74	17.01	0.006
H11	-0.109	0.293	0.76	18.70	0.005
H12	-0.094	0.245	0.77	19.48	0.004
H13	-0.085	0.231	0.40	4.02	0.092

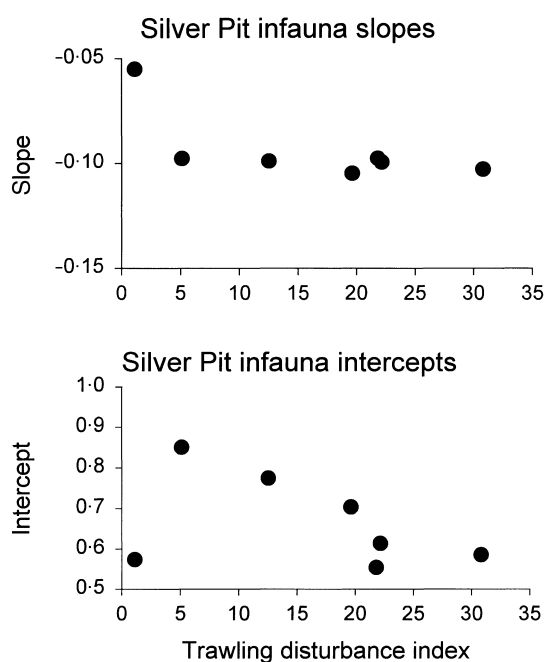


Fig. 7. Relationships between the slopes and intercepts of normalized size spectra and trawling disturbance for the infaunal communities at the Silver Pit sites.

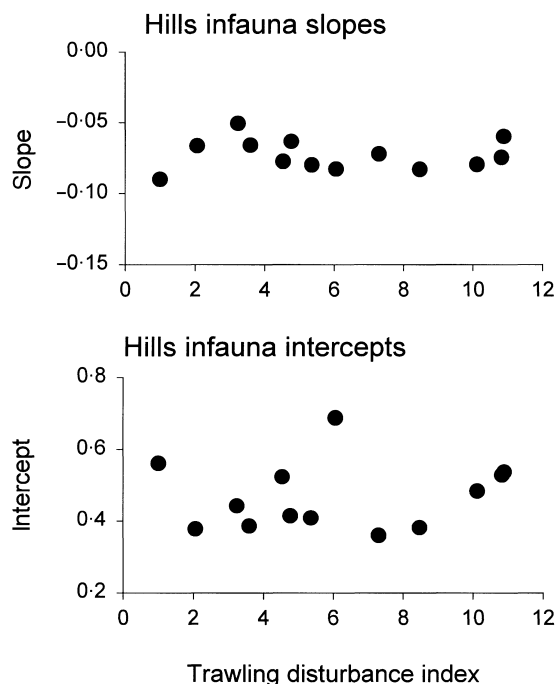


Fig. 8. Relationships between the slopes and intercepts of normalized size spectra and trawling disturbance for the infaunal communities at the Hills sites.

that there were significant negative relationships between normalized biomass by size class and body size (Table 2). In the Silver Pit region, slopes ($F_{1,5} = 4.56$, $P = 0.086$) and intercepts ($F_{1,5} = 1.11$, $P = 0.341$) of the infaunal size spectra were not significantly related to trawling disturbance (Fig. 7). Similarly, for polychaetes alone (Fig. 5; Table 3), slopes ($F_{1,5} = 0.00$, $P = 0.967$) and intercepts ($F_{1,5} = 0.39$, $P = 0.560$) were not significantly

related to trawling disturbance. The slopes ($F_{1,11} = 0.02$, $P = 0.903$) and intercepts ($F_{1,11} = 0.22$, $P = 0.645$) of infaunal size spectra in the Hills region were also not significantly related to trawling disturbance (Fig. 8), although for polychaetes alone (Fig. 6; Table 3), slopes became significantly more negative ($F_{1,11} = 4.64$, $P = 0.054$) and intercepts significantly more positive ($F_{1,11} = 7.08$, $P = 0.022$) as trawling disturbance increased.

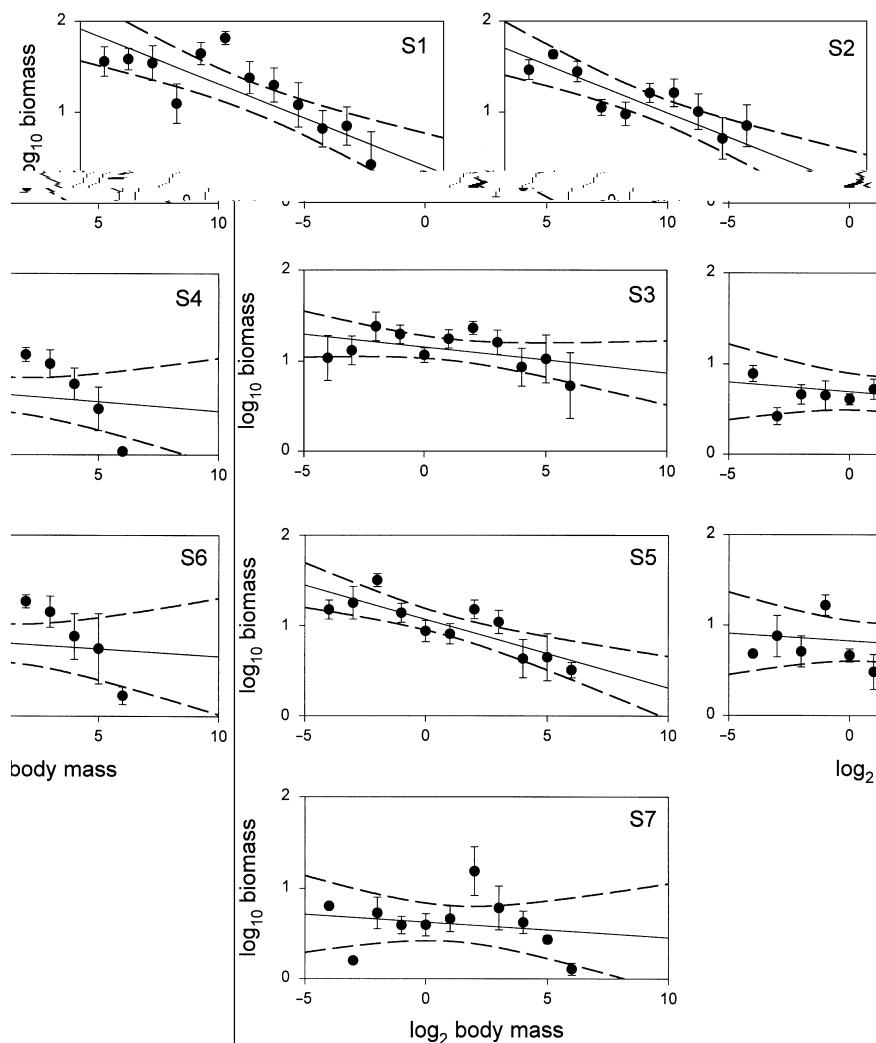
Table 4. Slopes, intercepts and significance of linear regressions used to describe epifaunal size spectra (plots of \log_{10} normalized biomass by \log_2 size class vs. \log_2 size class)

Site	Slope	Intercept	r^2	$F_{1,12}$	P
S1	-0.119	1.390	0.76	37.43	< 0.001
S2	-0.128	1.160	0.87	79.57	< 0.001
S3	-0.096	1.120	0.61	19.08	0.001
S4	-0.059	0.677	0.41	8.40	0.013
S5	-0.109	1.050	0.83	58.22	< 0.001
S6	-0.067	0.803	0.40	7.88	0.016
S7	-0.053	0.614	0.36	6.82	0.023
H1	-0.112	0.932	0.83	60.24	< 0.001
H2	-0.131	1.100	0.78	43.62	< 0.001
H3	-0.119	0.956	0.91	114.70	< 0.001
H4	-0.133	1.040	0.90	106.21	< 0.001
H5	-0.078	0.730	0.47	10.44	0.007
H6	-0.096	0.825	0.74	34.49	< 0.001
H7	-0.073	0.651	0.65	22.01	< 0.001
H8	-0.099	0.992	0.59	17.48	0.001
H9	-0.086	0.787	0.60	18.09	0.001
H10	-0.130	1.010	0.85	67.78	< 0.001
H11	-0.095	0.846	0.76	37.19	< 0.001
H12	-0.074	0.743	0.38	7.30	0.019
H13	-0.075	0.677	0.58	16.57	0.002

For the epifaunal community, there were significant negative relationships between normalized biomass by size class and body size (Table 4) at the Silver Pit (Fig. 9) and Hills (Fig. 10) sites. However, at both Silver Pit (Fig. 11) and Hills (Fig. 12) sites, slopes and intercepts were not significantly related to trawling disturbance (Silver Pit: slopes $F_{1,5} = 0.04$, $P = 0.847$, intercepts $F_{1,5} = 0$, $P = 0.987$; Hills: slopes $F_{1,11} = 2.54$, $P = 0.139$, intercepts $F_{1,11} = 2.76$, $P = 0.125$).

There was a significant relationship between P:B and body mass (B) (Fig. 13; $F_{1,75} = 66.70$, $P < 0.001$). This was described by the relationship $\log_{10} \text{P:B} = -0.233 \log_{10} \text{B} - 0.197$. The phylogeny (Fig. 14) was used to identify paired contrasts for the comparative analysis. The comparative analysis confirmed that the relationship was positive. The null expectation was that contrasts would go in either direction, but 20 of 22 contrasts were positive and only 2 of 20 were negative (Fig. 15). A binomial test indicated that this was highly significant ($P < 0.001$). Thus, even if the allometric equation contains some phylogenetic bias, the positive relationship between P:B and B is valid.

The production of infauna in the Silver Pit was significantly and negatively related to levels of trawling

**Fig. 9.** Normalized size spectra for epifaunal communities at the Silver Pit sites. Normalized biomass data are means \pm SD. The continuous lines are linear regressions fitted to these data, and broken lines are the 95% confidence limits for the regressions.

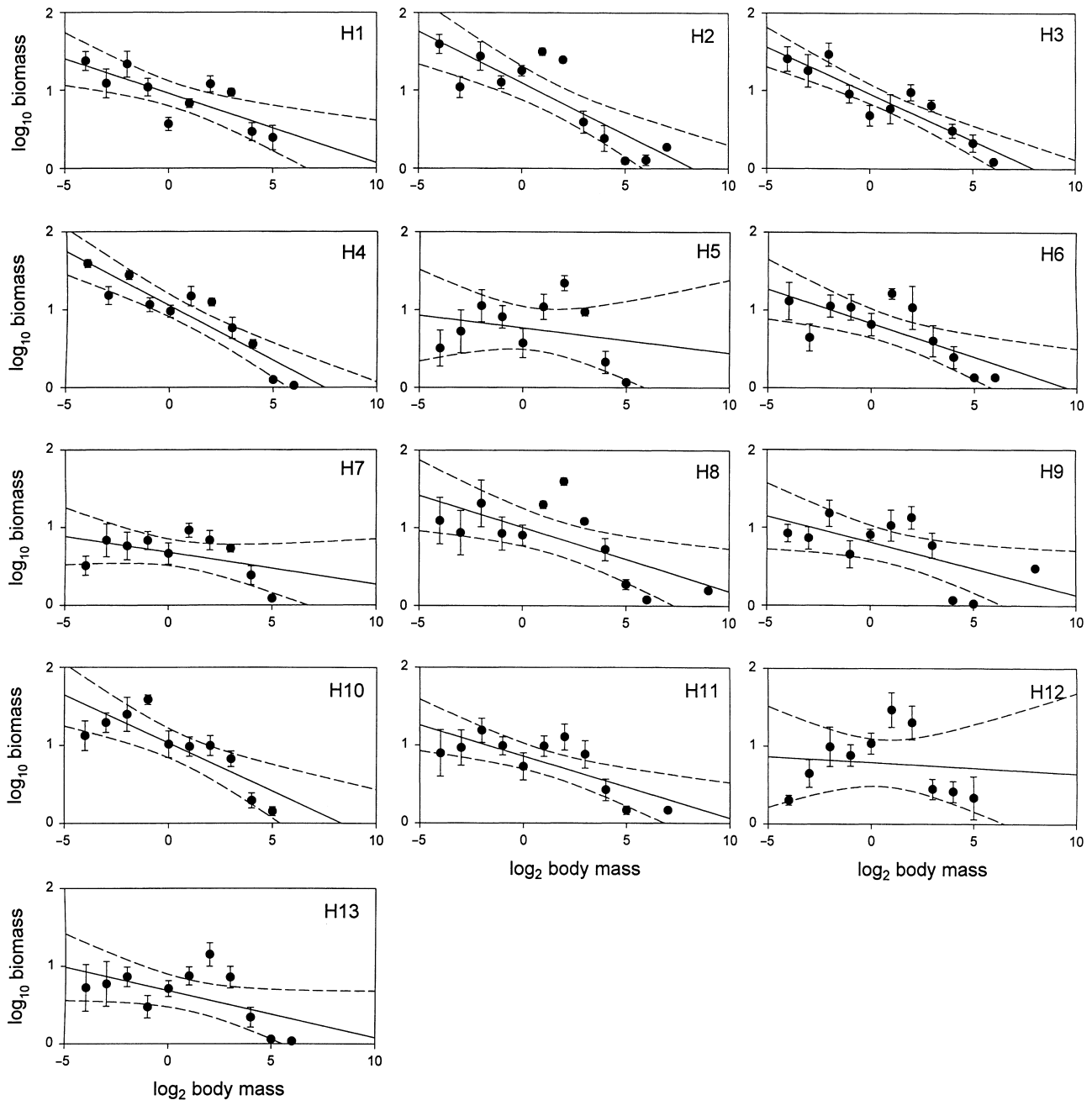


Fig. 10. Normalized size spectra for epifaunal communities at the Hills sites. Normalized biomass data are means \pm SD. The continuous lines are linear regressions fitted to these data, and broken lines are the 95% confidence limits for the regressions.

disturbance (Fig. 16a; $F_{1,5} = 130.82$, $r^2 = 0.96$, $P < 0.001$). When components of the infauna were considered separately, the production of polychaetes did not fall in response to disturbance ($F_{1,5} = 0.05$, $r^2 = 0.01$, $P = 0.831$), while that of bivalves and spatangoids did ($F_{1,5} = 56.06$, $r^2 = 0.92$, $P < 0.001$). The P:B ratio of the entire infaunal community rose significantly with disturbance (Fig. 16b; $F_{1,5} = 168.43$, $r^2 = 0.97$, $P < 0.001$), but this did not compensate for the loss of overall biomass and production. For epifauna in the Silver Pit region, there was no significant relationship between disturbance and production (Fig. 16c; $F_{1,5} = 0.02$, $r^2 = 0.01$, $P = 0.900$) or between disturbance and mean P:B of the whole community (Fig. 16d; $F_{1,5} = 0.40$, $r^2 = 0.07$, $P = 0.555$).

In the Hills region, infauna production was not significantly related to trawling disturbance (Fig. 17a; $F_{1,11} = 0.09$, $r^2 = 0.09$, $P = 0.764$), and nor was spatangoid and bivalve production ($F_{1,11} = 0.19$, $r^2 = 0.02$, $P = 0.620$). However, polychaete production increased significantly with disturbance ($F_{1,11} = 11.71$, $r^2 = 0.52$, $P = 0.006$). The P:B ratio of the entire infaunal community was not significantly related to disturbance (Fig. 17b; $F_{1,11} = 0.06$, $r^2 = 0.06$, $P = 0.805$). For epifauna in the Hills region, there was no significant relationship between disturbance and production (Fig. 17c; $F_{1,11} = 1.32$, $r^2 = 0.11$, $P = 0.274$) and there was no consistent change in the mean P:B of the whole community (Fig. 17d; $F_{1,11} = 0.07$, $r^2 = 0.06$, $P = 0.802$).

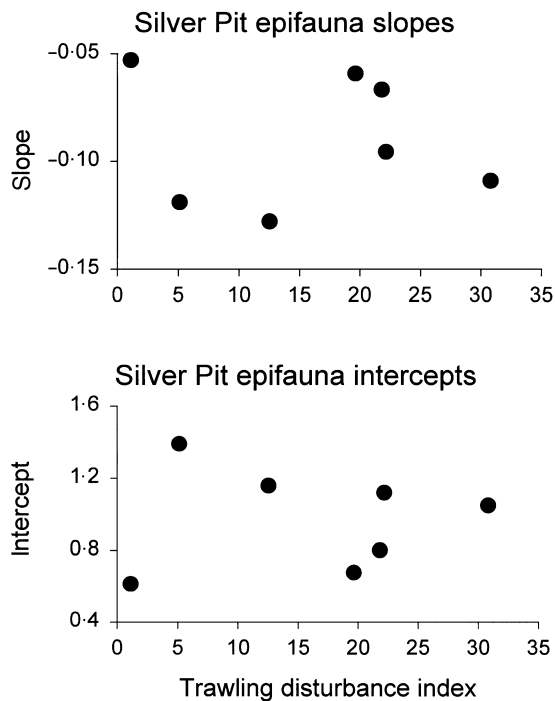


Fig. 11. Relationships between the slopes and intercepts of normalized size spectra and trawling disturbance for the epifaunal communities at the Silver Pit sites.

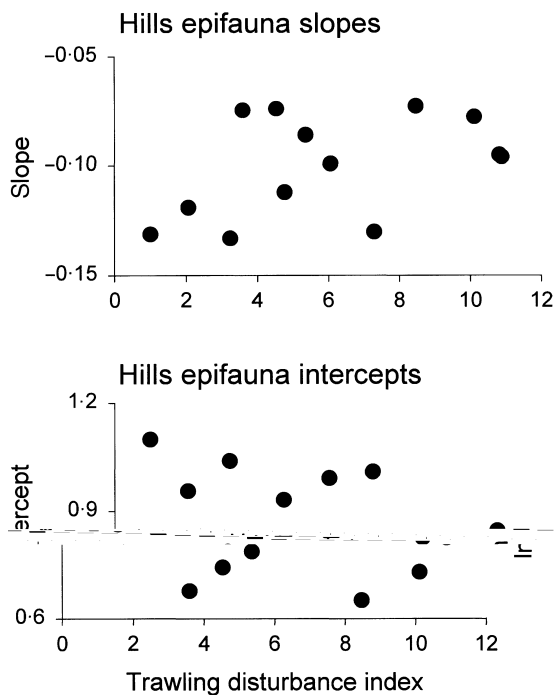


Fig. 12. Relationships between the slopes and intercepts of normalized size spectra and trawling disturbance for the epifaunal communities at the Hills sites.

Discussion

This was the first large-scale study of trawling effects on benthic production and size structure across quantified gradients of disturbance. Trawling disturbance led to reductions in the production of larger infaunal inverte-

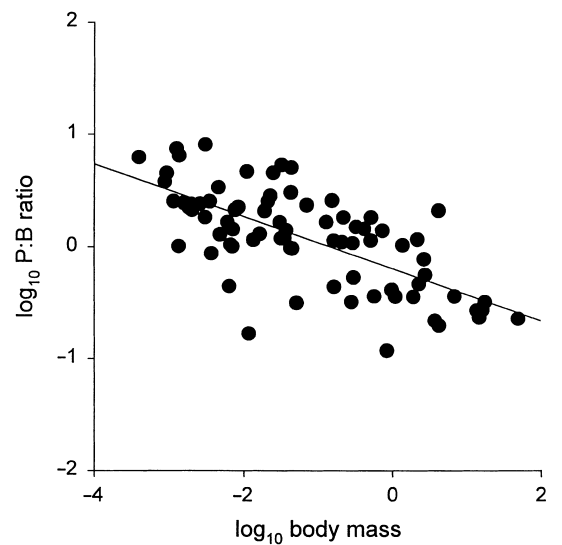


Fig. 13. The relationship between body mass and P:B ratio for marine invertebrates. The continuous line is the linear regression fitted to the data.

brates in the more heavily trawled and deeper region. The P:B ratio of the infaunal community rose with increased disturbance, but this reflected the differential loss of larger individuals rather than the proliferation of smaller ones, and total production fell. Our results are broadly consistent with studies of the effects of natural disturbance on production. Thus the correlative study of Emerson (1989) suggested that natural disturbance created by wind stress limited benthic production in shallow areas. Consistent gradients in environmental factors could have explained differences in the benthic communities among sites. However, there was no evidence for such gradients (Jennings *et al.* 2001).

Epifauna biomass and production were not significantly related to trawling disturbance. While trawling causes high levels of mortality among epifaunal species (Lindeboom & de Groot 1998; Bergman & van Santbrink 2000), changes in abundance may not have been detected because epifaunal mobility was high in relation to the spatial separation of sites subject to different levels of trawling disturbance (e.g. Dare 1982; Freeman, Seed & Richardson, *in press*). Thus the effects of mortality would have been dissipated across a wide area and could not have been detected by spatial comparisons. A significant relationship between epifauna biomass and trawling disturbance was recorded in the Silver Pit region during winter (Jennings *et al.* 2001). The Silver Pit region was much more heavily trawled in the October–November period that preceded the winter survey than the March–April period that preceded the summer survey (K.J. Warr, unpublished). Thus the link between epifauna biomass and disturbance in winter may have reflected the immediate effects of local fishing mortality.

In the Hills region, there was no significant reduction in the biomass of bivalves and spatangoids with trawling disturbance. This may have reflected the lower

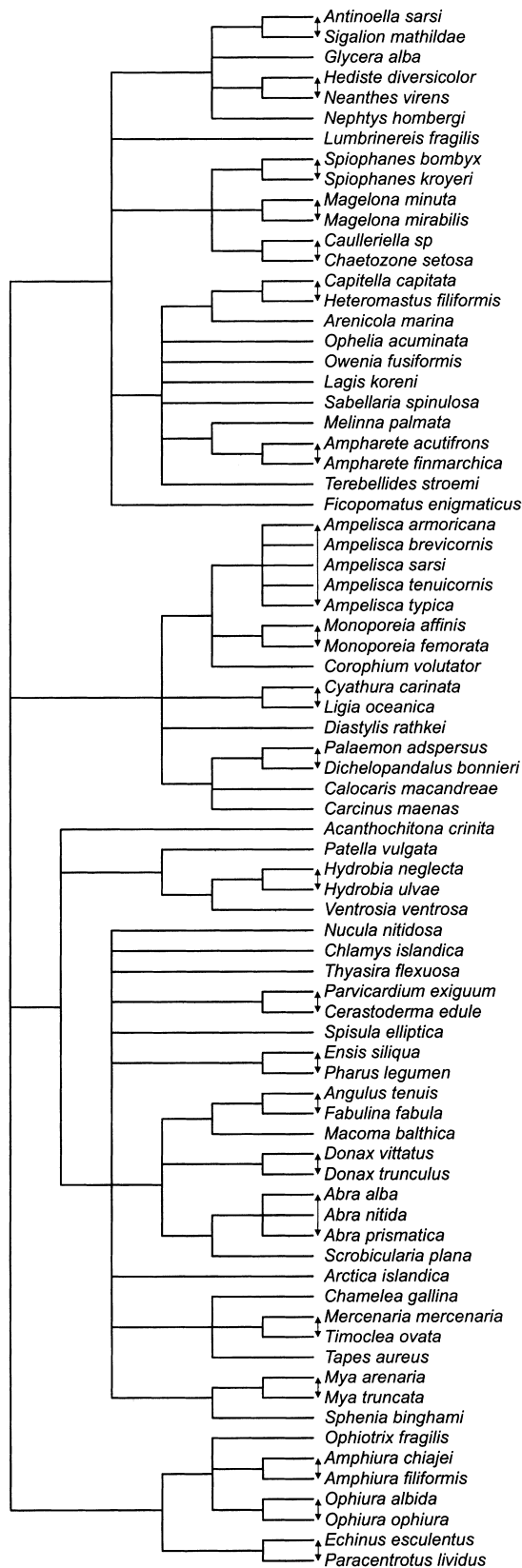


Fig. 14. Phylogenetic relationships among marine invertebrates. Branch lengths were set to unity and vertical arrows indicate paired comparisons among species.

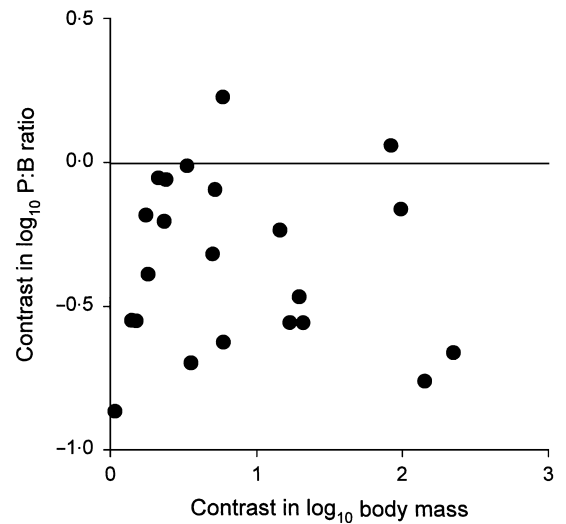


Fig. 15. Relationship between contrasts in P:B and contrasts in body mass for marine invertebrates.

range of trawling intensities in this region, since the decrease in biomass of bivalves and spatangoids was relatively small across this range of trawling intensities in the Silver Pit region. In addition, the bivalve community in the Hills region was dominated by fast-burrowing species such as *Ensis*, that are associated with mobile sands, rather than the more vulnerable *Arctica islandica* (Bergman & van Santbrink 2000) that was found in the Silver Pit. *Ensis* may have been able to bury in advance of beam trawls. Moreover, natural disturbance due to currents and waves is expected to be higher in the shallower Hills region and the fauna in that region may be less susceptible to trawling effects because it is already well adapted to natural disturbance (e.g. Hall 1994; Kaiser & Spencer 1996).

There was some evidence for the proliferation of smaller infaunal species at sites subject to moderate trawling disturbance. In the Hills region, where the disturbance index ranged from 1 to 10, there was a rise in polychaete biomass with trawling disturbance. Over a similar range of disturbance indices in the Silver Pit, polychaete biomass also appeared to increase, although there were insufficient sites at lower disturbance levels to determine whether this was statistically significant. In the Hills region, the slopes of the polychaete size spectra became increasingly negative, and the intercepts increasingly positive, as trawling disturbance increased. This change was consistent with the proliferation of smaller individuals. At higher levels of disturbance in the Silver Pit, polychaete biomass appeared to decrease, possibly because higher rates of direct or indirect mortality could not be sustained. Direct mortality could have resulted from contact with the gear, and indirect mortality from exposure of animals to invertebrate and fish predators, since many scavenging species are found in heavily trawled areas (Ramsay *et al.* 1997; Ramsay, Kaiser & Hughes 1998). The increases in the biomass or production of polychaetes had minimal effects on biomass or production of the whole community, since

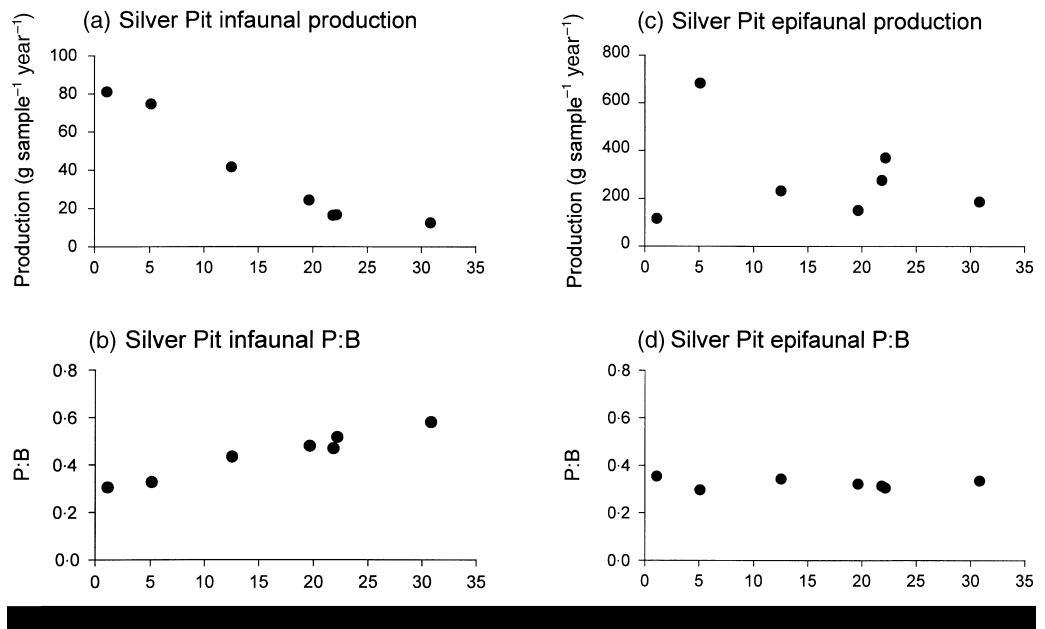


Fig. 16. The relationship between trawling disturbance and (a) infaunal production, (b) infaunal P:B, (c) epifaunal production and (d) epifaunal P:B in the Silver Pit region.

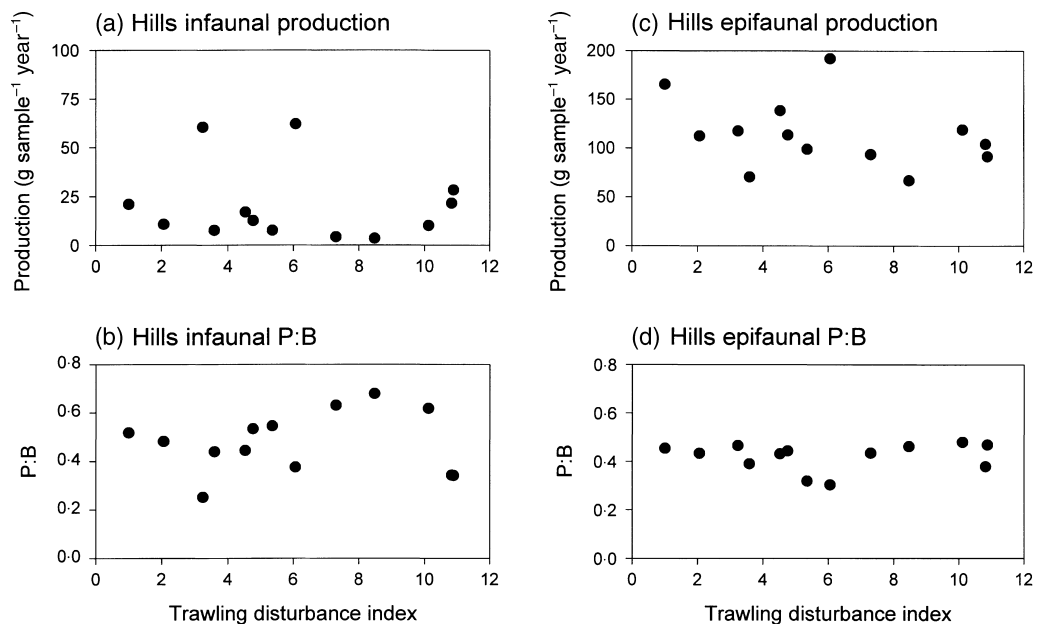


Fig. 17. The relationship between trawling disturbance and (a) infaunal production, (b) infaunal P:B, (c) epifaunal production and (d) epifaunal P:B in the Hills region.

they were very small in relation to losses in overall community biomass and production that resulted from the depletion of larger individuals. The largest increases in polychaete biomass that we observed did not approach 100%, and were less than the temporal increases in biomass that occurred in the southern North Sea during recent years (Kröncke 1992; Kröncke *et al.* 1998).

A number of mechanisms could have accounted for increases in small polychaete production at sites subject to moderate levels of trawling disturbance. First, the reduction in biomass of larger species and larger individuals may release small polychaetes from competi-

tion or predation. Secondly, trawling disturbance could enhance local production by increasing rates of contact between detritus and bacteria. Thirdly, trawling disturbance could increase the depth of the aerobic layer and increase the biomass and production of meiofauna that are consumed by larger polychaetes. Finally, trawling disturbance could alter the redox state of the sediment and increase rates of nutrient recycling. Our study suggests that none of the proposed mechanisms had a large effect on the production of polychaetes, since the spatial comparisons showed that any increases in polychaete biomass and production were minor.

However, the impacts of trawling could boost production on much larger scales, and we could not have detected these effects. Large-scale effects could have occurred if trawling released nutrients from the sediment and these nutrients enhanced primary production. Trawling disturbance is well known to resuspend large quantities of sediment (Schubel *et al.* 1978; Churchill 1989; Riemann & Hoffman 1991), and this would lead to nutrient release. The nutrients would be transported over large areas, and could enhance primary production in areas of nutrient limitation. This process is poorly understood, as is the relative contribution of nutrient release due to bioturbators (many of which are reduced in abundance by trawling disturbance), currents and storms. The present study suggests that much more research should focus on the magnitude and effects of large-scale nutrient release.

Our results suggest that recent temporal increases in the productivity of smaller polychaetes in the North Sea were not primarily a response to local disturbance by beam trawls. Rather, we suggest that they were predominantly a response to increased primary production, that resulted in a greater food supply for benthic fauna (Reid *et al.* 1998a, 1998b). Increased biomass may be observed among polychaetes and smaller bivalves, because these species are the only ones that can withstand the high rates of mortality now imposed by trawling. Since polychaetes are a favoured food of commercially important North Sea flatfishes such as plaice and sole, it is possible that the recent increases in plaice and sole growth (Veen 1976, 1978; Millner & Whiting 1996; Rijnsdorp & van Leeuwen 1996) were a response to increased benthic production following increased primary production, with trawling disturbance favouring species that were a preferred food and periodically exposing them to fish predation (Millner & Whiting 1996; Rijnsdorp & van Leeuwen 1996).

Primary production in the central North Sea has increased in recent years. The increase began from 1985 to 1987, as evidenced by greater densities of phytoplankton recorded over a longer period of each year (Reid *et al.* 1998b; Reid, Planque & Edwards 1998a). This coincided with the period when benthic biomass increased (Kröncke *et al.* 1998). From 1965 to 1985, however, primary production was low and variable. The increase in primary production has been attributed to an increase in sea temperature (Reid *et al.* 1998b), as determined by the strength of the North Atlantic Oscillation (Becker & Pauly 1996). It is possible that increases in primary production during recent years were also driven by nutrient release following trawling. However, the beam trawling fleet in the North Sea grew most rapidly in the period from 1966 to 1976 (Millner & Whiting 1996; Rijnsdorp & van Leeuwen 1996; Jennings *et al.* 1999a), but there were no consistent increases in primary production prior to 1985 (Reid *et al.* 1998a, 1998b).

Overflight estimates of trawling disturbance imply that all out study sites were fished at some time during the period 1994–98. However, the use of SPUE data

as an index of trawling disturbance do not necessarily give an accurate indication of the actual frequency of disturbance at the sites where invertebrates were sampled because the scales at which the overflight data and benthic samples can be collected were different (Jennings *et al.* 2001). Accurate knowledge of trawling history at a specific sampling site will only become available for the whole North Sea following some years of satellite tracking of fishing vessels. These data cannot be used at present since tracking has only been in operation since 1 January 2000.

A mean SPUE of 0.01 beam trawlers per visit corresponds to the entire area of a 1-nm² box being fished 6.8 times each year, or every 54 days on average (Jennings *et al.* 2001). Thus the frequency with which the entire area of the sites was trawled ranged from 0.2 to 6.5 times year⁻¹ (every 1574–56 days) in the Silver Pit and 0.2–2.3 times year⁻¹ (every 1819–158 days) in the Hills (assuming trawling is randomly distributed). Increases in polychaete biomass and production were only observed at estimated trawling frequencies of up to 2.3 times year⁻¹, and fell at higher levels of disturbance. Since many of the beam trawling grounds are fished more frequently than this (Rijnsdorp *et al.* 1998), polychaetes are unlikely to benefit from disturbance in many areas. However, larger bivalves and spatangoids are likely to be depleted (Bergman & van Santbrink 2000). Production to biomass ratios are quite low in the parts of the macrofauna community we considered (individuals > 0.0625 g), and there may be an increase in production in smaller size classes with faster turnover times, as these could take advantage of an increased food supply or reduced predation, but easily withstand any mortality imposed by trawling. Our smallest size class (arithmetic mean wet mass = 0.09375 g) has a P:B of 1.1 : 1, implying a 'turnover time' of 332 days and thus relatively low rates of mortality could prevent population growth. Turnover times significantly faster than the frequency of trawling are only seen in the meiofauna. For example, Schwinghamer *et al.* (1986) quote turnover times of 24 days and less for organisms < 2.1*10⁻⁷ g (converted from kCal; Brey, personal communication). If we are looking for increases in production that result from trawling disturbance then the effects are likely to be seen only in the smallest macrofauna and meiofauna. Increases in the production of these small species are unlikely to provide additional food for adult fishes of commercial importance as these fishes tend to feed on larger polychaetes (e.g. Braber & de Groot 1973; De Clerck & Buseyne 1989).

Ecological theory suggests that the assembly of organisms can be described using size spectra because these spectra reflect energy flow from prey to predators (Kerr 1974; Platt & Denman 1977, 1978; Dickie, Kerr & Boudreau 1987; Boudreau, Dickie & Kerr 1991; Thiebaut & Dickie 1992, 1993). In the infaunal community, a size-based assessment of trophic level using stable isotope analysis has shown that the size distribution of organisms is not consistently related to trophic level.

For the smaller infauna, predominantly the polychaetes, trophic level increases with body size (Jennings *et al.* 2001). This suggests that larger predatory polychaetes eat smaller deposit feeding polychaetes, in accordance with diet studies (Schubert & Reise 1986; Beukema 1987). However, the larger bivalves and spatangoids often feed at lower trophic levels than the polychaetes, and changes in the size spectra for the whole infaunal community reflect the differential loss of large animals with slow life histories rather than a reduction in trophic level of the infaunal community.

The estimation of production from body mass is fraught with difficulty and the relationships used do not account for phylogenetic nonindependence of data and the characteristics of the environment in which specific studies were conducted (Banse & Moser 1980; Schwinghamer *et al.* 1986; Tumbiolo & Downing 1994; Brey 1999). While our estimates of production may be imprecise, the direction of trends we report are expected to be valid, since we confirmed the validity of the general relationship using a phylogenetic comparative approach. The general relationship between P:B and body mass is consistent with relationships in other animal populations, where larger species have slower life histories than smaller ones (Beverton & Holt 1959; Charnov 1993). If greater resources were available, it would still be useful to make direct measurements of production for communities in areas subject to different levels of trawling disturbance.

Our results can probably be generalized to other shallow, trawled, sand and mud habitats dominated by free-living species, but we would expect very different results in areas where the habitat is more complex, where there are many biogenic species and where there was no previous history of fishing activity (e.g. Dayton *et al.* 1998). For example, when Collie, Escanero & Valentine (1997) compared cobble substrata that were scallop dredged at different intensities on Georges Bank, north-west Atlantic, the infrequently fished areas were characterized by abundant growths of bryozoans, hydroids and tubeworms that increased the three-dimensional complexity of the habitat while heavily fished areas were very different, with lower species diversity and reduced habitat complexity, and were dominated by species resistant to fishing activities. We would expect massive changes in production processes and trophic structure in such areas as many of the most vulnerable animals, such as bryozoans, are those responsible for forming habitat.

Our results suggest that future studies of trawling effects on ecosystem function should focus on the production and dynamics of the meiofauna and the smallest macrofauna, because these groups, along with bacteria, are the only large groups of species that have sufficiently fast life cycles to proliferate in intensively trawled areas and process the carbon and nitrogen that cannot be processed by depleted populations of larger animals. If these studies also show that the rate of production is reduced by disturbance, then trawling disturbance could have indirect effects on the strength

of benthic–pelagic coupling and the rate of detritus accumulation in marine ecosystems.

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