

Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities

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ABSTRACT: Bottom trawling causes chronic and widespread disturbance to the seabed in shallow shelf seas and could lead to changes in the trophic structure and function of benthic communities, with important implications for the processing of primary production and the wider functioning of the marine ecosystem. We studied the effects of bottom trawling on the trophic structure of infaunal and epifaunal benthic communities in 2 regions (Silver Pit and Hills) of the central North Sea. Within each region, we quantified long-term (over 5 yr) differences in trawling disturbance at a series of sites (using sightings data from fishery protection flights), and related this to differences in the biomass and trophic structure of the benthic community. There were 27- and 10-fold differences in levels of beam trawl disturbance among the Silver Pit and Hills sites respectively, and we estimated that the frequency with which the entire area of the sites was trawled ranged from 0.2 to 6.5 times yr⁻¹ in the Silver Pit and 0.2 to 2.3 times yr⁻¹ in the Hills. The impacts of fishing were most pronounced in the Silver Pit region, where the range of trawling disturbance was greater. Infaunal and epifaunal biomass decreased significantly with trawling disturbance. Within the infauna, there were highly significant decreases in the biomass of bivalves and spatangoids (burrowing sea-urchins) but no significant change in polychaetes. Relationships between trophic level (estimated using nitrogen stable isotope composition, $\delta^{15}\text{N}$) and body mass (as log₂ size classes) were rarely significant, implying that the larger individuals in this community did not consistently prey on the smaller ones. For epifauna, the relationships were significant, but the slopes or intercepts of the fitted linear regressions were not significantly related to trawling disturbance. Moreover, mean $\delta^{15}\text{N}$ of the sampled infaunal and epifaunal communities were remarkably consistent across sites and not significantly related to trawling disturbance. Our results suggest that chronic trawling disturbance led to dramatic reductions in the biomass of infauna and epifauna, but these reductions were not reflected in changes to the mean trophic level of the community, or the relationships between the trophic levels of different sizes of epifauna. The trophic structure of intensively trawled benthic invertebrate communities may be a robust feature of this marine ecosystem, thus ensuring the efficient processing of production within those animals that have sufficiently high intrinsic rates of population increase to withstand the levels of mortality imposed by trawling.

KEY WORDS: North Sea · Fishing effects · Benthic infauna · Benthic epifauna · Trophic relationships · Stable isotopes · Community structure · Beam trawling · Food webs

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INTRODUCTION

Many studies have described the impacts of bottom trawling on the structure of benthic communities (reviews: Dayton et al. 1995, Jennings & Kaiser 1998, Lindeboom & de Groot 1998, Hall 1999, Kaiser & de Groot 2000). They have focused on changes in the relative abundance of different species in the benthic

community, but have not dealt directly with changes in the trophic structure or function of that community. We might expect trawling to have profound effects on the trophic structure and function of benthic communities, because certain functional groups, such as large filter-feeding bivalves, are more vulnerable to trawling disturbance than others (Lindeboom & de Groot 1998).

A large proportion of the seabed in northeast Atlantic shelf seas is disturbed by bottom trawling (Rijnsdorp et al. 1996, Kaiser 1998, Greenstreet et al.

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1999, Jennings et al. 1999a), and small (10s of km²) intensively fished areas in the southern North Sea may be trawled 10 or more times each year (Rijnsdorp et al. 1998). If quantified levels of bottom trawling disturbance could be linked to quantifiable changes in the trophic structure of benthic communities, this would be a first step towards describing and mitigating any indirect effects of fishing on ecosystem function. To date, the best evidence for fishing effects on trophic structure comes from changes in the trophic level of global catches. Pauly et al. (1998) documented a decrease in the trophic level of catches as larger and more vulnerable species at the highest trophic levels were depleted and fishers 'fished down the food chain' in order to maintain yields. However, fishing has many impacts other than those on target species (Jennings & Kaiser 1998, Hall 1999). Bottom trawls, for example, crush benthic invertebrates in the path of the net and lead to the mortality of invertebrates that are caught in the net and subsequently discarded because they have little or no commercial value (Jennings & Kaiser 1998, Lindeboom & de Groot 1998, Hall 1999, Kaiser & de Groot 2000). The mortality suffered by larger benthic species is generally greater than that of smaller species (Gilkinson et al. 1998, Lindeboom & de Groot 1998), and larger species, with lower intrinsic rates of natural increase (Brey 1999), are more likely to decline in abundance at a given rate of mortality. Since larger species are often those at higher trophic levels (because predators are usually larger than their prey; Cohen et al. 1993), the reductions in abundance of larger species might be expected to reduce the mean trophic level of the community.

Short-term reductions in benthic biomass and shifts in community structure following trawling disturbance are well known from experimental studies (Bergman & Hup 1992, Thrush et al. 1995, Currie & Parry 1996, Kaiser & Spencer 1996, Tuck et al. 1998, Bradshaw et al. 2000). The effects of trawling on infauna are more noticeable in areas where levels of natural disturbance are low than where they are high (Brylinsky et al. 1994, Kaiser & Spencer 1996), because the community is already adapted to disturbance (Jennings & Kaiser 1998). Recovery of the community following trawling also depends on levels of natural disturbance. At a site with strong tidal currents and mobile substratum, Kaiser & Spencer (1996) showed that experimental trawling changed the community, but 6 mo later, there were no significant differences between trawled and untrawled sites (Kaiser et al. 1998). Similarly rapid recovery of fauna in a coarse sand was observed by Thrush et al. (1995) in New Zealand. In more stable areas, recovery is longer. Tuck et al. (1998) studied trawling effects in a previously untrawled muddy area, and changes were still apparent after 18 mo. Similarly, Collie et al. (1997)

showed recovery from scallop dredging took at least 2 yr. Collie et al. (2000) synthesised recovery data from a variety of studies in a meta analysis. Their results suggested that the fauna of sandy seabeds often recovered in around 100 d and could tolerate 2 to 3 trawl passes a year. We must assume that measured rates of recovery for mobile species are largely due to immigration, since what is known of the life histories of benthic species (Brey 1999) suggests that population regeneration would not occur on this time scale. This means that the effects of repeated trawling over large areas, as occurs in real fisheries, may have collective effects that would not be detected by studies of recovery in small experimental areas.

Small-scale experimental studies provide a statistically powerful way of detecting trawling effects, but do not replicate the large-scale and long-term disturbance that occurs in real fisheries (Kaiser et al. 2000). Study of trawling effects at the scale of the fishery is especially important if we are to understand effects at the ecosystem scale. For example, there have been dramatic and long-term changes in the benthic fauna of the southern and central North Sea, and trawling could easily be implicated as a cause, because trawling effort has risen over the same period (Lindley et al. 1995, Heessen & Daan 1996). In the southern North Sea, there has been a shift towards a community of higher biomass that is dominated by polychaetes rather than larger bivalves (Kröncke 1990, 1992, Kröncke et al. 1998). The reduction in bivalves has been attributed to the mortality caused by contact with trawls (Lindeboom & de Groot 1998), while polychaetes could proliferate because they suffer lower mortality and have life histories that imply higher intrinsic rates of population increase (Brey 1999). Reductions in the abundance of larger burrowing urchins (spatangoids) are also an expected consequence of trawling disturbance, as these can suffer 10 to 50% mortality in the path of trawls (Lindeboom & de Groot 1998). Intriguingly, the temporal changes in North Sea benthos (Kröncke 1990, 1992, Kröncke et al. 1998) during a period of increasing beam trawling effort (Jennings et al. 1999a), have mimicked those demonstrated in experimental studies, where bivalves became scarce and polychaetes proliferated (Tuck et al. 1998). However, eutrophication and climatic effects are predicted to be responsible for much of the proliferation of polychaetes in the North Sea (Kröncke et al. 1998), and quantitative assessment of the relationship between trawling disturbance and polychaete abundance would help to resolve the relative roles of eutrophication, climate and disturbance.

A major impediment to the study of trawling disturbance of benthic communities is the paucity of data that quantify levels of trawling disturbance on appro-

priate spatial and temporal scales; in addition, with few exceptions, trawling effects have not been examined across quantifiable gradients of disturbance (Collie et al. 1997, Thrush et al. 1998, Kaiser et al. 2000). In the North Sea, international trawling effort data are collated by ICES statistical rectangle (211 boxes of 0.5° North–South and 1° East–West). These are very large areas (3720 km² at 53° N) and trawling effort in the rectangles is very patchy (Rijnsdorp et al. 1998). Since benthic sampling can only be conducted on spatial scales several orders of magnitude below that of the rectangle, it is impossible to know if a sampling site has actually been disturbed by trawling. One alternative is to attempt to quantify trawling disturbance on much smaller scales using biological indicators. For example, rates of scarring in the shells of large bivalves such as *Arctica islandica* (Witbaard & Klein 1994) and *Glycymeris glycymeris* (Kaiser et al. 2000), or the whelk *Buccinum undatum* (Mensink et al. 2000) reflect the frequency with which they are hit by bottom trawls. However, not all individuals recover when they are hit by trawls, and larger bivalves in the path of a beam trawl typically suffer mortality of 20% or more (Lindeboom & de Groot 1998, Bergman & van Santbrink 2000). As a result, species such as *Arctica islandica* have been extirpated in heavily trawled areas (Rumohr & Krost 1991, Craeymeersch et al. 2000) and cannot be used to differentiate between higher levels of disturbance.

An alternative method for quantifying trawling disturbance on relatively small scales is to use records of vessels sighted by aircraft that patrol the fishing grounds around the United Kingdom. The crew on these aircraft record the description and location of all vessels they see fishing. Relative trawling disturbance can be estimated as the number of actively fishing trawlers sighted per unit of search effort per unit area. While the spatial resolution of fishery protection data is not quite as good as that collected from position loggers on trawlers or satellite tracking, the former has not been applied to all trawlers that prosecute the southern and central North Sea fisheries and the latter has only been applied since 1 January 2000.

We describe the trophic structure of benthic invertebrate communities by using stable isotopes of nitrogen as an index of trophic level. Studies of nitrogen stable isotope (¹⁴N and ¹⁵N) composition can provide indices of trophic level and thus provides a useful tool for investigating trophic relationships (Peterson et al. 1985, Owens 1987, Peterson & Fry 1987, Fry & Sherr 1989, Preston 1992). The $\delta^{15}\text{N}$ in the tissues of predators is typically ~3‰ greater than their prey and thus ¹⁵N studies have been used to define the trophic levels of organisms in systems where feeding relationships are not known (Minawaga & Wada 1984, Owens 1987,

Hobson & Welch 1992, Fry & Quinones 1994), although in reality, there is variation around the mean level of enrichment due to differences in C:N ratios of the tissue and nutritional status (Adams & Sterner 2000). Stable isotope analysis allows the estimation of trophic level for species such as small invertebrates, for which it would be impossible to quantify diet on a systematic basis (Minawaga & Wada 1984, Owens 1987).

In the present study we compare benthic communities among sites subject to different levels of trawling disturbance in 2 regions of the North Sea. The fauna in these regions is dominated by free-living infauna and epifauna living in mobile sediment, typical benthic communities of North Sea beam trawl grounds (e.g. Kunitzer et al. 1992). We focus on aggregate responses of the community to trawling rather than those of individual species. We attempt to link structural changes in the abundance of species groups to those in the trophic structure of the community. This is a fundamental step towards understanding the impacts of trawling disturbance on patterns of production and energy use in marine ecosystems. We focus on differences among sites that have been subject to different levels of trawling disturbance for at least 5 yr. We seek to address the following questions: (1) How does trawling disturbance affect the total biomass of infauna and epifauna? (2) Is there evidence for a shift in the infaunal community from one that is dominated by bivalves and spatangoids to one that is dominated by polychaetes? (3) Does trawling disturbance favour species from lower trophic levels and lead to a fall in the trophic level of the community? (4) Does trawling disturbance affect any size-based predator-prey relationships that are seen in the community?

METHODS

Study sites. The impact of trawling disturbance on the trophic structure of infaunal and epifaunal benthic communities was investigated in 2 series of sites subject to different levels of fishing disturbance in 2 regions of the North Sea (Fig. 1). The regions were chosen because a preliminary analysis showed that there were marked variations in trawling effort within each region, even though the depths, sediments and temperature regimes in each region were similar (Lee & Ramster 1981, British Geological Survey unpubl. data, CEFAS unpubl. data). The first region was the Silver Pit, where the depth ranges from 60 to 80 m and the sediment is muddy sand (mean particle diameter in Silver Pit = 0.02 to 0.09 mm; British Geological Survey unpubl.). The second region was the Hills, where depths are 40 to 60 m and the sediment is sandy (mean particle diameters in Hills = 0.250 to 0.350 mm;

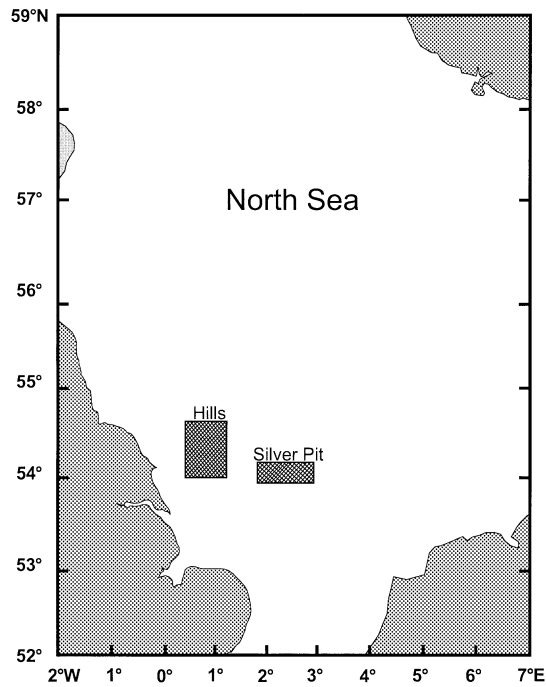


Fig. 1. The Hills and Silver Pit regions in the North Sea. The shaded boxes show the areas in which sampling sites were selected. The boundaries of the shaded boxes correspond to the boundaries of the boxes shown in Figs. 2 & 3. Note that 1° of latitude is 60 nautical miles (approx. 111 km)

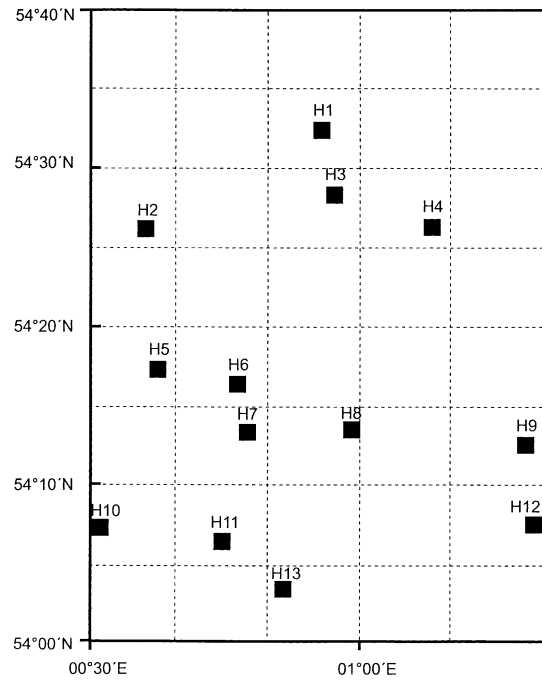


Fig. 3. The 13 study sites (H1–H13) in the Hills region of the North Sea. Each study site is shown as a shaded square of 1 n mile². The broken lines show the boundaries of the areas where trawling disturbance was assessed

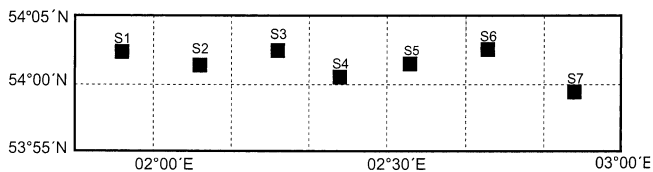


Fig. 2. The 7 study sites (S1–S7) in the Silver Pit region of the North Sea. Each study site is shown as a shaded square of 1 n mile². The broken lines show the boundaries of the areas where trawling disturbance was assessed

British Geological Survey unpubl.). Preliminary study of the invertebrate communities in each region showed that free-living species accounted for most of the total biomass and numerical abundance of the epifaunal (Jennings et al. 1999b) and infaunal (S.J. et al. unpubl.) community. Seven sites subject to different levels of trawling disturbance were studied in the Silver Pit (Fig. 2), and 13 sites in the Hills (Fig. 3). Each site was designated as an area of 1 n mile North–South (1 n mile = 1853 m) by 1 n mile East–West.

Estimation of trawling disturbance. The trawling disturbance at each site was determined from records of vessel sightings by fishery protection aircraft. These aircraft patrol the fishing grounds around the United

Kingdom and record a description and location of all vessels that they observe fishing. In the southern and central North Sea, fishery protection flights visit most ICES (International Council for the Exploration of the Sea) sub-rectangles (there are 4 sub-rectangles per rectangle, each sub-rectangle is 0.5° North–South by 0.5° East–West) around 100 times yr⁻¹. Relative trawling disturbance can be estimated as the number of trawlers sighted per unit of searching effort (SPUE) (Jennings et al. 2000).

The Silver Pit and Hills regions (Fig. 1) were divided into 5 n mile (9265 m) (North–South) by 6 n mile (11 118 m) (East–West) areas, working south from the northern limit of the maps in Figs. 2 & 3. Within each area, the mean number of beam or otter trawls SPUE was calculated (effort was measured as the number of visits by a fishery protection aircraft). We used records of all sightings of actively fishing beam and otter trawlers in the Silver Pit and Hills regions from 1 January 1994 to 31 December 1998. In this period, aircraft visited sub-rectangles in the Silver Pit with a mean frequency of 103.7 to 153 visits yr⁻¹, and sub-rectangles in the Hills with a mean frequency of 121.2 to 160.2 visits yr⁻¹ (Jennings et al. 2000). Trawling effort in the 1 n mile² (3.43 km²) study sites within the 30 n mile² (103 km²) area was taken as 1/30th of that in the 30 n mile² area. This was preferable to calculating SPUE in

the 1 n mile² study sites, because the error associated with locating a vessel inside or outside such a small area is very large when modern beam trawlers fish at up to 7 knots (13 km h⁻¹) and can travel 1 n mile (1853 m) in less than 10 min. For the quantitative analysis of differences in community and trophic structure among sites, we assumed that SPUE was directly and linearly proportional to trawling effort and trawling disturbance. We expressed the level of trawling disturbance as an index, where the lowest level of disturbance was given a value of 1 on a linear scale. Clearly, our approach assumes that trawling and aircraft search patterns within the areas are random. We recognise that this assumption will be violated and introduce some bias, but 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 track frequency and SPUE are correlated and that tracks cross the more heavily fished sites in many directions (S.J. unpubl. data). However, with existing data, we cannot quantify the bias that trawling and aircraft search patterns introduce.

Since the relative impacts of beam trawls on the benthic community are considerably greater than those of otter trawls (Lindeboom & de Groot 1998, Bergman & van Santbrink 2000), we related changes in trophic structure to differences in beam trawling effort. However, otter trawler SPUE data have been provided for comparative purposes. In all analyses we assume that the rate of SPUE is directly and linearly proportional to fishing effort and disturbance.

Sampling of benthic community. Epibenthic invertebrates were sampled with a 2 m beam trawl and infaunal invertebrates with an anchor dredge. The beam trawl was fitted with a chain mat and a 1 mm mesh liner and was fished from the stern gantry of the RV 'Corystes', using a warp length of 3 times the water depth. Three randomly located replicate tows were completed at each site. Each tow was 5 min in duration at a speed of 1 knot (1.853 km h⁻¹). The 5 min period was timed from the moment that the net contacted the seabed until the moment of hauling from the seabed. Operational constraints meant that the distance trawled had to be confirmed retrospectively, using Sextant software linked to the ship's differential global positioning system (DGPS). The design and operation of the 2 m beam trawl is described in detail by Jennings et al. (1999b). Three randomly located replicate tows of 1 min duration were also made with an anchor dredge (Kaiser et al. 2000). The sediment collected was emptied on the deck of the ship and a 0.2 m³ sub-sample removed. This was sieved through 1 mm square mesh, and all infaunal species retained by the mesh were removed for processing. All sampling was conducted from 29 October to 8 December

1999, and depth was measured at the location where each gear was first deployed.

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 of m²) and integrate small-scale patchiness of the benthic fauna. We assumed that the catchability of different species did not change from site to site, so bias in abundance estimates was consistent. Only free-living (species not anchored to shell, stone, rock or sand) epifaunal species were retained from the beam trawl samples, and free-living infauna from the anchor dredge samples. Epifauna were defined as those species that live on the seabed or burrow into it temporarily, while infauna were defined as those that live predominantly in the substrate.

All infauna from the replicate anchor dredge samples and epifauna from the replicate beam trawl samples were identified, individually weighed on heave compensated balances and assigned to log₂ size classes. Hermit crabs (Paguridae) were weighed after removal from their shells, but animals that secreted their own shells were weighed with the shells intact. To obtain tissue samples for stable isotope analysis, animals from the same size class in each of the 3 replicate samples of (a) infauna and (b) epifauna from each site were combined and homogenised in an electric blender, usually with added water, to produce a thoroughly mixed suspension that poured smoothly. Approximately 7 ml of this suspension was frozen to -20°C in a glass vial. Shells were removed from all bivalves before blending.

Stable isotope analysis. The frozen samples of homogenised tissue were freeze dried, and the freeze dried material was crumbled or ground to a fine powder (particles <60 µm). The ¹⁵N composition of the samples was determined using continuous flow isotope ratio mass spectrometry (CF-IRMS) (Preston & Owens 1983, Preston 1992). Weighed samples of 1.0 mg ground material were oxidised and the N₂ passed to a single inlet dual collector mass spectrometer (Automated Nitrogen Carbon Analysis [ANCA] SL 20-20 system). This was a continuous flow system, so 2 samples of reference material (an internal standard—in this case homogenised cod *Gadus morhua* tissue with similar nitrogen content to the samples we analysed) were analysed after every 5 tissue samples in order to calibrate the system and compensate for drift with time (ANCA-SL Dual Isotope v3.4 software).

Ratios of ¹⁵N:¹⁴N were expressed relative to N₂ in air for nitrogen and calculated as:

$$\delta^{15}\text{N} = \left(\frac{{}^{15}\text{N}:{}^{14}\text{N}_{\text{sample}}}{{}^{15}\text{N}:{}^{14}\text{N}_{\text{standard}}} - 1 \right) \times 10^3$$

The mean $\delta^{15}\text{N}$ for the infaunal or epifaunal community at each site was calculated as a weighted mean of $\delta^{15}\text{N}$ by size class. The SD for the repeated $\delta^{15}\text{N}$ measurements made with the reference material was 0.1%. Two samples were excluded from the final analysis. First, an infaunal sample in the 8.1 to 16.0 g size class from Site S4 which contained only 0.202% N, below the recommended tolerance of the ANCA system and significantly below the mean nitrogen content ($9.3 \pm 2.75\%$) for other samples in this size class taken at Silver Pit. Second, an infaunal sample in the 1.1 to 2.0 g size class from Site H13 which contained only 0.435% N, also below the recommended tolerance of the ANCA system and significantly below the mean nitrogen content ($9.8 \pm 1.61\%$) for other samples in this size class taken at the Hills sites. We do not know why the N content of these samples was so low.

RESULTS

All the study sites were trawled. There was a 27-fold range in beam trawl SPUE among the Silver Pit sites and 10-fold among the Hills sites, and the most intensively trawled site in the Silver Pit was trawled almost 3 times more often than the most frequently trawled

sites in the Hills (Table 1). Sites with high beam trawling disturbance were usually subject to high otter trawling disturbance too, and the ranking of sites within regions by total trawling disturbance and beam trawling disturbance was relatively similar. Mean depths at the Silver Pit sites ranged from 58.9 to 72.2 m and from 44.0 to 62.2 at the Hills sites (Table 1).

The total biomass (all references to biomass refer to biomass per sample) of infauna and epifauna decreased significantly with trawling disturbance in the Silver Pit (linear regression: infauna $r^2 = 0.68$, $F_{1,5} = 10.78$, $p = 0.022$; epifauna $r^2 = 0.60$, $F_{1,5} = 7.34$, $p = 0.042$; Fig. 4). The slope of the relationship between infaunal biomass and trawling disturbance ($b = 0.0376$) suggested that there would be an order of magnitude decrease in infaunal biomass when trawling disturbance was increased 27-fold. For epifauna, the slope ($b = 0.0162$) suggested an equivalent decrease when trawling disturbance increased 62-fold. Trends in total biomass of infauna and epifauna in relation to fishing disturbance were not significant at the Hills sites (infauna: $F_{1,11} = 0.10$ $p = 0.761$; epifauna: $F_{1,11} = 0.80$, $p = 0.389$; Fig. 4).

Analysis of the gross composition of the infaunal community at Silver Pit (Fig. 5) showed that there was a highly significant decrease in biomass of bivalves

Table 1. Mean sightings per unit searching effort (SPUE) of beam trawlers and otter trawlers by fishery protection flights in the Silver Pit and Hills areas of the North Sea. SPUE is assumed to be directly and linearly related to trawling effort and trawling disturbance. Rank 1 corresponds to the highest fishing effort. Apparent discrepancies in the additions of beam and otter trawl effort and calculations of indices are due to rounding. Depth is the mean of depths recorded on deployment of the three 2 m beam trawls and 3 anchor dredges at each site

Site	Beam trawl effort (SPUE $\times 10^3$)	Otter trawl effort (SPUE $\times 10^3$)	Total trawl effort (SPUE $\times 10^3$ and rank)	Index of relative beam trawl disturbance (index and rank)	Depth (m) (mean \pm SEM)
Silver Pit					
S1	1.57	1.91	3.48 (6)	5.12 (6)	72.2 \pm 1.20
S2	3.87	1.50	5.37 (5)	12.53 (5)	69.0 \pm 1.56
S3	6.86	1.22	8.08 (4)	22.18 (2)	66.6 \pm 0.67
S4	6.08	3.98	10.06 (3)	19.65 (4)	64.9 \pm 0.70
S5	9.51	9.09	18.60 (1)	30.82 (1)	59.5 \pm 2.88
S6	6.72	11.22	17.94 (2)	21.82 (3)	58.9 \pm 0.19
S7	0.34	1.70	2.04 (7)	1.12 (7)	60.3 \pm 0.82
Hills					
H1	1.47	0.05	1.52 (8)	4.76 (8)	55.4 \pm 0.64
H2	0.29	0.93	1.22 (10)	1.00 (13)	62.2 \pm 1.07
H3	0.64	0.05	0.69 (13)	2.06 (12)	58.3 \pm 2.04
H4	0.98	0.15	1.13 (12)	3.24 (11)	53.7 \pm 2.83
H5	3.14	0.29	3.43 (4)	10.12 (3)	53.4 \pm 2.30
H6	3.38	3.58	6.96 (1)	10.88 (1)	45.9 \pm 4.19
H7	2.60	1.08	3.68 (3)	8.47 (4)	44.0 \pm 2.11
H8	1.86	0.20	2.06 (6)	6.06 (6)	54.9 \pm 1.58
H9	1.67	0.00	1.67 (7)	5.35 (7)	57.2 \pm 1.26
H10	2.25	0.15	2.40 (5)	7.29 (5)	51.7 \pm 0.76
H11	3.33	1.47	4.80 (2)	10.82 (2)	51.8 \pm 0.79
H12	1.42	0.05	1.47 (9)	4.53 (9)	51.9 \pm 0.67
H13	1.13	0.05	1.18 (11)	3.59 (10)	47.1 \pm 2.13

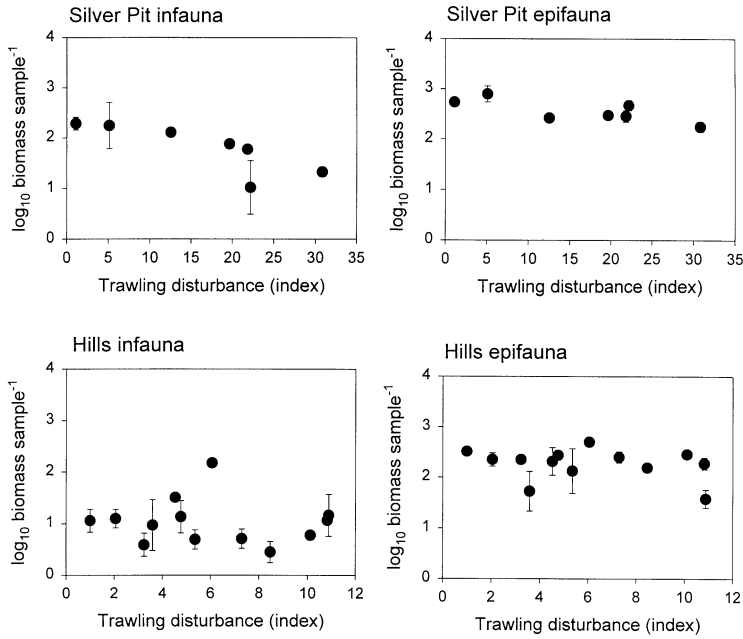


Fig. 4. Relationships between trawling disturbance and the mean biomass (\pm SD) of infauna and epifauna in samples from the Silver Pit and Hills regions of the North Sea

and spatangoids with fishing effort (linear regression $r^2 = 0.78$; $F_{1,5} = 17.56$, $p = 0.009$) but no significant change in polychaetes ($F_{1,5} = 0.03$, $p = 0.865$). At the Hills site (Fig. 6), there was no significant change in bivalves and spatangoids with effort ($F_{1,11} = 0.36$; $p = 0.560$), but an increase in polychaetes ($r^2 = 0.53$; $F_{1,11} = 12.26$; $p = 0.005$). Changes in the biomass of the species groups at the Silver Pit sites were reflected in significant changes in the proportions of these species (by biomass) in the community (Fig. 5). The proportion of bivalves and spatangoids decreased significantly ($r^2 = 0.90$; $F_{1,5} = 42.50$; $p = 0.001$), while the proportion of polychaetes increased ($r^2 = 0.68$; $F_{1,5} = 10.82$; $p = 0.022$). At the Hills sites (Fig. 6), decreases in the proportion of bivalves and spatangoids with trawling disturbance were also significant ($r^2 = 0.39$; $F_{1,11} = 7.00$; $p = 0.023$), but increases in the proportion of polychaetes were significant only at $p < 0.1$ ($r^2 = 0.24$; $F_{1,11} = 3.43$; $p = 0.090$). A range of exploratory analyses confirmed that the small depth variations between sites did not account for the differences in faunal biomass and faunal composition that were observed among sites within either the Silver Pit or the Hills region. Our sampling

confirmed that the community was dominated by free-living species, since they accounted for $>96\%$ of infaunal and $>98\%$ of epifaunal biomass at all sites.

There was no significant and positive relationship ($p > 0.1$ in all cases) between $\delta^{15}\text{N}$ and body size for infauna at any of the Silver Pit (Fig. 7) or Hills sites (Fig. 8), implying that the largest organisms in this community fed at lower trophic levels. In general, the larger organisms in samples were the bivalves and spatangoids, while the polychaetes were smaller (Table 2).

The relationships between $\delta^{15}\text{N}$ and body size for epifauna at the Silver Pit sites (Fig. 9) and Hills sites (Fig. 10) were generally positive and the relationships were well described using linear regression (Table 3). The relationships were significant at all Silver Pit sites and 10 of 13 Hills sites (Table 3). The relationships between the slopes and intercepts of these plots and levels of fishing disturbance were investigated (Fig. 11). In no cases were the slopes or intercepts significantly related to trawling disturbance (linear regression, $p > 0.05$), though intercepts were higher at Silver Pit sites than at Hills sites (Silver Pit: mean \pm SD = 11.67 ± 0.22 ; Hills: mean \pm SD = 11.29 ± 0.26 ; t -test: $t = 3.52$, $p = 0.003$).

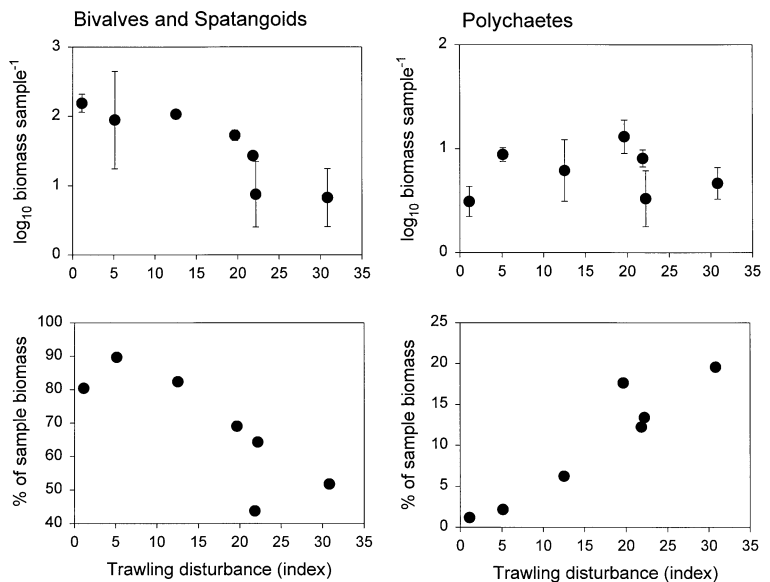


Fig. 5. Relationships between trawling disturbance and mean sample biomass (\pm SD) of infaunal bivalves/spatangoids and polychaetes (upper panels) and between trawling disturbance and mean percentage biomass of infaunal bivalves/spatangoids and polychaetes (lower panels) in the Silver Pit region of the North Sea

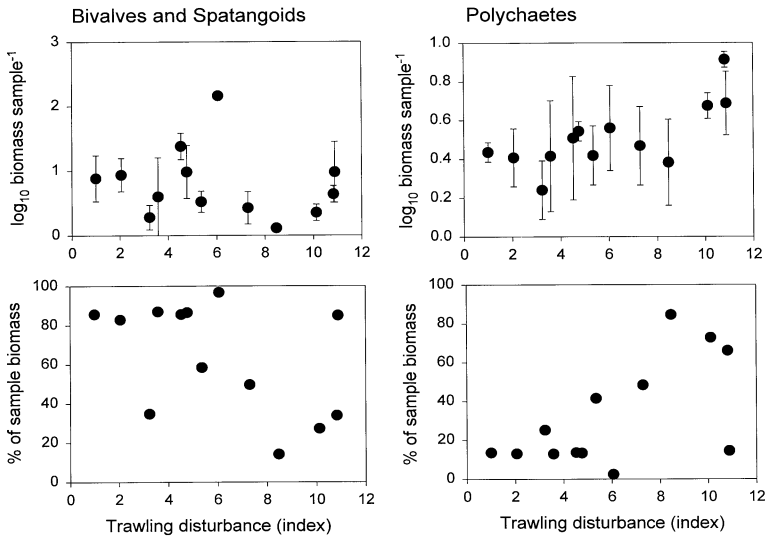


Fig. 6. Relationships between trawling disturbance and mean sample biomass (\pm SD) of infaunal bivalves/spatangoids and polychaetes (upper panels) and between trawling disturbance and mean percentage biomass of infaunal bivalves/spatangoids and polychaetes (lower panels) in the Hills region of the North Sea

Mean $\delta^{15}\text{N}$ of the sampled infaunal and epifaunal communities were remarkably consistent across sites and were not significantly related to trawling disturbance (Fig. 12). Mean $\delta^{15}\text{N}$ was significantly higher for epifauna than infauna within the Silver Pit (infauna:

mean $\delta^{15}\text{N} \pm \text{SD} = 9.07 \pm 0.92$; epifauna: mean $\delta^{15}\text{N} \pm \text{SD} = 12.27 \pm 0.19$; t -test: $t = 9.02$, $p < 0.001$) and Hills (infauna: mean $\delta^{15}\text{N} \pm \text{SD} = 9.53 \pm 1.05$; epifauna: mean $\delta^{15}\text{N} \pm \text{SD} = 11.82 \pm 0.55$; t -test: $t = 6.95$, $p < 0.001$) regions.

DISCUSSION

Our results suggest that intensive trawling disturbance has led to reductions in the biomass of infauna and epifauna in the Silver Pit, and dramatic changes in the composition of the infauna. However, these changes are not reflected in the mean trophic level of the community, or the relationships between the trophic levels of different sizes of infauna. We suggest that the trophic structure of intensively fished communities has not changed, despite changes in species composition, and that this ensures the continued processing of production by those remaining invertebrates that can withstand the levels of mortality imposed by trawling.

Clearly, factors other than trawling disturbance could have explained the patterns in biomass and trophic structure that we observed. We deliberately chose to work in 2 regions where sediment type (within region) was relatively homogeneous; the relatively small varia-

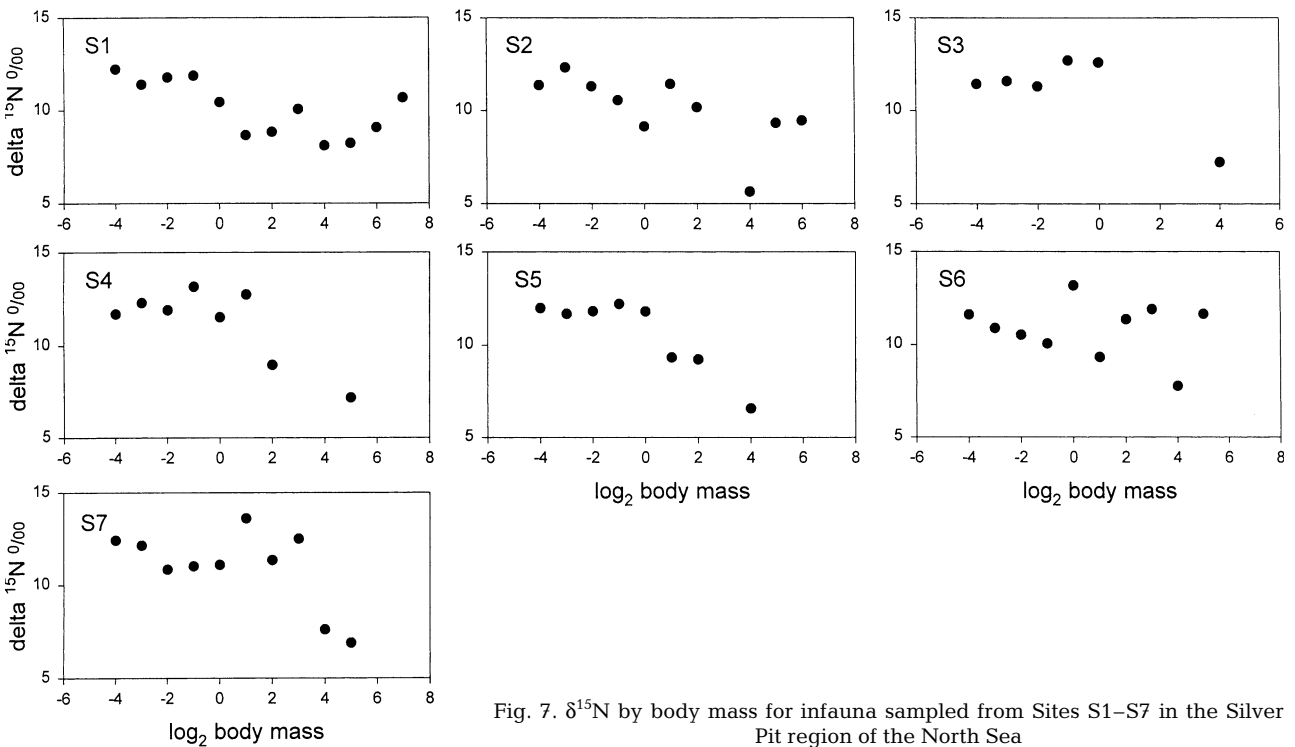


Fig. 7. $\delta^{15}\text{N}$ by body mass for infauna sampled from Sites S1–S7 in the Silver Pit region of the North Sea

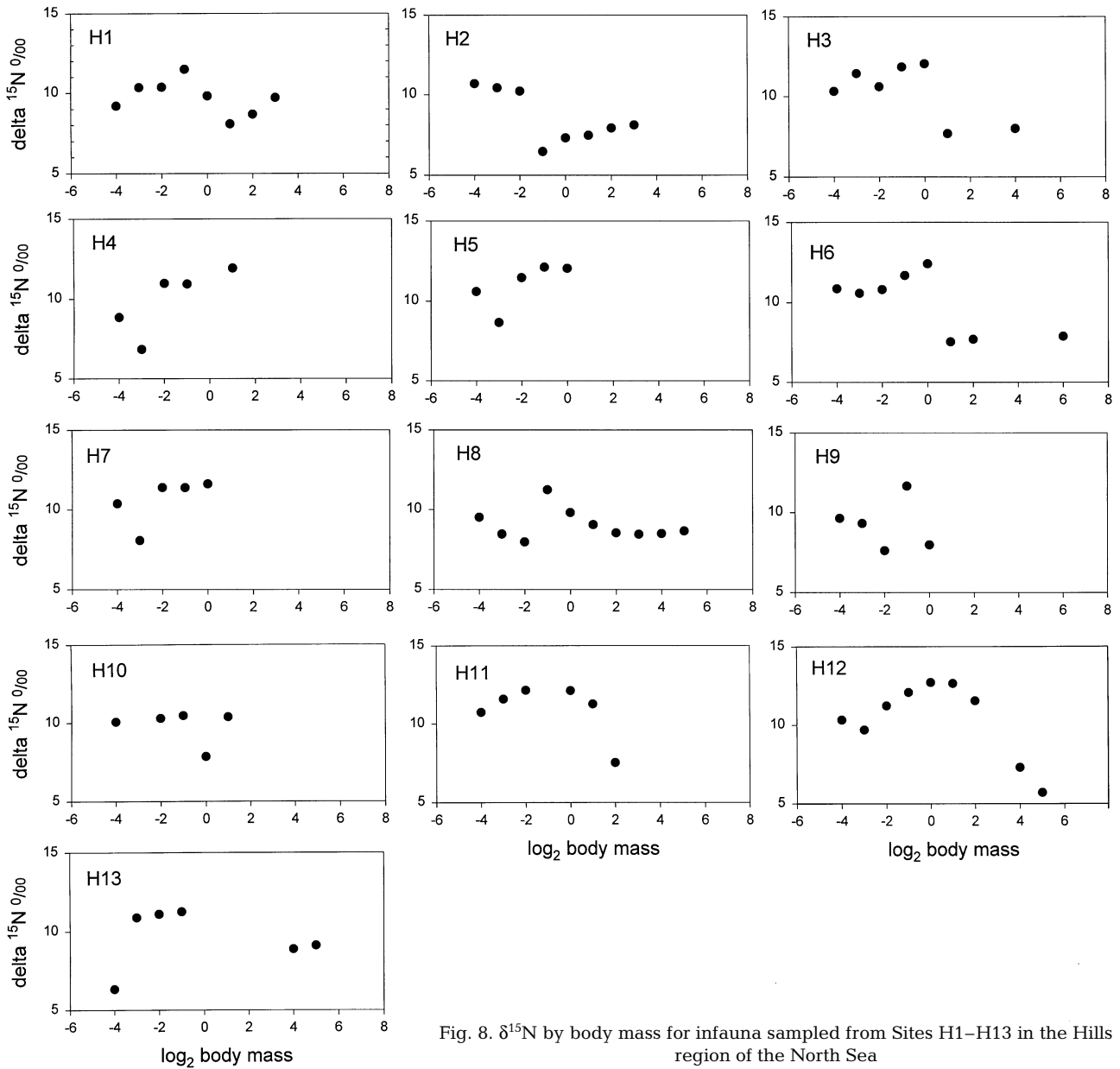


Fig. 8. $\delta^{15}\text{N}$ by body mass for infauna sampled from Sites H1–H13 in the Hills region of the North Sea

tions in mean sediment particle size reported within each region (Silver Pit: 0.02 to 0.09 mm diameter; Hills: 0.250 to 0.350 mm diameter; British Geological Survey unpubl.) would not be expected to account for the large differences in infaunal biomass among sites (e.g. Kunitzer et al. 1992). Moreover, depth variations among sites within regions were modest, and did not account for observed differences in faunal biomass and faunal composition. Many other factors, such as primary production, temperature regimes and currents, determine benthic community structure, but on the scales at which we worked it is unlikely that there were large and consistent differences in these factors among sites. The ge-

ographical location of sites with different fishing intensities within each grid does not follow a consistent pattern, so any gradients in community structure across each region are unlikely to confound our results. For example, in the Silver Pit (Fig. 2), the sites subject to the lowest fishing intensities (S1 and S7) are at the easternmost and westernmost extremes of the grid, with several more intensively fished sites in between. In the Hills region (Fig. 3), the most heavily fished sites are geographically close, but are mixed amongst sites subject to lower trawling intensities.

The SPUE data imply that all our study sites were fished at some time in the period 1994 to 1998. This

Table 2. Biomass of spatangoids/bivalves and polychaetes by size class as a percentage of the total biomass of all infauna taken in anchor dredge samples from the Silver Pit and Hills regions

Size class (\log_2)	Silver Pit		Hills	
	Bivalves and spatangoids	Polychaetes	Bivalves and spatangoids	Polychaetes
-4	0.04	1.46	0.72	2.20
-3	0.29	0.37	0.89	0.59
-2	0.21	0.79	1.83	2.95
-1	0.29	1.08	0.77	3.41
0	0.37	0.61	2.92	2.14
1	0.70	0.64	8.17	0.65
2	1.75	0.35	19.43	0.93
3	9.23	0.00	10.69	0.00
4	14.31	0.00	21.66	0.00
5	17.79	0.00	11.58	0.00
6	14.86	0.00	7.11	0.00
7	19.99	0.00	–	–

means that we cannot infer anything about the differences between trawled and untrawled sites from this study. The use of SPUE data as an index of trawling disturbance does not give an accurate indication of the actual frequency of disturbance at the site where invertebrates were sampled. This is because the scales at which the overflight data and benthic samples can be collected are very different. Since trawling effort is very patchy, it is possible that some benthic samples were taken from unfished sites while others were taken from

sites fished more frequently than SPUE sites suggest. Accurate knowledge of trawling history at a specific sampling site requires effort data with the highest spatial and temporal resolution. From 1 January 2000, this can be obtained through satellite tracking of larger trawlers (>24 m), although at present, it is too expensive to track all trawlers in the fleet at appropriately short time intervals. With a trawler fishing at 6 knots and a position fix every 6 min, the trawler will still have travelled over 1000 m between fixes.

With some assumptions we can make tentative predictions of the mean frequency of disturbance at each site. If we assume the average beam trawler tows two 12 m wide beams at a speed of 6 knots, then 267 264 m² of seabed, or 7.76% of the area of a 1 n mile² site, will

be disturbed each hour. Thus a mean sightings rate of 0.01 beam trawlers per visit corresponds to the entire area of the box being fished 6.8 times yr⁻¹. Thus the frequency with which the entire area of the sites was trawled ranged from 0.2 to 6.5 times yr⁻¹ in the Silver Pit and 0.2 to 2.3 times yr⁻¹ in the Hills. These calculations assume that trawling effort is evenly distributed in the box. The estimates of trawling frequency allow us to compare these levels of disturbance with those

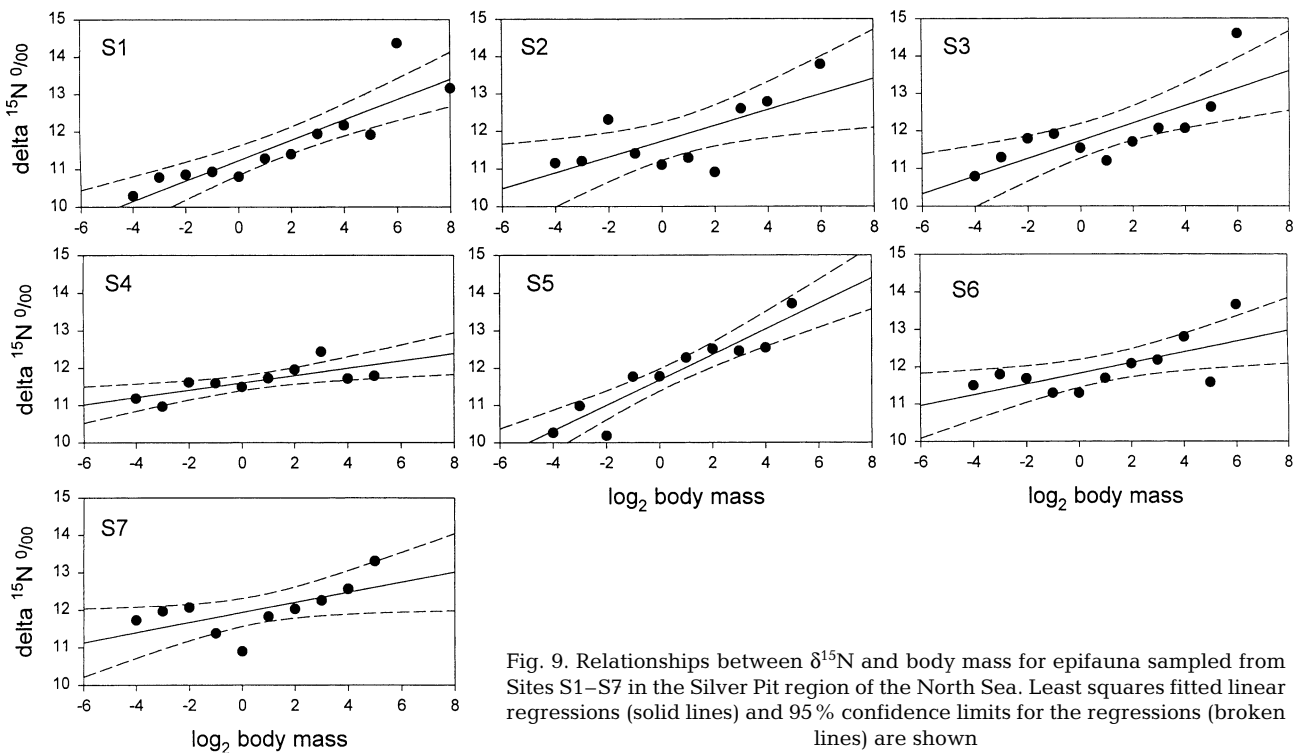


Fig. 9. Relationships between $\delta^{15}\text{N}$ and body mass for epifauna sampled from Sites S1–S7 in the Silver Pit region of the North Sea. Least squares fitted linear regressions (solid lines) and 95% confidence limits for the regressions (broken lines) are shown

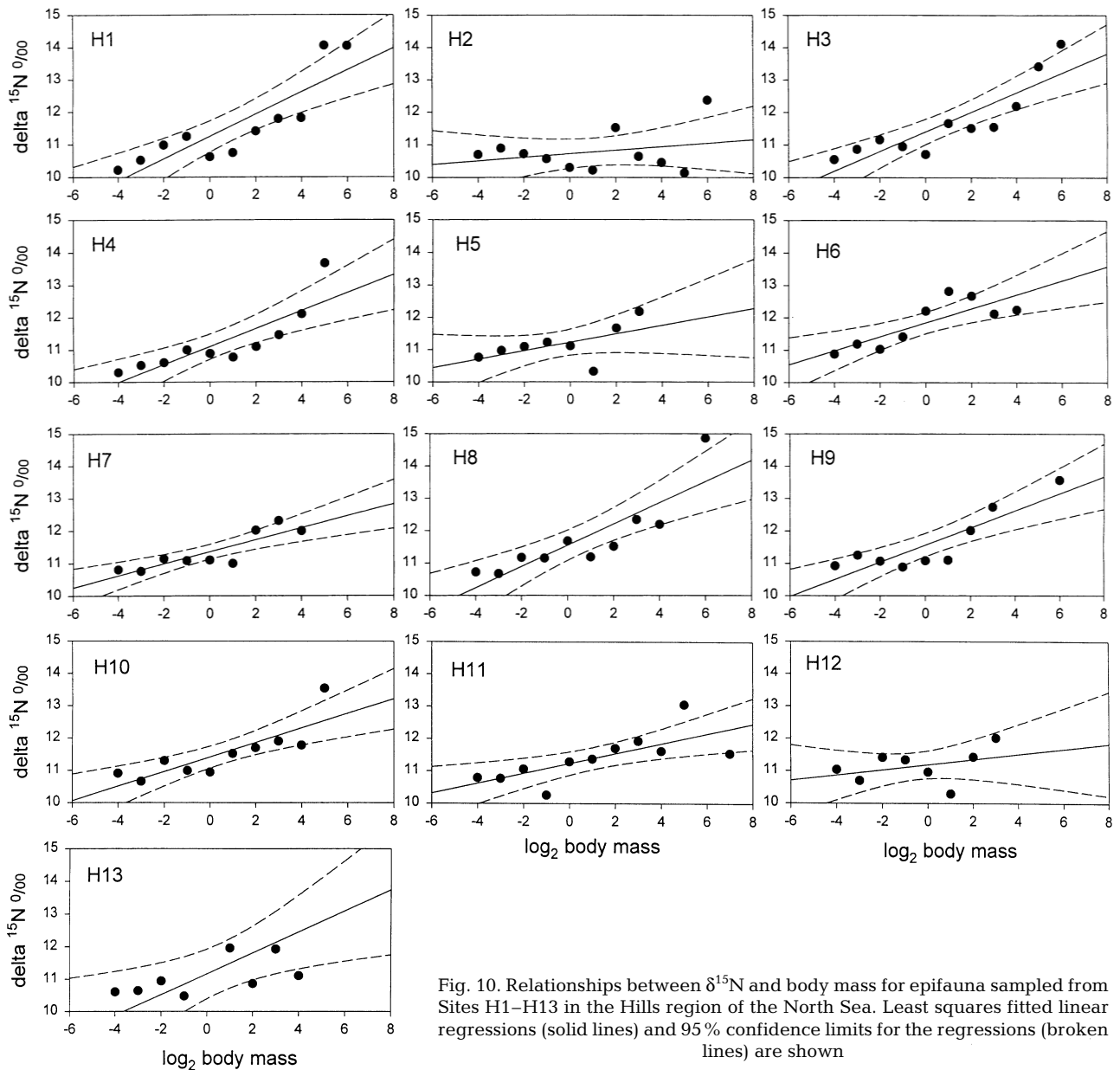


Fig. 10. Relationships between $\delta^{15}\text{N}$ and body mass for epifauna sampled from Sites H1–H13 in the Hills region of the North Sea. Least squares fitted linear regressions (solid lines) and 95% confidence limits for the regressions (broken lines) are shown

reported in other studies. The range of trawling intensities we observed at the Silver Pit spans most of the range attributed to the Dutch beam trawl fleet in many other areas of the southern and central North Sea (Rijnsdorp et al. 1998).

Since our sampling methods estimate the abundance of infauna and epifauna on different scales, it is impossible to integrate data for infaunal and epifaunal communities. Drawing a distinction between the 2 communities is rather arbitrary, as many smaller infaunal species are likely to be eaten by larger epifauna. However, to take true quantitative samples of larger epifauna on a scale appropriate to fishing effects requires gears that integrate patchiness. Given the scarcity of

many of the larger epifauna (Rumohr & Krost 1991, Craeymeersch et al. 2000), and that any gear that would ensure equal catchability for all species could not be used to sample larger areas, we believe the benefits of sampling on a relatively large scale outweigh the disadvantages of the loss of other information. Given that beam trawlers impact swathes of seabed from 16 m wide (two 8 m beams) to 36 m wide (two 18 m beams) in these regions, we would gain little from higher replication with smaller sampling devices.

The effects of trawling on biomass and gross composition of the community were most apparent at the Silver Pit sites, where differences in trawling disturbance exceeded 30-fold and the most intensively trawled site

Table 3. Parameters and significance of linear regressions of $\delta^{15}\text{N}$ on \log_2 body size class of epifaunal invertebrates at sites in the Silver Pit and Hills areas of the North Sea

	Slope	Intercept	r^2	F	df	p
Silver Pit						
S1	0.271	11.2	0.77	33.56	1,10	<0.001
S2	0.210	11.7	0.49	7.81	1,8	0.023
S3	0.233	11.7	0.59	13.11	1,9	0.006
S4	0.098	11.6	0.54	9.50	1,8	0.015
S5	0.340	11.7	0.87	51.88	1,8	<0.001
S6	0.143	11.8	0.45	7.30	1,9	0.024
S7	0.135	11.9	0.40	5.23	1,8	0.051
Hills						
H1	0.341	11.2	0.74	25.32	1,9	<0.001
H2	0.054	10.7	0.07	0.74	1,9	0.413
H3	0.301	11.4	0.77	30.16	1,9	<0.001
H4	0.278	11.1	0.71	19.84	1,8	0.002
H5	0.130	11.2	0.33	2.91	1,6	0.139
H6	0.217	11.8	0.66	13.81	1,7	0.007
H7	0.184	11.4	0.75	20.61	1,7	<0.001
H8	0.328	11.6	0.73	22.12	1,8	<0.001
H9	0.265	11.6	0.77	23.22	1,7	<0.001
H10	0.226	11.4	0.69	17.72	1,8	0.003
H11	0.153	11.2	0.52	9.82	1,9	0.012
H12	0.081	11.2	0.14	0.99	1,6	0.357
H13	0.322	11.2	0.50	7.95	1,8	0.022

was fished 3 times more intensively than the most intensively fished Hills site. Only the decrease in the biomass of infauna was significant in the Hills, and of smaller magnitude than in the Silver Pit. If changes in biomass are examined at those Silver Pit sites that are not fished any more intensively than the Hills sites (S1 and S7), then the effects of trawling disturbance are not apparent, so differences in trawling disturbance alone may explain the responses of the community. Moreover, it is reasonable to assume that the benthic communities in the Silver Pit region may be more vulnerable to trawling disturbance, since there are greater depths, slower tidal flows and finer sediments than in the Hills region (British Geological Survey and British Admiralty unpubl. data), suggesting a regime of lower natural disturbance. Our results, however, should not be interpreted as evidence that low levels of trawling disturbance have no effect on community structure. All the sites we considered were trawled to differing degrees, and so there may still be significant differences between all our sites and any that are unfished. Previously unfished sites are often the most vulnerable to fishing effects (Jennings & Kaiser 1998).

The Silver Pit and Hills regions are typical of many beam trawling grounds in the southern and central North Sea. As such, the results of our studies are likely to be applicable to other beam trawling grounds in the North Sea where the fauna is dominated by free-living infauna and epifauna. Attached and sessile organisms form only a minor proportion of total biomass. The dominance of free-living species is probably a function of natural rather than trawling disturbance since, at the least intensively trawled sites, large bivalves such as *Arctica islandica* were still found. These bivalves are very vulnerable to trawling mortality due to their slow life histories (Witbaard & Klein 1994). Mortalities of 20% or more have been measured for *A. islandica* in the path of a 12 m beam trawl (Lindeboom & de Groot 1998, Bergman & van Santbrink 2000). These rates are as high as those for many attached species. Moreover, *A. islandica* have slower growth rates, greater longevity and lower natural mortality than many habitat forming organisms, suggesting they would have lower intrinsic rates of natural increase and be more vulnerable to trawling disturbance. If trawling had been responsible for the loss of attached fauna then *A. islandica* would be unlikely to persist at our least frequently trawled study sites. Our results are applicable to free-living fauna of mobile substrates. It is unlikely they can be extrapolated to deeper areas with lower natural disturbance where many habitat forming species are particularly vulnerable to disturbance (Auster et al. 1996). Here, loss of habitat will have important consequences

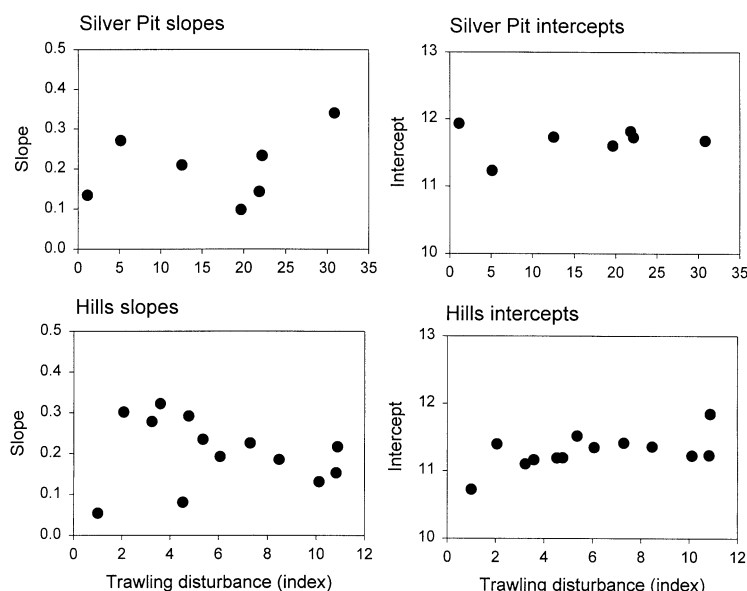


Fig. 11. Relationships between trawling disturbance and the slopes and intercepts of linear regressions fitted to relationships between $\delta^{15}\text{N}$ and body mass for epifauna samples from the Silver Pit and Hills regions of the North Sea

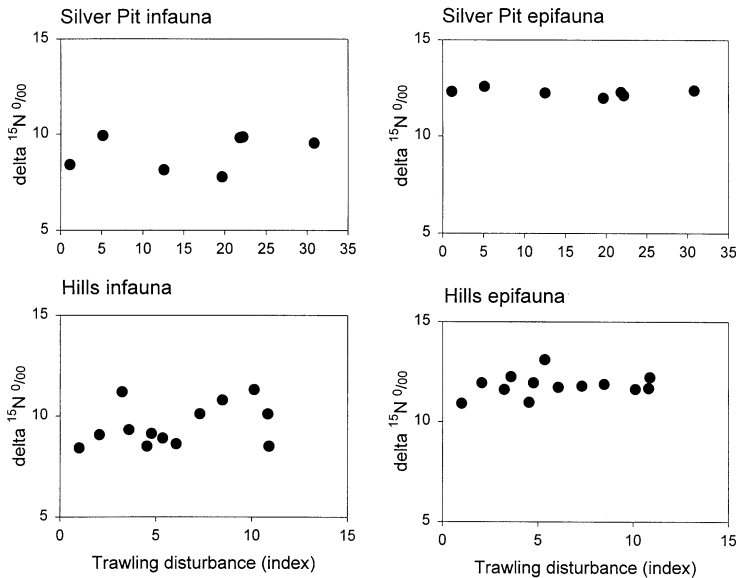


Fig. 12. Relationships between mean $\delta^{15}\text{N}$ and trawling disturbance for infauna and epifauna in the Silver Pit and Hills regions of the North Sea

for many species, and stability in trophic structure is unlikely to be observed as biomass falls.

Some of the structural changes in the infauna that we observed and that appear to be related to fishing disturbance are consistent with changes that have occurred in time-series studies of infauna in specific areas of the southern and central North Sea (Kröncke 1990, 1992, Kröncke et al. 1998). Thus the proportion of small polychaetes has increased while that of bivalves and spatangoids has decreased. However, it is noticeable, that the changes in proportion of polychaetes were not strongly reflected in changes in abundance. This is interesting, since studies of long-term changes in the biomass of infauna in the southern North Sea suggest large absolute increases in polychaete biomass, but changes in community composition similar to those we observed. On this basis, the shift in community composition observed in the time-series data appears to be a fishing effect, but the increase in biomass is likely to be due to other factors as predicted by Kröncke (1990, 1992) and Kröncke et al. (1998). From a comparison of our spatial study with existing temporal studies, we would make the tentative suggestion that increases in biomass are less influenced by trawling disturbance that favours smaller polychaetes than by the recent increases in primary productivity of the plankton community in the southern North Sea (Reid et al. 1998a,b). Increased growth rates of plaice *Pleuronectes platessa* and sole *Solea solea* (de Veen 1976, 1978, Millner & Whiting 1996, Rijnsdorp & van Leeuwen 1996) could largely be a response to increases in primary production rather than the effects

of beam trawl disturbance (Rijnsdorp & van Leeuwen 1996). However, trawling disturbance will make many infaunal polychaetes more accessible to feeding fish and break open bivalves. It is well known to scientists and fishers that fish aggregate in trawl tracks to scavenge on exposed and damaged fauna (Kaiser & Spencer 1994, Ramsay & Kaiser 1997, Ramsay et al. 1998).

Since Minagawa & Wada (1984) implied that nitrogen isotope abundances could provide a powerful tool for the investigation of trophic pathways, it became commonplace to assume a ^{15}N enrichment of around 3‰ for each trophic step (e.g. Cabana & Rasmussen 1994, Vander Zanden et al. 1997, Post et al. 2000). However, as Adams & Sterner (2000) have commented, the fractionation of 3.4‰ reported by Minagawa & Wada (1984) was actually the numerical mean of reported values between 1.3 and 5.3‰, and this prompted many calls for experimental evaluation and validation (e.g. Gannes et al. 1997, Pinnegar & Polunin 1999, Ponsard & Averbuch 1999, Schoella 1999, Adams & Sterner 2000). In the present study we avoided assigning specific trophic levels to body mass classes on the basis of their $\delta^{15}\text{N}$ and did not use a single fractionation factor and an estimate of $\delta^{15}\text{N}$ of source material to calculate absolute trophic levels. Rather, we simply assumed linearity in the relationship between $\delta^{15}\text{N}$ and trophic level.

A positive cross-species relationship between body mass and $\delta^{15}\text{N}$ is the expected consequence of larger predators eating smaller prey (Cohen et al. 1993, France et al. 1998). The relationship between body mass and $\delta^{15}\text{N}$ was significant within the epifaunal communities at most Silver Pit and Hills sites, suggesting that larger epifauna fed on smaller ones. If epifauna only preyed on other epifauna, then the gradient of the relationship between body mass and $\delta^{15}\text{N}$ would indicate the mean ratio of epifaunal predator:prey body mass. However, epifauna also prey on infauna and fish, and the gradient will be affected by these feeding interactions. The gradient of the relationship between body mass and $\delta^{15}\text{N}$ was not consistently related to the level of trawling disturbance. Rather, it appears that the trophic position of epifauna in a specific size class is more or less independent of fishing disturbance. Given that biomass fell in response to fishing disturbance across the Silver Pit sites, we suggest that patterns of energy flow in the epifaunal community are largely unaffected by the increased rates of mortality caused by trawling disturbance.

Infauna did not show an increase in $\delta^{15}\text{N}$ with body size. The infaunal community was dominated by polychaetes, bivalves and spatangoids. The polychaetes

are generally small species with a \log_2 body mass of <0 , while bivalves and echinoderms tend to be larger but feed at low trophic levels, as shown by the low values of $\delta^{15}\text{N}$ in large body mass categories. It would seem that 2 groups of infauna may exist, a conventional 'food chain' of polychaetes where the larger species and individuals feed on smaller ones (Schubert & Reise 1986, Beukema 1987) and larger organisms, such as bivalves and spatangoids, that are deposit and filter feeders that feed at lower trophic levels. As such, there is little or no consumption of the smallest infauna by the largest. Polychaetes may be consumed directly by infauna and fish, while larger bivalves are only accessible if crushed by trawls or if their siphons can be nibbled by fish and epifaunal invertebrates.

Despite order of magnitude decreases in biomass of infauna, and a shift from a community dominated by bivalves and spatangoids to one dominated by polychaetes, the mean trophic level of these communities differed by less than 1 trophic level between sites and differences were not linked to levels of fishing disturbance. The lack of changes in the trophic level of the benthos could imply that the trophic structure of the community is relatively robust in the face of fishing disturbance because species less vulnerable to disturbance are taking the trophic roles of larger more vulnerable species. It would be very valuable to undertake an explicit study of whether smaller species with faster life histories begin to fill the trophic functions vacated by larger species with slower life histories because the latter cannot withstand the high mortality rates imposed by repeated trawling.

If the community is at the same trophic level, but biomass is lower, then production must increase relative to biomass if the community is to use primary production at the same rate. Alternatively, if the production to biomass ratio (P:B) does not increase, then a greater proportion of primary production will accumulate as detritus. Some modelling studies have predicted that increased accumulation of detritus may be an ecosystem response to intensive fishing (Christensen & Pauly 1998). It is also possible that bacteria, meiofauna and other groups we did not study may play a more significant role in cycling energy when the larger epifauna and infauna are reduced, or that there is inefficient processing of energy in fished systems. The effects of fishing on energy cycling is an area that warrants much more investigation and could have implications for fish production in systems disturbed by trawling.

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