Chronic fishing disturbance has changed shelf sea benthic community structure

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Summary

1. Bottom fishing using towed nets and dredges is one of the most widespread sources of physical disturbance to the continental shelf seas throughout the world. Previous studies suggest that degradation and ecosystem changes have occurred in intensively fished areas. Nevertheless, to date it has been difficult to attribute habitat and benthic community changes to fishing effort at a spatial scale that is truly representative of commercial fishing activities.
2. In this study we present convincing evidence that chronic bottom-fishing disturbance has caused significant and widespread changes in the structure of two distinct soft-sediment benthic assemblages and habitats.
3. Our study compared the benthic fauna found in areas that have been exposed to either high or low levels of bottom-fishing disturbance over the past 10 years. We were able to validate the fishing effort data in some areas using scars in the shells of a long-lived bivalve mollusc (*Glycymeris glycymeris*) which result from fishing disturbance. Shell scars occurred most frequently in bivalves collected from the area of highest fishing effort.
4. Multivariate analyses and the response of abundance/biomass curves indicated that chronic fishing has caused a shift from communities dominated by relatively sessile, emergent, high biomass species to communities dominated by infaunal, smaller-bodied fauna. Removal of emergent fauna has thus degraded the topographic complexity of seabed habitats in areas of high fishing effort. The communities within these areas currently may be in an alternative stable state.

Key-words: abundance/biomass curves, bivalves, chronic fishing disturbance, seabed, shell scarring.

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Introduction

Natural disturbance events are some of the most important agents that determine the structure of benthic communities (Grassle & Saunders 1973; Van Blaricom 1982; Probert 1984; Hall 1994; Thrush *et al.* 1996). The frequency and scale of natural disturbance events varies from small-scale (< 1 m) predator feeding disturbances to large-scale (> 1 km) interannual glacial scouring events (Hall, Raffaelli &

Thrush 1994). Bottom fishing activity with towed nets and dredges has occurred for centuries (de Groot 1984) and on such a large scale that it is thought to be one of the greatest sources of anthropogenic disturbance to marine benthic communities (see reviews by Dayton *et al.* 1995; Jennings & Kaiser 1998). Mobile bottom fishing gears are used on every continental shelf in the world (Collie *et al.* 2000). These gears are used to catch species that live within, on or in close contact with the seabed such as scallops, shrimp and flatfishes. As nets and dredges pass over the seabed, they unintentionally damage *in situ* and remove a large biomass of the resident biota (Sainsbury 1987). Recently, the effects of disturbance of the seabed by mobile fishing gear

on structurally complex habitats and fauna has been compared to forest clear-cutting (Watling & Norse 1998). This issue is of pressing importance and has been highlighted in the United States by recent amendments to the Magnuson–Stevens Fishery Conservation and Management Act which require fisheries managers to define 'essential' fish habitat and address the impact of fishing gear in their management plans (Auster & Langton 1999).

While it has been possible to demonstrate short-term changes in benthic fauna using relatively small-scale experimental field studies (Bergman & Hup 1992; Thrush *et al.* 1995; Currie & Parry 1996; Kaiser & Spencer 1996; Tuck *et al.* 1998), these do not adequately replicate the scale of the disturbance regime imposed by a commercial fishing fleet. A more powerful approach would be to infer fishing effects from comparative studies of areas exposed to different intensities of fishing effort (Collie, Escanero & Valentine 1997; Thrush *et al.* 1998). However, in many fishing effort data are either not collected, or are collected at such large scales that they lack the resolution necessary for meaningful comparative studies undertaken using small-scale ($< 100\,\mathrm{m}^2$) remote benthic sampling techniques (Kaiser *et al.* 1996; Rijnsdorp *et al.* 1998). In the seas of northern Europe, fishing effort data is collected from International Council for the Exploration of the Seas (ICES) statistical rectangles approximately $3500\,\mathrm{km}^2$ in area. Rijnsdorp *et al.* (1998) have demonstrated that fishing effort within these areas can be highly aggregated, hence benthic samples collected at random from a supposedly intensively fished area may, with a relatively high probability, be taken from relatively undisturbed areas.

In the present study, we have partially overcome the general problem of the poor resolution of fishing effort data by studying the effects of fishing in a sea area for which relatively accurate fishing effort data are collected. Fishing intensity can also be related to the relative frequency of the occurrence of physical damage imposed during the capture process as determined from damage in the body tissues of certain organisms like bivalves and echinoderms (Kaiser 1996). Previously, Witbaard & Klein (1994) have demonstrated that the incidence of shell scars for the bivalve *Arctica islandica* increased with increasing fishing effort in the southern North Sea. We used this technique to corroborate the level of fishing intensity at each study site by collecting live bivalve molluscs in the hope that they would provide us with a direct *in situ* measure of the relative intensity of past fishing effort. At each of our study sites we examined the structure of infaunal and epifaunal communities which had been subjected to either high or low fishing intensities over a period of 10 years. Our aim was to use this information to investigate the relationship between the benthic community structure found in areas of the seabed that have been subjected to differing levels of disturbance at the scale of a commercial fishery.

Methods

We based the present study around the Isle of Man, UK, which is the centre of one of the most heavily fished scallop fisheries in Europe. Fishing effort data have been collected for over 10 years for one-third of the scallop dredging fleet via logbooks maintained by the scallop fishers. Fishers are paid to record their effort per 5×5 nautical mile box that is subsequently multiplied up to give total effort for the fleet (Kaiser *et al.* 1996). Each scallop dredge is 0·75 m wide. As fishers record the number of dredges fished on each trip it is possible to express effort as the sum of the width of the total number of dredges deployed times the total number of hours fished (mh). The number of hours fished relates directly to distance towed over the seabed as fishers generally tow scallop dredges at a constant speed of 2·5 knots. For the purposes of this study we focused our sampling effort on 10 different areas of the seabed; five areas that have been subjected to high ($47\,526 \pm 14\,464\,\mathrm{m\ h\ year^{-1}}$) and five subjected to low ($9335 \pm 5416\,\mathrm{m\ h\ year^{-1}}$) fishing effort based on fishing effort data collected between 1986 and 1996 (mean $\pm 95\%$ CI metres of dredge width deployed $\times$ h fished per 10 years) (Fig. 1). As expected, mean effort was significantly different for these areas (*t*-test, $t = -6·29$, $P < 0·002$).

ENVIRONMENTAL AND BIOLOGICAL SAMPLES

Within each of these 10 areas we collected three samples by day grab for sediment particle-size and organic content analysis (for methodology of sediment and organic analyses refer to Kaiser & Spencer 1996) and three qualitative, but comparable, infaunal samples using an anchor dredge (Kaiser *et al.* 1998) deployed for 1 min on the seabed. We used an anchor dredge as it samples less common, large infauna more effectively than smaller grabs and deep corers that would not work in coarse sediment (Collie *et al.* 1997; Kaiser *et al.* 1998). Collected sediments were sieved over a 10-mm wire mesh as we were most interested in the effects of fishing on larger macrofauna that are more likely to be sensitive to physical disturbance than smaller individuals (Kaiser *et al.* 1998). In addition, three quantitative samples of the epifauna were collected from each site using a 2-m wide beam trawl towed for a standard duration of 5 min. Small beam trawls are particularly effective for sampling less common emergent high-biomass epibiota that might be expected to be most vulnerable to the impact of bottom-fishing activities (Kaiser, Rogers & McCandliss 1994). At sea, large and easily identified species were counted

Fig. 1. Map showing the Isle of Man in the Irish Sea, and the location of the 10 areas subjected to either high or low scallop dredging (fishing) effort. Each area was located within a different 5×5 nautical mile box, which is the resolution at which fishing effort is recorded by the participants in the Isle of Man scallop fishery. The limits of each area indicate the area from which the samples were collected in this study and are less than 5×5 miles in dimension. Within each area, the spatial separation of each sample was a distance of approximately 500 m.

and weighed using motion-compensated balances. Shell fragments and stone material were also sorted from catches and weighed separately as these may provide information about gross characteristics such as the coarseness and topographic complexity of the seabed habitat. In the laboratory faunal samples were sorted and identified to species level whenever possible and the total number of each species and their biomass [flesh (g) dried to constant weight] quantified. Data collected with the beam trawl were standardized to numbers or biomass $1000 \, \text{m}^{-2}$ ascertained by calculating the area of seabed sampled based on the shot and hauled positions of the net determined from a differential global positioning system on-board ship.

DATA ANALYSES

The data collected with the anchor dredge and beam trawl were analysed separately as they were considered to sample distinctly different components of the benthic community. Anchor dredges are particularly effective at collecting large samples of infauna that might be considered to be less vulnerable to fishing disturbance than the surface-dwelling epifauna that were sampled most effectively with the beam trawl. The analyses of community data were undertaken using the PRIMER software package (Clarke & Warwick 1994). After root-root transformation to downweight the influence of extremely abundant or high biomass species, the species abundance and biomass data were clustered separately using the Bray–Curtis index of similarity. This downweighting of the influence of high biomass taxa within our samples means that our analyses are conservative with respect to our investigation of the effects of fishing on the benthic community. Multidimensional scaling ordination was then performed on each of the resulting similarity matrices. The programme BIOENV was then used to explore which of the five environmental variables (median sediment particle size, sediment organic content, depth, weight of

stones and weight of broken shell) might best fit the ordination of faunal samples. The BIOENV procedure selects the abiotic variable subset that maximizes the rank correlation (ρ) between biotic and abiotic (dis)similarity matrices. A significant relationship that indicated habitat differences among the areas that differed in fishing effort would need to be taken into account by using a two-way analysis of similarities test (ANOSIM) with fishing effort and habitat-type set as the fixed factors. ANOSIM is a nonparametric permutation procedure applied to the similarity matrix underlying the ordination of samples. It is analogous to a parametric ANOVA except that it is not presently possible to examine interaction terms with the ANOSIM test. ANOSIM uses a general randomization approach to generate significance levels (Clarke & Green 1988; Clarke 1993; Clarke & Warwick 1994). K-dominance curves of data for high and low fishing intensity areas were then plotted using untransformed data to investigate any possible difference in community structure related to fishing intensity. These curves show typical responses to environmental stress; in unstressed communities the biomass curve lies above the abundance curve, indicating a predominance of individuals with a high biomass, in stressed communities the abundance curve lies above the biomass curve, indicating high abundances of low biomass taxa (Lambshead, Platt & Shaw 1983). After $ln + 1$ transformation, the differences in the total number of species, total number of individuals and diversity indices (Hill's N1 and N2) were investigated using a general linear model (GLM) ANOVA with fishing effort and habitat set as the fixed factors.

DETERMINATION OF DISTURBANCE HISTORY

Where they occurred, bivalves were separated from the samples for analysis of shell scars in the laboratory. However, the long-lived (> 30 years) bivalve *Glycymeris glycymeris* was abundant at only one of the high intensity and three of the low intensity fishing sites. These animals were collected from the dredge and trawl samples outlined above and their shells were examined microscopically in the laboratory for the incidence of scars caused by fishing activity. Each shell was sectioned from the umbone to the middle of the posterior margin of the shell. Each of these sections was then ground and polished and etched in 0·1 N hydrochloric acid. Subsequently acetate peels were made of the etched face of the shell cross-section and examined for the incidence of damage and scarring (see Witbaard & Klein 1994 and Gaspar, Richardson & Monteiro 1994 for more details). Witbaard & Klein (1994) identified scars that had been caused by fishing activity from the occurrence of sand grains within the shell matrix

that become lodged between the animal's mantle tissue and the growing edge of the shell at the time of damage (see also Gaspar *et al.* 1994). As in other bivalve species, *G. glycymeris* record annual growth rings in their shell matrix, hence for each individual bivalve it is possible to determine the frequency of scarring for the period for which fishing effort data were extracted. Thus bivalve shells have the potential to provide a historical record of disturbance of the precise piece of seabed sampled. Although *G. glycymeris* occurred in only four of the 10 seabed areas sampled, the information that they provide at least provides an indication of the validity or otherwise of the fishing effort data. The relationship between the yearly incidence of shell scars and fishing effort was investigated using regression analysis.

Results

ENVIRONMENTAL AND BIOLOGICAL SAMPLES

Multivariate analysis revealed almost identical results for the biomass and abundance data collected from either the anchor dredge or 2-m beam trawl, hence hereafter we will refer mainly to the biomass data (which includes data for the emergent colonial organisms) and only refer to the abundance data when differences occurred. Cluster analyses revealed that the first dichotomy in the anchor dredge and 2-m beam trawl data was related to habitat differences as revealed using the BIOENV procedure. This split in the data was best explained by median sediment particle size (either gravel or coarse sand habitats) and depth at the different sites for both the anchor dredge and 2-m beam trawl data (Fig. 2; anchor dredge data, $R = 0.32$, $P < 0.001$; 2-m beam trawl data, $R = 0.49$, $P < 0.001$).

Before undertaking an analysis to test for the effects of fishing disturbance, it was necessary to account for this habitat effect in a two-way analysis of similarity matrices using the ANOSIM procedure. These analyses revealed that both the habitat and fishing effort factors were significant for the abundance (ANOSIM, $R = 0.24$, $P < 0.005$) and biomass ($R = 0.34$, $P < 0.001$) data for the 2-m beam trawl (epifauna) samples. Although similar differences were apparent for the biomass data for the anchor dredge (infauna) samples ($R = 0.16$, $P < 0.05$) they were not apparent for the abundance data ($R = 0.09$, $P > 0.05$).

Analysis of the summary data (total number of species, individuals and the Hill's N1 and N2 diversity indices) using a GLM ANOVA revealed no significant differences for either habitat or fishing effort effects, except for the total number of individuals
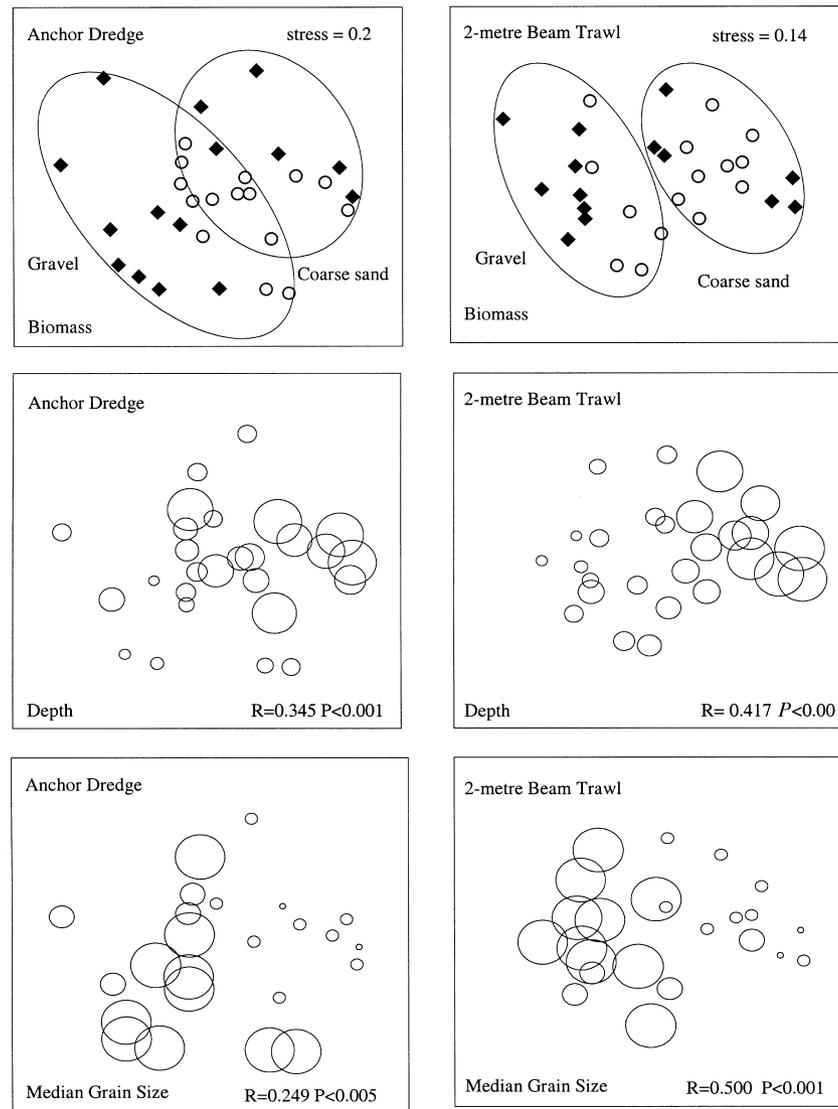
Fig. 2. The first two dimensions of the MDS ordination plot for the biomass of fauna collected with the anchor dredge (infauna) and the 2-m beam trawl (epifauna). The ordination for the infaunal samples has a stress level of 0·20 which is on the borderline for visual interpretation, however, a three-dimensional plot would make it difficult to relate this plot to the data plots for the environmental variables. The main habitat split identified by the cluster analyses is indicated by the ellipse that encircles the appropriate sample points. Within each of these groupings, the areas subjected to high fishing intensity (◆) are significantly different from the low fishing intensity sites (○). The plots of the relative values (lowest value = smallest circle, highest value = largest circle) of depth and median sediment grain size are also shown in the corresponding location for each sample point as depicted in the MDS plot for the biomass data.

for the epifauna data for which there was a significant effect of fishing effort (high intensity, 4856 ± 4666; low intensity, 2312 ± 1696 mean ± 95% CI no.1000 m^{-2}; $F_{1,26} = 5·1$, $P < 0·03$).

K-dominance curves were then plotted for the biomass and abundance data for both infaunal and epifaunal samples. In both cases, the plot for the low fishing effort areas shows that the biomass curve lies above the abundance curve. These curves tend to converge in the high fishing effort areas which indicates increased levels of physical stress (Fig. 3). The K-dominance plots suggest that the communities in the heavily fished areas are dominated by higher abundances of smaller-bodied organisms, whereas the less intensely fished areas are dominated by fewer, larger-bodied biota. In order to determine which species accounted for the differences between the high and low intensity fishing areas we analysed the biomass data for the epi- and infauna using the SIMPER procedure (Clarke & Warwick 1994). The SIMPER procedure computes the average dissimilarity between all pairs of inter-group samples (i.e. samples collected from low vs. high intensity fishing areas). This average is then
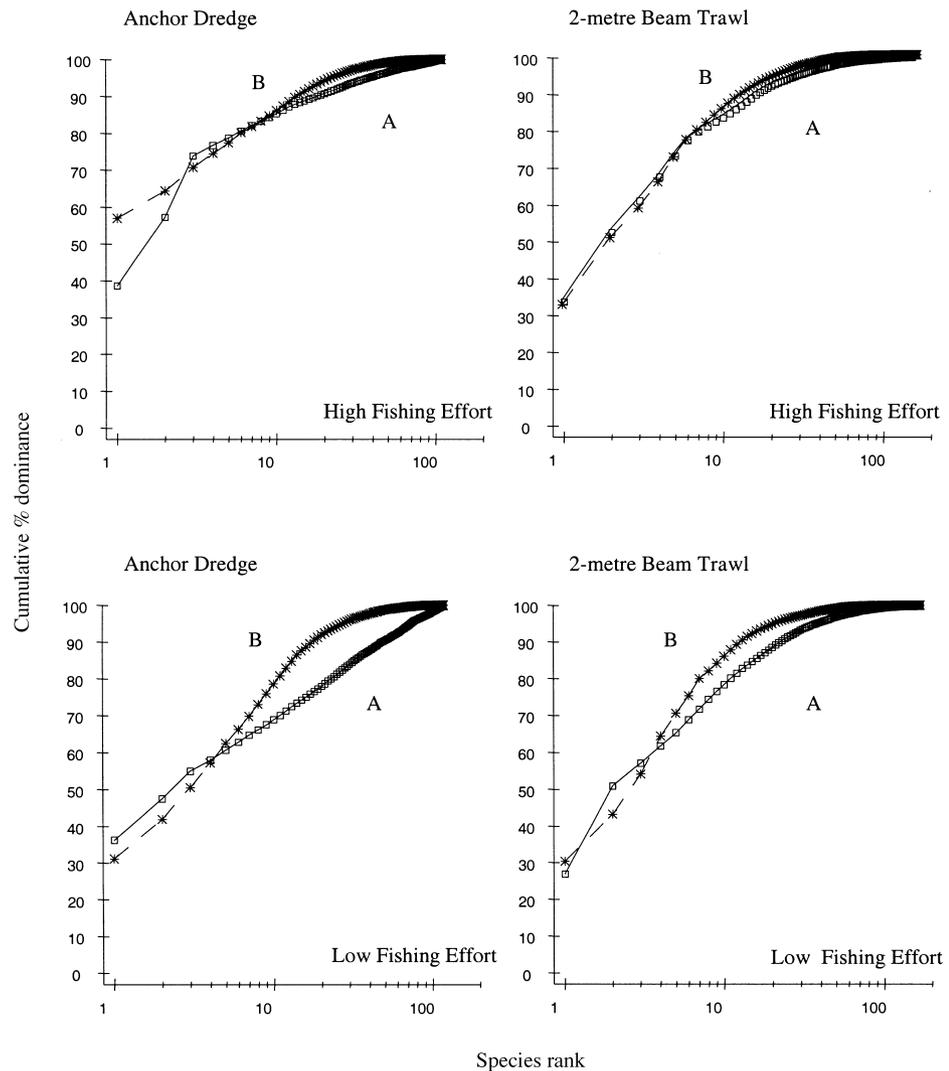
Anchor Dredge

2-metre Beam Trawl

Anchor Dredge

2-metre Beam Trawl

Cumulative % dominance

Species rank

Fig. 3. Abundance–biomass curves (ABC curves) for the beam trawl (epifauna) and dredge (infauna) from the areas subjected to low and high intensity fishing. The curves are derived from the pooled data from all the samples in either low or high intensity fishing areas. In unstressed environments, the biomass (B) curve lies above the abundance (A) curve, as stress increases (e.g. in a grossly polluted environment) the curves tend to converge or cross.

broken down into the separate contributions from each species to the dissimilarity between each group. Interestingly, this analysis revealed that the biomass of the emergent soft coral *Alcyonium digitatum*, the large sea urchin *Echinus esculensis*, the bivalve *G. glycymeris* and the gastropod *Buccinum undatum* was lowest in the areas of high fishing effort. In contrast, the biomass of brittlestars such as *Ophiura albida* and *Ophiocomina nigra* was highest in these areas (Table 1).

DETERMINATION OF DISTURBANCE HISTORY

As predicted, the *G. glycymeris* collected from the most heavily fished area had a significantly higher incidence of trawl damage scars per annual growth ring than those collected from the three less intensively fished areas (Fig. 4). Although this corroborates the fishing effort for only a proportion of our study sites, these data provide us with tangible proof of physical disturbance intensity for the actual pieces of seabed sampled in this study as the bivalves came from the same samples from which the community data were analysed.

Discussion

The results of this study provide compelling evidence that chronic fishing (scallop dredging) disturbance has led to detectable changes in benthic community structure in two different habitats in the Irish Sea and the literature suggests most probably in other areas of the world (Saila, Kocic &

Table 1. The SIMPER analysis (Clarke & Ainsworth 1993) of the top six species that contributed most (cumulative percentage contribution) to the dissimilarity between the areas subjected to high and low fishing effort. Data for the samples collected with the 2-m beam trawl are expressed as biomass dry wt g $1000\,m^{-2}$ (mean $\pm$ 95% CI), whereas data for the samples collected with the anchor dredge are expressed as biomass dry wt g sample

Species	Common name	Low fishing effort	High fishing effort	Cumulative percentage
Trawl samples				
Alcyonium digitatum	Dead men's fingers	2157 ± 2564	1513 ± 792	4.5
Echinus esculensis	Sea urchin	3584 ± 2497	2640 ± 2323	8.7
Glycymeris glycymeris	Dog cockle	1516 ± 1629	57 ± 69	12.6
Ophiothrix fragilis	Brittlestar	1277 ± 1477	4708 ± 7782	16.3
Ophiocomina nigra	Brittlestar	255 ± 411	973 ± 1183	19.6
Buccinum undatum	Common whelk	561 ± 291	37 ± 41	22.8
Dredge samples				
Psammechinus miliaris	Sea urchin	2·6 ± 2·7	6·1 ± 4·3	4.5
O. fragilis		2·3 ± 3·0	54·5 ± 70·3	8.9
E. acutus	Sea urchin	9·5 ± 9·8	2·7 ± 2·9	12.5
G. glycymeris		27·4 ± 36·0	0 ± 0	16.1
Ophiura albida	Brittlestar	3·1 ± 4·7	3·6 ± 4·2	19.7
Aporrhais pespelecani	Pelican's foot shell	4·7 ± 5·1	2·7 ± 3·8	22.5

McManus 1993; Dayton *et al.* 1995; Jennings & Kaiser 1998; Collie *et al.* 2000). It would be misleading to place too much emphasis on the fact that this is a scallop dredge fishery as any of the large, bottom-fishing gears such as rock-hopper otter trawls and beam trawls will have similar effects. Nevertheless, scallop dredges and rock-hopper otter trawls are often fished in areas that support more diverse and sensitive communities than areas in which beam trawls are operated, i.e. stable gravel habitats cf. shallow sandy substrata (Kaiser *et al.* 1998; Collie *et al.* 2000).

Previous attempts to compare areas subjected to different levels of commercial bottom-fishing disturbance have had to assume that the exact area of seabed sampled is representative of the average disturbance regime in that area (Collie *et al.* 1997). Collie *et al.* (1997) used the occurrence of dredge marks on the seabed as ascertained from side-scan

sonar surveys to validate the fishing effort in their study area and to improve the precision of their sampling. However, these marks are relatively ephemeral and last from a few days to no more than a year in coarse sediments (De Groot & Lindeboom 1994; Lindeboom & De Groot 1998). Unlike previous studies, the examination of shell scars provides confirmation that at least 40% of our samples of the benthic fauna were collected from areas of the seabed that have been physically disturbed by fishing gear at different intensities over many years (see Ramsay *et al.* in press for a detailed description of the bivalve records used in this study). Large bivalve species, such as *Arctica islandica* and *G. glycymeris*, are relatively sedentary and therefore remain *in situ* for the majority of their life and their shells provide us with a historical record of the physical disturbance regime applied to the sediment in which they lived. Our use of shell scars as an index of relative
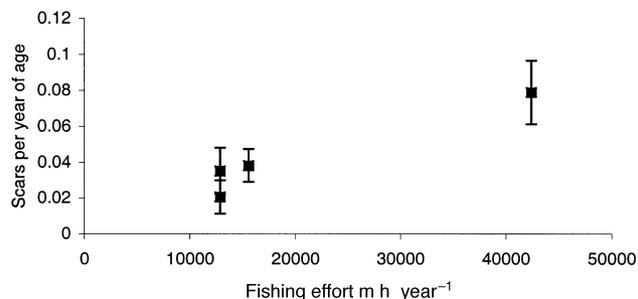

Fig. 4. The number of scars per year of age between 1986 and 1997 for the bivalve *Glycymeris glycymeris* collected at three of the low intensity and one of the high intensity fishing effort sites, plotted against total annual fishing effort for the years 1986–96. The highest mean number of scars occurred in the shells of those bivalves collected from the area that had been subjected to the highest mean intensity of fishing, ANOVA $F_{3,172} = 15\cdot21$, $P < 0\cdot0001$.

fishing disturbance has provided us with independent evidence of fishing effort intensity that has been lacking in previous studies. Ideally, we would have collected *G. glycymeris* from each of the areas studied and one might speculate that their absence from the majority of high fishing effort areas is indicative of this activity. Although this represents a drawback to using this technique to corroborate fishing effort data we propose that it is the only current method that gives a spatially accurate description of disturbance history when fishing effort data are lacking. The future introduction of accurate ($\pm$ 5 m) position recorders on board fishing vessels would greatly enhance our ability to study the effects of fishing activity on seabed habitats.

The benthic communities sampled in this study show responses to chronic disturbance that concur with theoretical predictions (Lambshead *et al.* 1983). The abundance–biomass curves for both infaunal and epifaunal samples (Fig. 3) tend to converge in the high fishing intensity areas where physical disturbance is greatest, whereas the biomass curve lies well above the abundance curve in the areas that are less intensively disturbed. This indicates that relatively large-bodied fauna have been removed by repeated bottom fishing such that these benthic communities are now dominated by smaller-bodied organisms which are presumably less susceptible to physical disturbance. Fauna such as sessile soft corals and sea urchins which have a fragile test and long-lived bivalves and gastropods are the most severely affected fauna (Table 1). Soft corals, *Alcyonium digitatum*, are attached directly to solid substrata, shell or cobbles and stones. If detached from their substratum, it is doubtful that soft corals will be able to survive once discarded overboard. The large sea urchin, *Echinus esculensis*, is relatively fragile because of its brittle test and its relatively large size (up to 20 cm diameter) increases its catchability. Although gastropods might appear to be protected from the effects of physical damage by their robust shell, laboratory and field studies have demonstrated that they experience increased predation mortality from starfish as a result of direct contact with towed fishing gear (Ramsay & Kaiser 1998). Furthermore, the egg masses laid by these gastropods are also vulnerable to bottom trawling as they are attached to the substratum. Benthic communities in heavily fished areas tend to be dominated by fauna that are resilient to physical damage, either through life-history adaptations or their ability to regenerate damaged body parts (e.g. starfish, crabs, small polychaetes and small bivalves).

Experimental studies have shown that scavenging taxa aggregate in comparatively high numbers in areas of recent fishing disturbance. They are drawn to these disturbances by the odours of damaged biota from a distance of < 50 m. However, these aggregations persist for a maximum of 3 days after the disturbance event (Kaiser & Ramsay 1997; Ramsay *et al.* 1997). Collie *et al.* (1997) also reported that scavenging organisms tended to dominate communities found in areas that experienced heavy dredging disturbance on a commercial scale. Thus communities dominated by scavenging fauna may be indicative of areas that experience high levels of physical disturbance.

The removal of epifaunal organisms that contribute to habitat complexity, and potentially 'essential' fish habitat, may lead to the degradation of habitat such that it is no longer suitable for associated species (Peattie & Hoare 1981; Sainsbury *et al.* 1998; Auster & Langton 1999; Kaiser, Rogers & Ellis 1999). Preliminary analyses suggest that for flatfish communities even slight changes in habitat topography may favour one species over another according to feeding mode and predator avoidance mechanisms (Kaiser *et al.* 1999). For example, the predation rate of juvenile Atlantic cod (*Gadus morhua*) increases with decreasing habitat complexity (Walters & Juanes 1993). Thus, while most fisheries science has been preoccupied with the need to manage stocks of target species, the habitat on which those species relied may have been altered to such an extent that it is no longer suitable for them.

Our study leaves us in no doubt that in certain areas bottom fishing with towed gears has led to wide-scale changes in benthic habitats and communities as indicated by the few other comparative studies conducted at similar spatial scales (Collie *et al.* 1997; Thrush *et al.* 1998). There now exists a growing body of literature that indicates the pressing need for fisheries management to be applied at both the species and habitat level (Auster *et al.* 1996; Auster, Malatesta & Donaldson 1997; Jennings & Kaiser 1998; Kaiser & De Groot 2000). We conclude that fisheries managers will need to consider seriously the exclusion of towed bottom-fishing gears from some areas of the seabed that support structurally complex habitats and benthic fauna that may have an important functional role for both non-commercial and commercially important species.

Acknowledgements

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