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Disturbance of intertidal soft-sediment benthic communities by cockle hand raking

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Recent awareness of the ecosystem effects of fishing activities on the marine environment means that there is a pressing need to evaluate the direct and indirect effects of those activities that may have negative effects on non-target species and habitats. The cockle, *Cerastoderma edule* (L.) is the target of a commercial and artisanal fishery that occurs in intertidal and estuarine habitats across Northern Europe. Cockles are harvested either mechanically using tractor dredges or suction dredges or by large numbers of individual fishers using hand rakes. This study examined the effects of hand raking on the non-target species and under-sized cockles associated with intertidal cockle beds and the effects of size of the patch of sediment disturbed on subsequent recolonisation. Hand raking led to an initial three-fold increase in the damage rate of under-sized cockles compared with control plots. The communities in both small and large raked plots showed community changes relative to control plots 14 days after the initial disturbance. The small raked plots had recovered 56 days after the initial disturbance whereas the large raked plots remained in an altered state. Samples collected over a year later indicated that small-scale variations in habitat heterogeneity had been altered and suggest that while effects of hand raking may be significant within a year, they are unlikely to persist beyond this time-scale unless there are larger long-lived species present within the community. © 2001 Elsevier Science B.V. All rights reserved.

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One of the most pressing issues in marine conservation is how to accommodate the wide range of uses and activities in the narrow coastal margin such that the ecology of intertidal and nearshore marine habitats is protected. In particular, fisheries management needs to consider both environmental and political sensitivities in coastal marine habitats owing to the extractive nature of harvesting processes, disruption to marine habitats and potential conflicts between multiple users (Jones, 1994, 2000; Symes and Phillipson, 1997). Fisheries management has traditionally concentrated on the conservation of sustainable stocks of the harvested target species. More recently, concern about the secondary environmental effects of sublittoral fishing activities on the marine environment has become increasingly prominent (De Groot, 1984; Messieh et al., 1991; Jones, 1992; Dayton et al., 1995; Jennings and Kaiser, 1998). Indeed, the minimisation of the negative secondary effects of fishing activities is perceived to be an important component

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Table 1
Definition of different intensities of commercial harvesting for species that occur in intertidal or shallow sublittoral soft-sediment habitats

Low	Collection of polychaetes or bivalves for personal use, which generally results in relatively small-scale disturbances less than several m^2. Target fauna are extracted using hand-held suction pumps that remove individual specimens (few environmental effects) or by digging (polychaetes) or raking (bivalves). However, the cumulative effects of many individuals exploiting a population for personal use could constitute a scale of disturbance similar to commercial exploitation rates as in level 3 below (Van den Heiligenberg, 1987; Beukema, 1995)
Medium	Semi-professional collection of bait or bivalves involving groups of individuals that employ the same techniques as for level 1 but on a larger scale. This can involve intense activity within small areas rapidly depleting local stocks (Olive, 1993)
High	Large-scale harvesting using mechanical extraction devices such as suction pumps (Kaiser et al., 1996), tractor dredges (Hall and Harding, 1997), boat propellers (Peterson et al., 1987), and suction dredges (Beukema, 1995). Generally these devices work in restricted areas until the target stocks have been reduced to a level that is no longer economically viable for exploitation

of fishery management plans in certain parts of the world (Benaka, 1999; Kaiser and De Groot, 2000).

Harvesting of marine invertebrates from intertidal areas is widespread and occurs either commercially or as a subsistence activity. Marine intertidal habitats can be divided into hard and soft substrata. Fauna that typically inhabit rocky shores are attached to the surface of the substratum. Consequently, harvested species tend to be easily accessible and little manipulation of the habitat is required to remove them, except where the target organisms are an essential component of the habitat (e.g. mussels, oysters). Nevertheless, removal of the target species may have consequences for other components of the community. For example, in a range of manipulative field experiments the protection of the predatory snail *Concholepas concholepas* from fishing pressure has demonstrated how increases in predation by this species led to a decline in mussel and barnacle prey (Moreno et al., 1984). Additional changes may occur in association with trampling over rocky shores to reach the harvesting area which also removes organisms and creates free space within the habitat (Moreno et al., 1984; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996).

In contrast to rocky shores, few soft-sediment fauna are found on the sediment surface at low tide (exceptions might include the protruding tubes of sand mason worms *Lanice conchilega*). As a consequence, harvesting of soft-sediment fauna requires the physical disturbance of the substratum. Moreover, these habitats tend to extend over large areas which, coupled with their low topography and the structure of the substratum, makes them amenable to extensive mechanical harvesting. The study of the ecosystem effects of harvesting in these habitats is of particular relevance as intertidal beaches, sand and mudflats of many estuaries provide important food resources for migratory and resident bird species and demersal fish species (e.g. Raffaelli and Milne, 1987; Lambeck et al., 1996; Norris et al., 1998).

In soft-sediment intertidal and shallow subtidal habitats, bivalve molluscs are harvested mostly for human consumption (e.g. Peterson et al., 1987; Hall and Harding, 1997; Spencer et al., 1997; Ferns et al., 2000). In contrast, those species harvested as bait for recreational fishing tend to be polychaete worms (Olive, 1993) and crustacea (Peterson, 1975, 1977). There are many similarities between both bivalve (Cotter et al., 1997; Hall and Harding, 1997) and polychaete harvesting (Olive, 1993; Beukema, 1995) and each can be categorised into different levels of scale and intensity (Table 1). The intensity and scale of habitat disturbance is an important consideration when assessing the potential ecological influence of harvesting activities in comparison with natural perturbations (Hall et al., 1994; Kaiser, 1998).

The present study focuses on the cockle fishery that occurs in the UK. While a number of authors have studied the environmental effects of mechanical tractor or suction harvesting, no one has as yet examined the possible effects of hand raking on cockles that is carried out by large numbers of individuals in estuaries around the UK. Similar activities occur elsewhere in the world for other bivalve species (e.g. *Tapes decussatus* in Portugal (pers. obs.) and *Mercenaria mercenaria* in North America (Peterson et al., 1983; Lenihan and Micheli, 2000)). While it is easy to perceive how a tractor harvester can cover large areas of the intertidal sandflats during a low tide, the

Fig. 1. The experimental site was located on a relatively uniform sandflat off the Point of Ayr in the River Dee Estuary UK. Cockle harvesting was simulated by raking each of the treatment plots that were described as a circular area scored into the sediment.

additive effects of large numbers of humans harvesting by hand could easily have similar effects on the environment. For example, commercial lugworm harvesting barges used in the Dutch Wadden Sea collect 18 million worms per annum whereas hand-diggers collect 14 million worms per annum (Beukema, 1995).

The aim of the present paper is to examine the initial ecological impact of hand raking for cockles and the effect of harvested patch size on recovery rate. We then compare our results to those of similar studies that have examined different scales and intensities of harvesting intertidal species with the aim of assessing the relative ecological importance of hand raking c.f. other harvesting techniques.

The study site was located on the sandflats at the Point of Ayr on the Dee Estuary, North Wales at approximately mid-tide level (Fig. 1). The substratum in the study area was predominantly silty sand with a relatively flat and uniform topography. The area was not (at that time) used for the commercial harvesting of cockles (D. B. Edwards, 1997 (pers. comm.)). Although cockles were abundant within this area they were smaller than the legal landing-size. Hence, in our experimental manipulation of the effects of cockle raking, cockles were not removed from the plots as they would have been discarded by commercial fishers. Had we located our experimental site within an area containing cockles of commercial size, we would have had no means of excluding commercial fishers from the site, which would have compromised the experiment. Though under-sized, cockles were present within our experimental plots and hence the associated benthic fauna were considered to be representative of that normally associated with cockles.

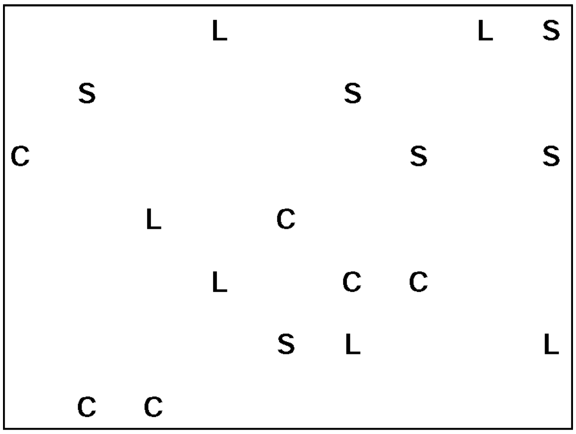

Fig. 2. Layout of each of the replicate plots for each of the control (C), small (S) and large (L) treatments at the experimental site (90 × 70 m).

The experiment comprised a total of 18 plots that were sampled on 08/10/1996 (day 1), 25/10/1996 (day 14), 18/12/1996 (day 56) and 23/02/1998 (day 503). Treatment plots were allocated randomly by drawing labelled pegs out of an opaque bag at haphazard intervals within the experimental site (Fig. 2). We simulated the effects of cockle hand raking by completely raking the sediment in treatment plots at low tide using rakes with 10 cm long teeth that disturbed the sediment in a manner very similar to that generated by commercially deployed hand rakes (Fig. 1). The experimental design incorporated six control plots (undisturbed; size = 9 m^2), and six small (approximately 9 m^2) and six large raked plots (approximately 36 m^2) that were positioned at random within a fixed area of the sandflat. Each plot was located at least 5 m away from the edge of any other plot to minimise interactions between them. The location of each plot was marked by placing a metal peg into the substratum from which it was possible to describe a circle (that defined the dimensions of the plot) with a line attached to the peg on each sampling occasion. Samples from within the large plots were collected haphazardly from the central 9 m^2 of each plot such that the area from which samples were collected was held constant.

On day 1, the treatment plots were completely raked once at low tide and then the control, small and large treatment plots were sampled for sediment characteristics and infaunal community composition. As the raking disturbance did not remove any fauna or sediment from the plots and any damaged or dead biota would be left in situ, there was no point in undertaking sampling immediately before raking. Therefore, the effects of the raking disturbance are unlikely to be detected until the following sampling occasion (day 14).

2.1. Sediment parameters

To examine changes in sediment particle size composition that might occur with each of the disturbance treatments, one core sample of sediment was collected haphazardly from each replicate plot by inserting a PVC cylinder (76 mm high × 74 mm diameter) into the sediment until it was flush with the sediment surface. The samples were oven dried in the laboratory before storage. Before sorting, the samples were oven dried at 60°C to dry weight. Then, 200 g of each sediment sample was soaked overnight in 1 dm^3 of an aqueous solution of sodium hexametaphosphate to facilitate separation of the sediment particles. Each sample was then washed through a 63 μm sieve with tap water to remove the silt fraction. The sediment was then re-dried in the oven to constant weight and separated into four size fractions using three sieves with mesh sizes of 250, 125 and 63 μm and a collecting container (for the remaining particles of <63 μm) on an electrically driven reciprocating shaker for 5 min. The four sediment fractions were then weighed to an accuracy of ±0.01 g.

Two sediment samples were also collected haphazardly from each replicate plot to ascertain the organic content of the sediment. Sediment cores were collected with a cylinder 70 mm long with a diameter of 15 mm, made from a hypodermic syringe with the nozzle end removed. These samples were also oven dried at 60°C in the laboratory. The two samples were pooled to provide representative data from the plots and a pestle and mortar used to grind the samples to an even consistency. Two subsamples were taken to improve the degree of accuracy and the mean taken to estimate the ash-free weight by weighing subsamples before and after combustion in a muffle furnace at 450°C for 24 h.

2.2. Sampling of the infauna

The infaunal community was sampled by taking four sediment cores haphazardly from each plot using a PVC cylinder (100 mm diameter × 120 mm deep). The cores were washed in situ over a 0.5 mm mesh and the residue preserved in a solution of 4% buffered formalin. In the laboratory, macrofauna were sorted and identified to species level whenever possible. We quantified cockle damage rates by counting the number of damaged cockles in each sample and that was then expressed as a percentage of the total cockles present in that sample. The cockles at the experimental site were below the minimum legal landing size, hence none were removed from the treatment plots except for those within the sediment cores.

2.3. Statistical treatment

The data for each of the four cores collected from each plot were pooled prior to undertaking further analyses. The PRIMER ecological statistical software package (Clarke and Warwick, 1994) was used to perform the multivariate analyses of the data. Cluster analyses on the community data were performed using the Bray–Curtis index of similarity on $\sqrt{\sqrt{}}$-transformed data followed by multi-dimensional scaling (MDS). Significant differences between the treatment and control plots on each sampling date were determined using an a priori one-way analysis of similarities (ANOSIM) test. In addition, using the same test, for each treatment we determined significant differences that occurred with time by direct comparison with the initial condition of the treatment or control plot. This procedure was repeated after removing mobile epifauna (e.g. the mud snail *Hydrobia ulvae*) that may have had an undue influence (due to their high abundance) on our ability to detect subtle changes in response to disturbance. The relationship between environmental factors and the benthic community characteristics over the duration of the experiment was investigated using the BIOENV procedure (Clarke and Warwick, 1994).

Differences in the gross characteristics of the infaunal benthic community were assessed by two-way ANOVA on the $\ln(x + 1)$ transformed data for the total number of individuals and the total number of taxa per replicate (pooled data from four cores). When significant differences were identified a further one-way ANOVA was performed for each date and differences between treatments were determined using the Tukey–Kramer multiple comparison test. The percentage particle size, percentage organic composition of the sediment and percentage of damaged cockles was arcsin transformed prior to undertaking a two-way ANOVA. When significant differences with time were identified a one-way ANOVA was performed for each sampling occasion. When significant differences were identified, differences between treatments were identified using a Tukey–Kramer multiple comparison test. A general linear model ANOVA of the rate of changes in sediment parameters with time in each of the treatments was also undertaken.

2.4. Power analysis

Soft sediment communities are notoriously variable. Hence, there is risk that our experimental design lacked sufficient statistical power to detect subtle changes in the fauna. For a given effective size, we investigated the probability of obtaining a statistically significant result given the experimental design and sample variance. We performed a power analysis (Cohen, 1977) for the ANOVA tests used for between treatment differences in the total numbers of individuals, total numbers of species, the abundance of particular taxa and the percentage silt and organic contents of the sediment. The power of the experiment to detect a certain level of change from the control situation varies for different species and parameters. Nevertheless, there is a 90% chance of detecting <10% changes in the total numbers of individuals and the total number of species, *Hydrobia ulvae* and *Macoma balthica*. There is an 80% chance of detecting changes of <50% for five of the six taxa listed (Table 2). Thus our experimental design had sufficient power to detect relatively subtle changes in the abundance of the most common species found at the experimental site.

3.1. Sediment parameters

Medan particle sizes were not significantly different among control and treatment plots during any of the sampling periods. Fine sand always comprised the largest fraction in any plot with a median grain size of 0.125 mm. Although the silt/clay fraction

Table 2
Results of a power analysis for the most abundant taxa, the total number of individuals and species and the organic and silt content of the sediment. The numbers in the table indicate the percentage change that could be detected with a given level of power within the design of the experiment. For example, there is a 90% chance of being able to detect a 3.5% change in the abundance of *Hydrobia ulvae*

Variable	Power 0.5	0.6	0.7	0.8	0.9
Hydrobia ulvae	1.1	1.7	2.3	2.9	3.5
Lacuna parva	22	25	28	32	36
Adult cockles	16	18	21	24	27
Juvenile cockles	29	32	36	40	47
Macoma balthica	5	6	7	8	9
Nephtys spp.	35	40	45	50	58
Corophium sp.	47	53	60	68	78
Total number of individuals	5	6	7	8	9
Total number of species	5	5	6	7	8
Percentage silt content	27	31	35	39	44
Percentage organic content	14	16	18	21	24

(<0.063 mm) appeared to be elevated in both the small and large treatments compared to the control plots 14 days after the initial disturbance, this was not a significant difference (Table 3). Power analysis indicated that there was a 90% chance of detecting a 44% change in the percentage of the sediment composed of the silt/clay fraction (Table 2).

In general, the organic content of the sediment was low (<1.6%). While there were no significant differences among the small and large treatments and control plots on the first day of the experiment, significant differences occurred thereafter, although these were not consistent on subsequent occasions (Table 4). Nevertheless, it is notable that on the first sampling occasion after the raking disturbance, the plots in both treatments had significantly higher levels of organic matter than the control plots. From day 1 to day 56 there was a consistent decrease in the organic content of the sediment, which increased again by day 503 (General Linear Model ANOVA test for variation with time, $F_{3,67} = 13.7$, $P < 0.001$). The rate of decrease in organic content between day 1 and 56 was greatest in the control plots ($T = 23.4$, $P < 0.001$).

3.2. Biological parameters

On the first day of the experiment at the point of sampling immediately after undertaking the raking disturbance, the benthic communities in the small and large treatment and control plots were significantly different from each other (Fig. 3, Table 5, ANOSIM). These differences coincided with a significantly higher mean abundance of individual organisms found within both the small and large treatment plots compared with the control plots (Fig. 4, T–K test, $P < 0.05$). Two weeks after the raking disturbance there were no significant differences in the benthic community among the different treatments (Fig. 3, Table 5). After 56 days, the small plots were significantly different from the control plots (Fig. 3, Table 5) but the control plots were not significantly different from the large treatment plots (Table 5). This also coincided with a significantly higher total number of individuals in the small plots compared with the control plots (Fig. 4, Table 6, T–K test $P < 0.05$). Similarly, the total number of individuals in the large plots appeared to be higher than in the control plots, but this difference was not significant (Fig. 4, Table 6, T–K test $P > 0.05$). After 503 days, there were no significant differences between either of the two treatments or the small treatment and control plots (Fig. 3, Table 5). However, the large treatment plot was significantly different from the control plot (Table 5). We repeated these analyses with a dataset that excluded the epifaunal component of the community because these organisms tend to be highly mobile

Table 3
Mean percentage (±95% confidence interval) silt and clay (<0.063 mm particle size) content of the sediment. No significant differences occurred between either the treatment or control plots on each sampling occasion

	Mean ± CI/core Day 1	Day 14	Day 56	Day 503
Control plots	5.20 ± 0.89	5.40 ± 1.04	4.41 ± 0.49	5.70 ± 2.30
Small plots	4.70 ± 1.13	7.30 ± 1.26	4.08 ± 0.83	5.44 ± 1.13
Large plots	5.45 ± 1.48	6.00 ± 1.80	4.76 ± 0.62	5.84 ± 1.31

Table 4
Mean percentage (±95% confidence interval) organic content of the sediment samples. Mean values in a column that share the same superscript letter are not significantly different (Tukey–Kramer, $P > 0.05$). Values with no superscript letter are significantly different from all other values in that column

	Mean ± Cl/core Day 1 repeat	Day 14	Day 56	Day 503
Control plots	1.37 ± 0.15^{a}	1.12 ± 0.08	1.06 ± 0.06^{a}	1.32 ± 0.22^{ab}
Small plots	1.52 ± 0.09^{a}	1.45 ± 0.10^{a}	1.20 ± 0.05^{b}	1.43 ± 0.06^{b}
Large plots	1.48 ± 0.10^{a}	1.32 ± 0.12^{a}	1.12 ± 0.11^{ab}	1.24 ± 0.12^{a}

and their distribution is often affected by tidal flow. The subsequent multivariate community analysis revealed the same patterns of community change on the first three sampling occasions. However, on day 503 there were no significant differences among the treatments when the epifauna were excluded from the analysis.

A BIOENV analysis revealed that there was no significant relationship between sediment particle size and organic content with the similarity/dissimilarity between different replicates of each treatment (sediment particle size, $\rho = 0.12$; organic content, $\rho = -0.06$). Hence, changes in the community composition and sediment parameters were not closely associated.

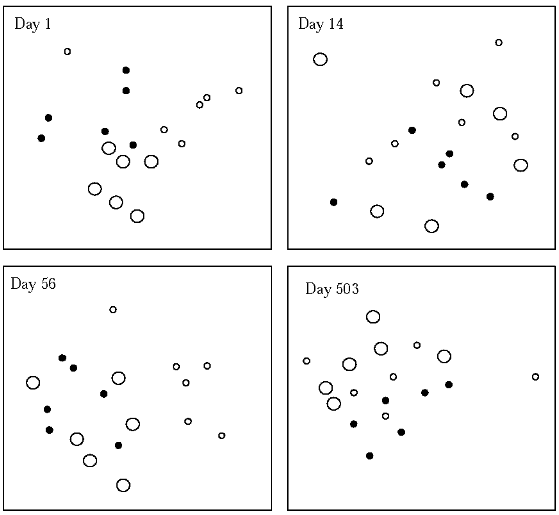

Fig. 3. Two-dimensional MDS ordination of community data found in each of the control and raked plots on day 1 (stress = 0.14), day 14 (stress = 0.18), day 56 (stress = 0.18) and day 503 (stress = 0.16). Filled circles: control plots, small clear circles: small plots, large clear circles: large plots.

The variation of the abundance of five selected taxa among treatments with time was also examined using a GLM ANOVA (Table 6). The abundance of all of the taxa examined changed significantly with time (Fig. 4), which was not surprising given the timing of each sampling occasion. Significant differences among the treatment and control plots were only detected for juvenile cockles, *Hydrobia ulvae*, *Corophium volutator* and the total number of individuals. For juvenile cockles and *H. ulvae* there was a significant interaction between treatment and time demonstrating that the differences among treatments were not consistent with time.

3.3. Damage to cockles

On day 1 of the experiment, there was a significant difference in the number of damaged cockles

Table 5
Pair-wise comparisons (ANOSIM) of the benthic community data from small and large treatments and control plots on each sampling occasion (see Fig. 3)

Sampling day	Treatment plots	R-statistic	P-value
Day 1	Control vs small	0.45	0.01
	Control vs large	0.32	0.01
	Small vs large	0.64	< 0.01
Day 14	Control vs small	0.07	0.27
	Control vs large	−0.15	0.97
	Small vs large	−0.02	0.56
Day 56	Control vs small	0.77	< 0.01
	Control vs large	0.02	0.46
	Small vs large	0.65	< 0.01
Day 503	Control vs small	0.04	0.32
	Control vs large	0.53	< 0.01
	Small vs large	−0.08	0.81

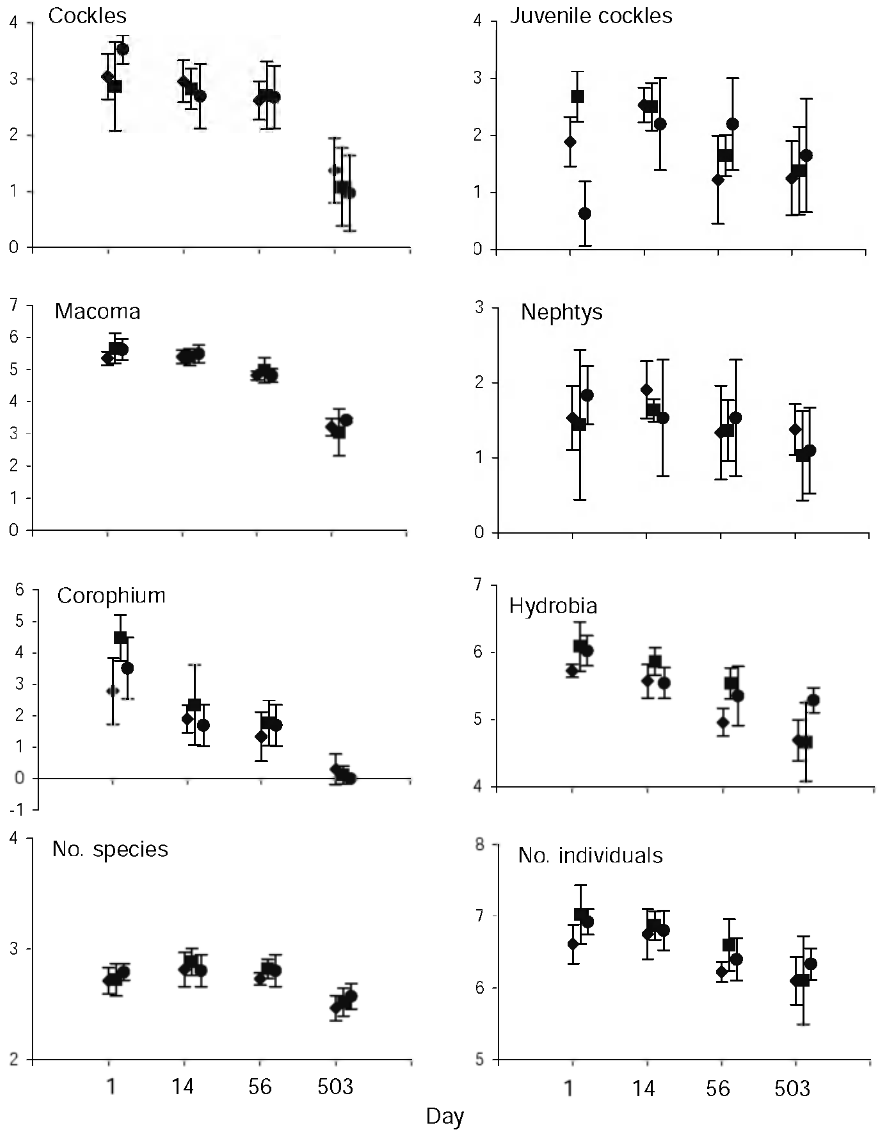

Fig. 4. Mean $\ln(x + 1)$ numbers per plot (±SD) for different taxa and the total number of species and the total number of individuals plotted against the sampling day during the experiment. Diamonds: control plots, squares: small treatment plots, circles: large treatment plots.

between the control and small treatment plots (T–K test, $P < 0.05$) and between the control and large treatment plots (T–K test, $P < 0.05$). Thereafter, the percentage of cockles that were damaged did not differ significantly among either of the treatment plots or the control plot although there is a surprising degree of variability between treatments on the last sampling date (Table 7).

Despite the homogeneous appearance of our experimental site (Fig. 1) and our random allocation of treatments across the area, there was a significantly higher number of individuals in the plots of both treatments compared with the control plots at the beginning of the experiment (Fig. 4). This is somewhat

Table 6
Summary of the outcome of the GLM ANOVA for the effects of sampling date and treatment and the interaction between these factors (see Fig. 4)

		F	*P*
Cockles	Time	54.7	0.001
	Treatment	0.4	0.66
	Interaction	1.2	0.31
Juvenile cockles	Time	10.4	0.001
	Treatment	7.9	0.001
	Interaction	5.6	0.001
Macoma balthica	Time	177	0.001
	Treatment	1.2	0.31
	Interaction	0.9	0.48
Nephtys spp.	Time	3.1	0.03
	Treatment	0.9	0.38
	Interaction	0.9	0.46
Corophium volutator	Time	58.2	0.001
	Treatment	4.1	0.02
	Interaction	1.5	0.18
Hydrobia ulvae	Time	43.4	0.001
	Treatment	5.6	0.006
	Interaction	2.9	0.013
Total no. species	Time	26.7	0.001
	Treatment	2.2	0.12
	Interaction	0.7	0.69
Total no. individuals	Time	17.6	0.001
	Treatment	3.4	0.04
	Interaction	0.8	0.58

surprising as we had anticipated no difference between any of the treatments on the first day of the experiment. Although the hand raking may have disturbed the fauna and damaged and killed some organisms, they would have remained in situ during our subsequent sample collection on the same day.

Table 7
Mean percentage (± 95% confidence interval) of damaged cockles. Mean values in a row that share the same superscript letter are not significantly different (Tukey–Kramer, $P > 0.05$)

	Control	Small	Large
Day 1	4.3 ± 3.1^{a}	13.2 ± 3.6^{b}	11.5 ± 3.9^{b}
Day 14	3.3 ± 3.1^{a}	6.5 ± 5.6^{a}	8.7 ± 6.9^{a}
Day 56	8.8 ± 7.2^{a}	8.8 ± 4.9^{a}	5.8 ± 6.3^{a}
Day 503	20.5 ± 31.5^{a}	16.7 ± 10.7^{a}	3.0 ± 5.9^{a}

Hence we did not anticipate any dramatic community changes on the day of the initial raking disturbance. Although by chance some of the small treatment plots were laid out in the upper right portion of the experimental area, the large treatment plots and control plots were well interspersed, yet still these were significantly different in terms of their resident benthic fauna (Figs. 2 and 3). Thus in the interpretation of the response of the community to raking disturbance it is necessary to examine the relative change in the community on subsequent sampling events. Fourteen days after the initial treatment the benthic community in the treatment and control plots was no longer significantly different. The total number of individual organisms in both the small and large treatment plots had decreased in abundance whereas the total number of individuals in the control plots was slightly increased compared with the first sampling day. Thus, as in other studies (Beukema, 1995; Hall and Harding, 1997), the short-term response to raking is a relative decrease in overall abundance of fauna in the treatment plots. The relative decrease in abundance was similar for both treatments as might be expected (i.e. no initial effect of the size of the disturbed patch) (Fig. 4). Thus, subsequent recovery might be represented by restoration of the community differences between the treatment and control plots. Accordingly, 56 days after the initial treatment the benthic community within the small treatment plots had become significantly different from the control plots. While the benthic community within the large treatment plots had begun to show signs of recovery (increase in relative abundance of taxa), the community remained similar to the control plots suggesting that the scale of disturbance was an important factor in recolonisation rate. The final sampling occasion was 447 days after the third sampling date in the late winter of 1998. Analysis of the infaunal component of the benthic community demonstrated that there were no infaunal differences among treatment and control plots although there were some differences when epifauna were included in the analysis. We conclude that larval settlement during the following summer and natural perturbations through the winter months had altered the small-scale patchiness of the habitat that led to the initial community differences detected on the first sampling occasion. It is possible that the site was altered by human harvesting activities; however we discount this possibility as the site still supported only under-sized cockles throughout the experiment and would not have attracted the attention of harvesters. It is unfortunate that we did not include an intermediate sampling date that might have quantified more precisely the time taken for the large treatment plots to recover from the disturbance treatment.

These results are perhaps not surprising in light of similar studies undertaken in estuarine environments that have considered larger-scale or more intensive forms of physical disturbance. Nevertheless, even within these habitats there is considerable variation in the recovery rate of both the habitat (sediment structure) and faunal communities. The rate at which trenches and depressions that result from harvesting activities are filled in depends on sediment bed-load transport, suspended sediment load in the water column, exposure to wave action and the harvesting technique used. Hall and Harding (1997) found that trenches made by tractor dredgers in the Solway Firth were no longer visible one day after harvesting. McLusky et al. (1983) found that basins made by bait digging were two thirds filled after approximately 14 days but that evidence of physical disturbance was still present 120 days later. The basins also trapped fine sediments and organic debris such as seaweed and detritus that increased the carbon and nitrogen levels in these sediments for 29–51 days. In contrast, all traces of disturbance had disappeared after 22 days when trenches were back-filled. Spencer et al. (1998) found that trenches made by a suction dredger in November (winter) were no longer visible 120 days later. In contrast, Kaiser et al. (1996) found that it took approximately seven months for similar trenches to disappear on a more consolidated clay sediment with an overlying mud veneer. Ferns et al.'s (2000) study in the Burry Inlet in south Wales emphasises that recovery time can vary for sites within 3 km of each other. At one site, with coarse sediment, physical signs of tractor dredging were obliterated within six months (probably sooner, but the exact time was not stated) by natural disturbances. In contrast at a nearby sheltered site, with muddy fine sand, the dredge tracks were still visible after six months.

In the study by Hall and Harding (1997), bedload transport processes shifted large amounts of sediment and adult fauna into areas that had been harvested by commercial tractor dredgers. This, in conjunction with a concomitant seasonal decline in the population of the adults of many species, meant that within only three months the community in the harvested areas was indistinguishable from adjacent unharvested control areas (Hall and Harding, 1997). This is a good example of an environment that experiences large-scale natural disturbances in which the resident fauna have life-histories that are appropriate for such a habitat. In McLusky et al.'s (1983) study of the effects of bait digging on soft-sediment fauna, the mounds of spoil and depressions created by normal hand digging were evident for at least four months, whereas back-filling of dug areas accelerated habitat restoration and faunal recolonisation. When back-filling was undertaken, the fauna was found to be similar to that in surrounding undisturbed areas only 22 days after harvesting. Restoration of the original fauna is unlikely to occur until remediation of the habitat. In the present study, the sediment is left in situ and the penetration depth of the rakes is relatively shallow (between 5 and 10 cm). Thus, relatively minor changes in the benthic community might have been anticipated with very rapid recovery. Nevertheless, changes were apparent in the disturbed plots and these persisted for more than 56 days in the large treatment plots. While the above studies, and the present study demonstrate relatively rapid (within one year) recolonisation by small infaunal species of soft-sediment habitats after physical disturbance, recolonisation by larger-bodied organisms is much slower. In Beukema's (1995) study of the recolonisation of areas of the Wadden Sea harvested by commercial lugworm dredgers, the majority of the infaunal community had recovered six months after harvesting ceased. Nevertheless, the biomass of the population of the large bivalve *Mya arenaria* remained lower than pre-harvesting levels two years after the cessation of lugworm harvesting.

What is clear from these studies is that the recovery rate of the sediment habitat and its associated fauna is highly variable according to sediment type, local environmental conditions and the type and frequency of harvesting process employed. This complicates any attempt to predict recovery rates and hence to make sensible management decisions that relate to the sustainability of such practices. Recently, Collie et al. (2000) overcame the inherent variability in habitat responses to disturbance by undertaking a meta-analysis of fishing impact studies. They were able to calculate recovery trajectories for a number of different habitats and were able to conclude that sandy habitats could, on average, sustain approximately three fishing-type disturbances per year. In the context of this study, the environments studied by Beukema (1995); Hall and Harding (1997) and McLusky et al. (1983) are probably the most comparable to the present study. The magnitude and intensity of the disturbances studied can be ranked as follows: lugworm harvesting > tractor dredging > bait digging > cockle hand raking. For each of the forms of disturbance the reported recovery rates of the benthic communities are similar (approximately two to six months) with the exception that the larger fauna (e.g. *Mya arenaria*) take much longer to recover. Thus for intertidal soft-sediment environments, communities composed of small-bodied, motile and opportunistic fauna would seem to be relatively tolerant of physical disturbance and able to recolonise the habitat within 6 months. In contrast, communities that contain large-bodied relatively sessile organisms that recruit infrequently, and those that contain biota that influence the stability of the sedimentary environment (e.g. seagrasses, spionid worms, mussel beds) and represent biogenic habitat will be far less tolerant of physical disturbance and recovery times will be measured in years rather than months (Dayton et al. 1995; Collie et al. 2000).

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