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Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch

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ABSTRACT: The effects of trawling disturbance on a benthic community were investigated with a manipulative field experiment in a fine muddy habitat that has been closed to fishing for over 25 yr. We examined the effects of extensive and repeated experimental trawl disturbance over an 18 mo period on benthic community structure and also followed the subsequent patterns of recovery over a further 18 mo. During the period of trawl disturbance the number of species and individuals increased and measures of diversity (Shannon's exponential H' and Simpson's reciprocal D) and evenness decreased in the trawled area relative to the reference site. The cirratulid polychaetes *Chaetozone setosa* and *Caulleriella zetlandica* were found to be most resistant to disturbance, whilst the bivalve *Nucula nitidosa* and polychaetes *Scolopolos armiger* and *Nephtys cirrosa* were identified as sensitive species. Multivariate analysis and abundance biomass comparison plots confirmed that community changes occurred following disturbance, with some differences between treatment and reference sites still apparent after 18 mo of recovery. Physical effects, examined with Side-scan and RoxAnn, were identifiable immediately after disturbance, but were almost indistinguishable after 18 mo of recovery. Such long recovery times suggest that even fishing during a restricted period of the year may be sufficient to maintain communities occupying fine muddy sediment habitats in an altered state.

KEY WORDS: Fishing disturbance · Physical disturbance · Trawling · Community dynamics

INTRODUCTION

There is now considerable interest in the role that physical disturbance by mobile fishing gears plays in determining the structure of marine benthic communities and there is a growing catalogue of studies and reviews which examine this issue (e.g. De Groot 1984, Eleftheriou & Robertson 1992, Hall 1994, Thrush et al. 1995, Currie & Parry 1996, Kaiser & Spencer 1996a). Most of the investigations conducted to date contain the important caveat that the study area may have been markedly affected by previous fishing activities. Thus, if the bulk of community change occurred during the initial period of trawling development, subsequently it may not be possible to detect trends or impacts from fishing, either because the community is resistant to further effects, or because the effects are relatively trivial compared to those that were caused before.

Clearly, it makes little sense to conduct experiments on the effects of fishing in areas which are unsuitable as fishing grounds. A better situation — an area which is suitable for fishing but which remains unfished — is rarely available. Some such areas do still exist however, and in this paper we report the results of one such study, conducted in Loch Gareloch, Inverclyde, Scotland, UK. Loch Gareloch is an area that has been closed to fishing for over 25 yr through the presence of a naval base, but which previously supported good fish catches. We examined the effects of extensive and repeated experimental trawl disturbance over an 18 mo period on benthic community structure and also followed the subsequent patterns of recovery over a further 18 mo.

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MATERIALS AND METHODS

Study site. Loch Gareloch, Inverclyde, Scotland, UK, is a sheltered fjordic sea loch, approximately 9 km long, averaging less than 1.5 km wide, and has an estimated volume of 261×10^6 m^3 at MHWS (mean high water spring) (Fig. 1). Fresh water input is negligible. Tidal currents of up to 5 knots occur over the shallow (12 m) sandy sill at the narrow (350 m) entrance to the loch, but in the deeper water of the main loch currents are greatly reduced and the seabed is muddy. The close proximity of the loch to the Clyde Estuary permits frequent intrusions of estuarine surface water throughout the year, thereby enhancing nutrient levels (Mackay & Halcrow 1976). Such frequent intrusions appear to inhibit bottom water stagnation and the associated reduction in dissolved oxygen concentrations that are recorded in other Clyde sea lochs (Edwards et al. 1986). The loch has a history of domestic sewage discharge (Haig 1986). Metal concentrations are high within the loch, but preliminary observations do not suggest any differences between the 2 experimental sites (P. Hayes, FRS MLA, unpubl. obs.).

Owing to the presence of the Royal Navy Faslane Clyde Submarine Base, fishing in the loch is presently prohibited by the Inshore Fishing (Prohibition of Fishing and Fishing Methods) (Scotland) Order 1989. Prior to this Order, fishing was restricted by the Clyde Dockyard Port of Gareloch and Loch Long Order 1967 Anecdotal evidence suggests that although good catches of fish have been taken from the loch, these were taken from the southern part and the deepest channel, and little if any trawling took place prior to the ban in the present study's experimental areas. The

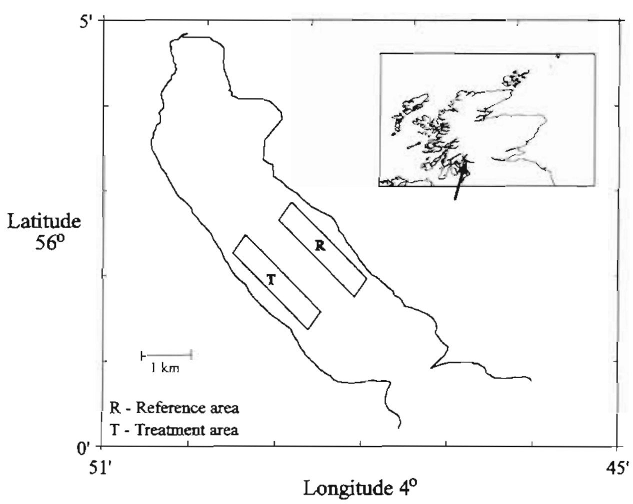

Fig. 1. Map showing Treatment and Reference area in Loch Gareloch, Scotland, UK

marine fauna has remained undisturbed by fishing for over 25 yr, and much longer than this in some places.

Experimental design. In analysing the effects of human activities on the environment, the basic Before/After, Control/Impact (or BACI) design of Bernstein & Zalinski (1983) and Stewart-Oaten et al. (1986) has been adopted by many researchers. Such a design involves replicated sampling over time (Underwood 1992). When multiple control and/or treatment sites are available, problems of spatial confounding (pseudoreplication; Hurlbert 1984) are avoided. Unfortunately, however, the unique nature (an area protected from fishing for almost 30 yr) and small size of Loch Gareloch meant that multiple treatment and control sites could not be established (access was limited by the presence of the naval base and extensive moorings to the north and south of the loch). Rather we were constrained to comparing a single impacted site with a single reference area. Such designs have been criticised as being only suitable to demonstrate differences between locations (Hurlbert 1984), and strictly speaking this is certainly true. However, by sampling our experiment at repeated points through time, during a period of impact and recovery, we feel that we have examined the effects of disturbance, and that the conclusions we draw for this site are likely to be of wider relevance.

A preliminary survey in November 1993 allowed 1 treatment and 1 reference area to be selected (Fig. 1). Both sites were at the same depth (30 to 35 m) and were closely matched with respect to sediment characteristics, topography and epifauna. Experimental trawling on the treatment site commenced in January 1994 and continued until April 1995 (16 mo). Fishing was conducted for 1 d each month when 10 tows of approximately 45 min duration were made over the treatment area at a speed of 2 knots. The width of the disturbed track produced by each tow, determined from acoustic measurements of the width between the trawl doors, was between 35 and 40 m. This net spread equated to a coverage of the treatment area of 140 to 160%.

Experimental trawling disturbance was carried out from a locally chartered fishing vessel (120 hp) using a modified rockhopper groundgear Because of the repeated and intensive nature of the trawling activity, the experiment was conducted using a trawl with no net. The rationale for this decision was that the direct disturbance effects of the net are small compared to the rest of the gear (Mayer et al. 1991, Anon 1996), although they would increase as the net became full, and that there was a risk that we would progressively deplete populations of scavenger species to low levels in the small and relatively enclosed loch if they were retained as catch. In the open sea, while large numbers of epibenthic scavengers would be removed if a

net was used, migrations into disturbed areas mean that it is unlikely there would be any noticeable local depletion of more mobile species (Kaiser & Spencer 1996b). In the present study, however, significantly reducing the epibenthic scavenger population could be possible. Since these scavengers are themselves potentially important mortality agents for exposed benthic fauna (Kaiser & Spencer 1994, 1996b, Ramsay et al. 1996) we felt that our experiment would be more realistic if their densities were preserved over the life of the experiment. The disadvantage of our approach is that the absence of a net makes the experiment conservative, particularly with respect to epifaunal species, only demonstrating the effects of the trawl doors and groundrope. Extra weight was added to the groundrope to compensate for the reduced weight of the gear.

Survey procedure. Full faunal surveys were conducted at the treatment and reference sites during May and October of 1994, 1995 and 1996. This corresponded to surveys after 5, 10 and 16 mo of disturbance and after 6, 12 and 18 mo of recovery. On each occasion, infaunal samples were taken at random locations within the designated areas using a 0.1 m^2 Day grab. (A total of 9 and 8 samples were taken from treatment and reference areas, respectively, during the preliminary survey, and 14 samples were taken from each in all subsequent surveys.) Samples were washed over a 0.5 mm mesh, fixed in 5% formalin and preserved in 75% alcohol. The infauna was counted and identified to species where possible. From each grab, a small sample of sediment was collected for either organic carbon or particle size analysis. Organic carbon was determined using an elemental analyser. Granulometric samples were analysed by laser granulometry using a Malvern Mastersizer/E granulometer (Malvern Instruments). Underwater television (TV) surveys were carried out with a camera mounted approximately 1 m above the seabed on a towed epibenthic sledge (Chapman 1985). The video signal was combined with a digital date/time signal and recorded for analysis. The position of the vessel was recorded during all TV sledge tows using differential GPS (global positioning system) with position fixes (±15 m) logged every 15 s. Seabed topography was examined using Side-scan (120 kHz transducer frequency) and RoxAnn (50 kHz transducer frequency) (Marine Microsystems Ltd). The latter is a seabed sediment discrimination system and provides quantitative measures of bottom texture that are conventionally expressed in terms of acoustic parameters, which roughly equate to the general sediment properties described as roughness and hardness. Details of the theoretical operation of RoxAnn are given by Burns et al. (1985). (Unfortunately, changes in the calibration of equipment between surveys mean that valid comparisons between RoxAnn data can only be made between areas on the same survey, not between surveys. A change of echo sounder transducer on the survey vessel following the 6 mo recovery survey means that the differences between areas on the last 2 surveys are not comparable with the previous RoxAnn data.)

Statistical analysis. For infaunal species, changes in the total numbers of individuals, number of species, biomass, species diversity indices, and the abundance of selected individual species were examined using 2-way ANOVA with site and date as fixed factors. Our BACI analysis infers an impact on the basis of the interaction term in the ANOVA model. This means it is trends over time at the 2 sites (and differences between the trends) that are examined, rather than absolute values. The power of our approach was investigated with a model assuming a constant effect during the period of disturbance, declining over the period of recovery. For simplicity, power was calculated assuming 14 samples were taken from each site at each date. Less samples were taken in the first survey, which would effectively mean power was slightly less than calculated. Following identification of effects, box plots (Tukey 1977) were constructed to visually examine the data and identify disturbance (interaction) effects. Abundance data were $\ln(x + 1)$ transformed prior to analysis to homogenise variances (confirmed through examination of residuals). In addition, effects on the proportion of individuals each phyla contributes to total abundance were examined with analysis of deviance using a binomial distribution of errors with a logit link (carried out within a generalized linear modelling framework). Multivariate community analyses were undertaken using non-metric multidimensional scaling based on a Bray-Curtis dissimilarity matrix calculated on 4th root transformed data (Field et al. 1982, Clarke & Green 1988, Faith et al. 1991). *A priori* differences between sites (treatments) and dates were tested with an 'analysis of similarities' randomisation test (2-way nested ANOSIM), available in the Primer statistical software package published by the Plymouth Marine Laboratory, with differences between individual sites and dates investigated with *a posteriori* pairwise tests. The SIMPER routine, a program within Primer, was then used to establish which species contributed most to the similarity (or dissimilarity) between sites or dates (Clarke 1993). SIMPER computes the average similarity (or dissimilarity) between all pairs of inter-group samples and then breaks this average down into contributions from each species. *k*-dominance curves (Lambshead et al. 1983) were also constructed to examine species frequency distributions for each

site and date, and effects were examined by comparing curves for abundance and biomass (ABC method; Warwick 1986).

We were unable to analyse some of the TV observations of epifaunal species, because of very poor underwater visibility (often <1 m). To overcome the problem of gaps in the TV transect data, densities of the identifiable epifaunal organisms were calculated for that portion of each tow in which visibility was adequate (from width of view and distance towed). These data were analysed using the same 2-way ANOVA model as for the infaunal data.

RESULTS

Seabed topography

The Side-scan record from the preliminary survey indicated that both the treatment and reference areas were flat and devoid of any distinct topographic features (not shown). This situation changed markedly during the period of experimental trawling, when the Side-scan records showed evidence of considerable physical disturbance in the treatment area, with tracks criss-crossing the area but running in a roughly northwest/southeast direction (Fig. 2). We assume that these are the tracks left by the trawl doors, an assumption supported by the fact that they run in the same direction as the experimental trawling. In a number of cases, parallel tracks could be seen 35 to 40 m apart, corresponding to the distance between the trawl doors. Disturbance tracks could still be seen in the treatment area 18 mo after the end of the trawling treatment, although the marks were very faint by this time. No comparable features were ever observed in the reference area.

An alternative measure of how seabed properties were altered by fishing can be obtained from the RoxAnn measurements. Fig. 3 shows the changes in the E1 (roughness) parameter for each survey after up to 6 mo of recovery. (These plots show a loess smooth of the E1 data in relation to distance from a nominal point at the southern end of each experimental area.) Prior to the experiment the roughness was greater in the treatment area, although this was not detected by the Side-scan sonar. The relative differences in roughness between the treatment and reference areas increased during the disturbance programme (Fig. 3b–d) and declined during the recovery period (Fig. 3e). The difference between sites at this time appeared similar to that prior to the experiment, suggesting a 6 mo recovery time for the effects detected by RoxAnn. No differences between the areas in the E2 (hardness) parameter were identified throughout the survey period.

Table 1. Sediment grain size median diameter and mean organic carbon in each experimental area for each survey

	Treatment area		Reference area	
	Median dia. (µm)	mg g^{-1}	Median dia. (µm)	mg g^{-1}
Nov 1993	110	48.2	123	42.4
May 1994	104	47.5	120	41.4
Oct 1994	114	49.6	123	41.1
May 1995	103	46.1	120	43.0
Oct 1995	104	44.3	119	38.8
May 1996	106	49.2	120	44.7
Oct 1996	103	49.6	121	46.1

Sediment particle size and organic carbon

The sediment in both areas of the loch was classified as poorly sorted fine silt (approx. 95% silt and clay), with a mesokurtic (nearly normal) distribution (Folk 1974). Grab penetration into the sediment was high at all times and did not vary between sites on any survey ($p = 0.535$). Two-way ANOVA of median particle diameter identified a significant difference between sites ($p < 0.001$), but neither the date ($p = 0.089$) nor interaction ($p = 0.402$) terms were significant (Table 1). Power analysis suggests that an interaction effect of 11% change in median particle diameter would have been detected with 90% probability. The sediment in the treatment area was somewhat finer (median diameter 103 to 114 µm) than that in the reference area (median diameter 119 to 123 µm). Although this difference between sites was consistent, differences between sites for individual surveys were not always significant, and trawling disturbance did not appear to have any effect upon the sediment characteristics over the duration of the study.

Organic carbon levels were high at both sites, suggesting organic enrichment, and varied significantly between treatment ($p < 0.001$) and date ($p < 0.0001$). The interaction term was, however, not significant ($p = 0.389$). An interaction effect of 0.5 mg g^{-1} would have been detected with 90% probability. Organic carbon levels were consistently higher in the treatment area than in the reference area (mean values: treatment, 47.8 mg g^{-1} sediment, cf. reference, 42.5 mg g^{-1}), although not always significantly so. At such levels a difference of 5 mg g^{-1} is not thought to be ecologically significant (D. C. Moore, FRS MLA, pers. comm.).

Community structure

A total of 147 infaunal invertebrate species were collected at the 2 sites during the study, comprising 50%

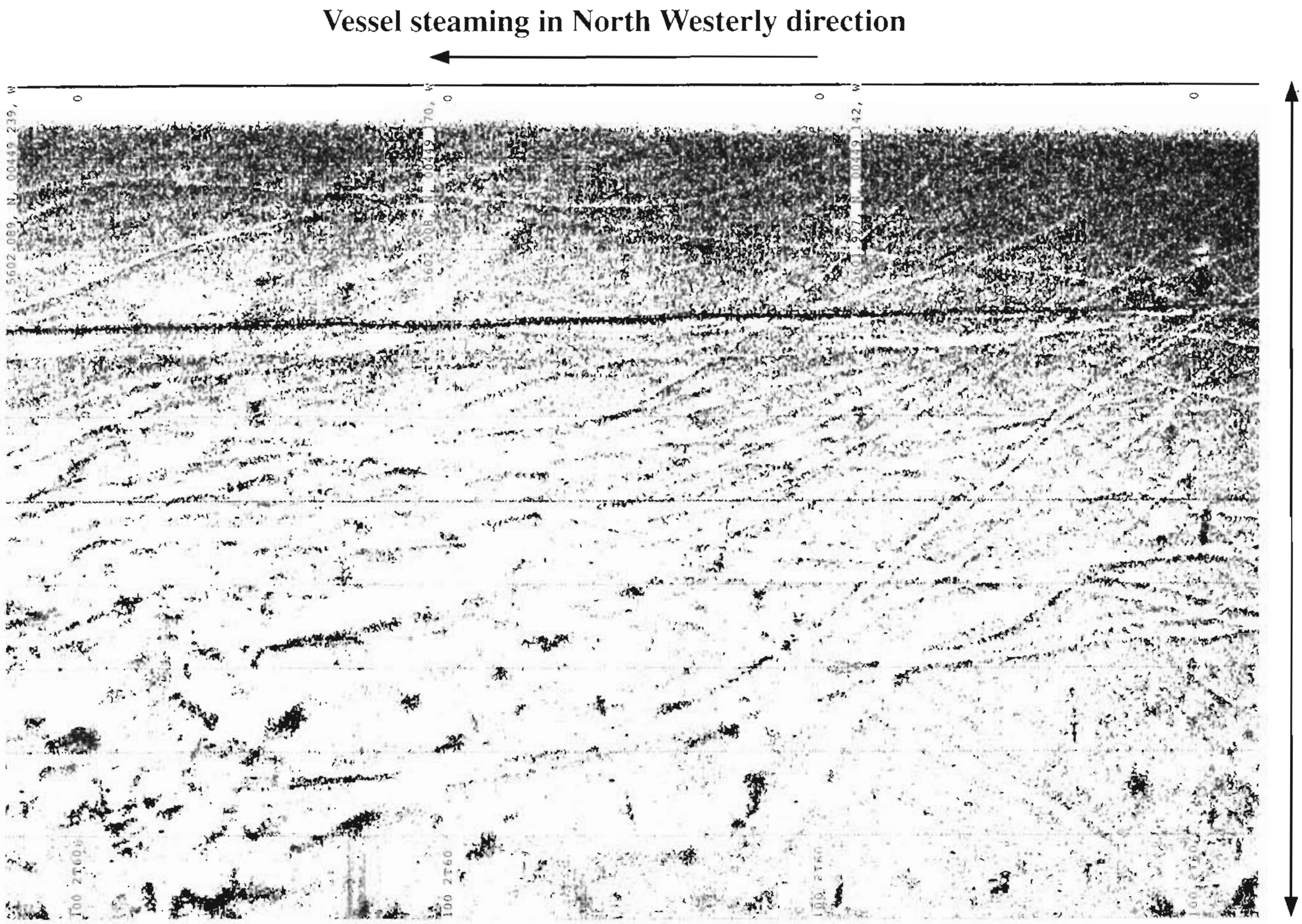

Fig. 2. Portion of the Side-scan sonar record obtained following 10 mo of disturbance, showing disturbed seabed in the treatment area

polychaetes, 22% molluscs and 15% crustaceans. Before the experimental disturbance, polychaetes and molluscs made up 84 and 14%, respectively, of the total abundance of individuals at the treatment site, and 77 and 22%, respectively, at the reference site. The differences in proportional abundance of these phyla between sites were consistent throughout the experiment [$\chi^2(1)$ = 13.04 and 13.22 for polychaetes and molluscs respectively, $p < 0.05$], but neither date nor interaction terms were significant for either phyla. For other phyla, neither site, date or interaction terms were significant.

It would appear that while changes over time occurred at both sites, the changes differed between sites for a number of parameters (Fig. 4). Two-way ANOVA of the number of species identified significant site and date effects ($p < 0.0001$), along with a significant interaction term ($p < 0.0001$) (Table 2). A significant interaction term implies that the trend over time differed between sites and therefore suggests a treatment effect. The number of species became significantly different between sites after 16 mo of disturbance (species numbers greater at treatment site) and remained so throughout the monitored recovery period (Fig. 4a). The numbers of individuals also showed significant site, date and interaction effects ($p < 0.0001$). The numbers of individuals were higher at the treatment site before the experiment (Fig 4a), and although the numbers were not significantly different after 5 mo of disturbance, they became significantly different between sites after 10 mo of disturbance (numbers greater at treatment site), only returning to similar levels after 18 mo of recovery. The disturbance had no detectable effect on infaunal biomass, since neither site, date or interaction terms were significant (Table 2). However, the data were quite variable (11.7 ± 12.1 g $0.1m^{-2}$, mean ± SD). An interaction effect change of 17 g $0.1m^{-2}$ would have been detected at 90% probability.

Treatment effects were also detected for measures of diversity and evenness. Two-way ANOVA of Shannon's exponential H' identified significant effects for

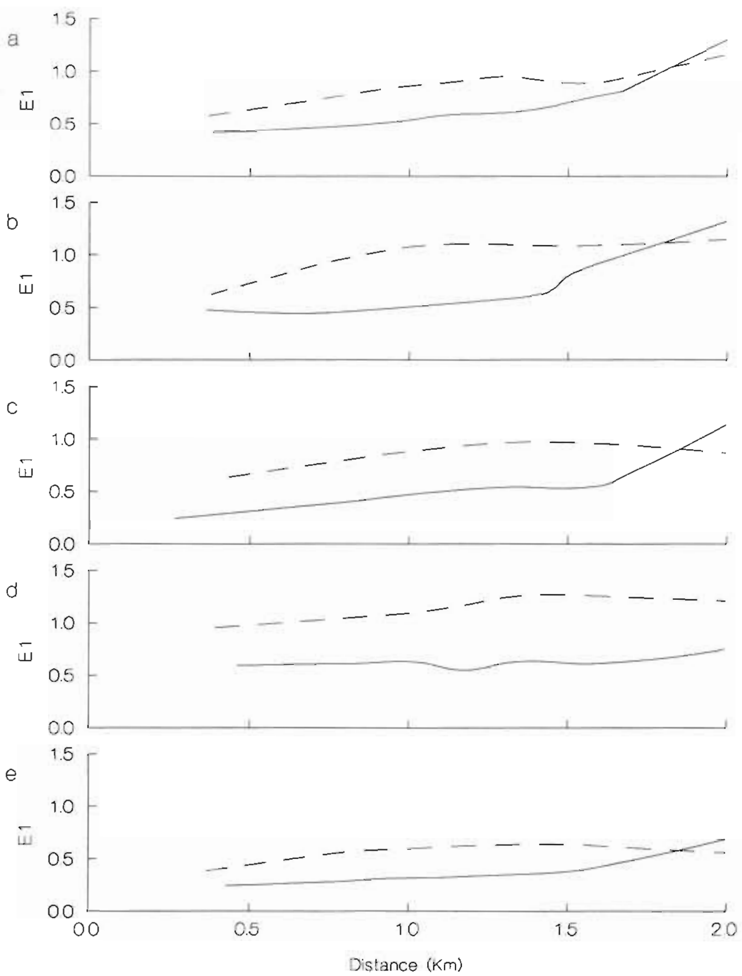

Fig. 3. Transect of E1 (roughness parameter) values along the loch for treatment (dashed line) and reference (solid line) areas. (a) Preliminary survey; (b) 5 mo of disturbance; (c) 10 mo of disturbance; (d) 16 mo of disturbance; and (e) 6 mo of recovery

site, interaction ($p < 0.0001$), and date terms ($p < 0.001$). Both Simpson's reciprocal D and Pielou's evenness measure showed similar changes in the community, with significant site, date ($p < 0.0001$) and interaction terms ($p < 0.001$). Each of the indices showed a similar temporal pattern between sites (Fig. 4b, Table 2), with significantly higher values for the reference site after only 5 mo of disturbance, returning to similar levels between sites after 12 mo of recovery. Since all 3 measures showed a significant treatment effect, the trawling disturbance can be seen to have had an effect on both rare (measured by Shannon's exponential H') and more abundant (measured by Simpson's reciprocal D) species in the community, along with the dominance structure (measured by Pielou's evenness). The changes shown in Fig. 4b indicate that when compared to the temporal changes at the reference area, the trawling disturbance reduced diversity and reduced evenness (increased dominance) at the treatment area.

Changes in the abundance [$\ln(x + 1)$ transformed] of the 20 commonest species were examined in relation to site and date using 2-way ANOVA. The results of these analyses are summarised in Table 3. Not all the species showed a significant treatment effect (Table 3), but of those that did, the more abundant species increased in density with disturbance, while the less abundant species decreased. An indication of the power of the tests is given by the % change required for an effect to be detected with 90% probability. Power varied between species, but most required a change of at least 50% in order for a change to be detected with a probability of 90%.

Box plots of abundance for selected species are shown in Fig. 5. Species that increased in abundance relative to the reference area in response to the disturbance are shown in Fig. 5a. The cirratulids *Chaetozone setosa* and *Caulleriella zetlandica* show a similar pattern, with density becoming greater at the treatment site after 10 mo disturbance. *C. setosa* appears to be a longer-term indicator, however, since median density was still significantly higher at the treatment site following 18 mo of recovery (although the whiskers extend well below the box, indicating some samples with low density), while *C. zetlandica* showed less difference between sites after 12 mo of recovery. *Mediomastus fragilis* showed a strong seasonal effect (densities greater in the autumn than in the spring) and was significantly more abundant at the treatment site throughout the disturbance period, with differences in densities becoming non-significant after 18 mo of recovery. The density of *Pseudopolydora paucibranchiata* became significantly different after 16 mo of disturbance, with differences becoming non-significant after 12 mo of recovery.

Species which declined in density relative to the reference area are shown in Fig. 5b. The density of the nutshell *Nucula nitidosa* fell in the treatment area after only 5 mo of disturbance and remained significantly lower than that in the reference area after 10 mo of disturbance. The densities of both *Scolopolos armiger* and *Nephtys cirrosa* declined in the treatment area relative to the reference area during the disturbance period. The density of *Terebellides stroemi* remained similar between areas throughout the disturbance period (although densities declined slightly in the treatment area), but increased relative to the reference area during the recovery period, becoming significantly greater after 18 mo of recovery.

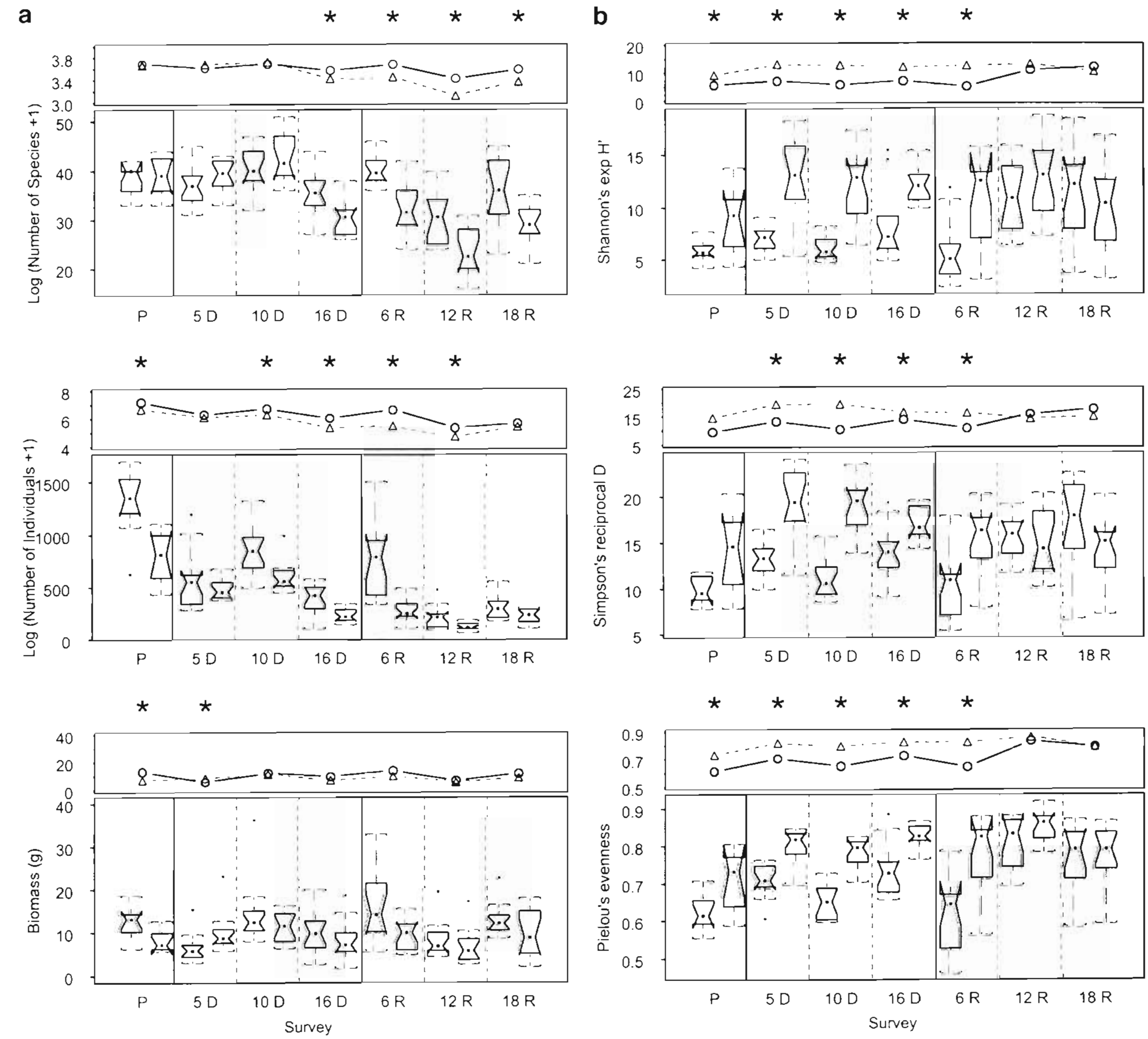

Fig. 4. Box plots of (a) number of species, individuals and biomass ($0.1\,m^{-2}$) and (b) Shannon's exponential H', Simpson's reciprocal D and Pielou's evenness (lower panels), along with the time series for the median values for each survey (upper panels). Box plots are arranged in pairs in time (survey) order, with the reference plot on the right for each pair. *Surveys in which medians of 2 sites were significantly different. P: preliminary survey; 5D: 5 mo of disturbance; 10D: 10 mo of disturbance; 16D: 16 mo of disturbance; 6R: 6 mo of recovery; 12R: 12 mo of recovery; 18R: 18 mo of recovery. Notches in boxes indicate 95% confidence intervals of the median. If the intervals around 2 population medians do not overlap, the population medians can be considered significantly different ($p < 0.05$). Dashed lines represent whiskers and extend to the largest observation that is less than or equal to the upper quartile plus 1.5 times the interquartile range (or the smallest observation that is greater than or equal to the lower quartile minus 1.5 times the interquartile range)

MDS plots of the reference and treatment areas are shown in Fig. 6. Owing to software limitations, a maximum of 125 stations can be plotted on any one figure, so data are presented on 2 plots, the first displaying the period from the preliminary survey to 6 mo recovery survey (Fig. 6a), and the second displaying the 16 mo disturbance to the 18 mo recovery survey (Fig. 6b). Stations which are more similar to one another in their infaunal community occur closer together on the figure, which shows that although the treatment and reference areas were partly separated in the preliminary survey, they became more distinct once the experimental trawling commenced (Fig. 6a), and the communities at both sites changed over time. The infaunal communities at the 2 sites remained distinct in the 6 mo recovery survey, and although they

Table 2. Analysis of variance table for the effects of site and date on log(x+1) transformed counts of total number of species and total number of individuals, and untransformed biomass, diversity and evenness from infaunal samples

	df	SS	MS	*F*	p
Number of species					
Site	1	0.027	0.027	28.85	<0.0001
Date	6	0.179	0.029	32.34	<0.0001
Site × Date	6	0.035	0.006	6.33	<0.0001
Residual	171	0.158	0.001		
Number of individuals					
Site	1	0.219	0.219	79.80	<0.0001
Date	6	1.261	0.210	76.39	<0.0001
Site × Date	6	0.074	0.012	4.52	<0.0001
Residual	171	0.470	0.003		
Biomass					
Site	1	82.710	82.711	0.557	0.456
Date	6	609.320	101.553	0.684	0.662
Site × Date	6	880.760	146.793	0.989	0.434
Residual	171	25367.340	148.347		
Shannon's exponential *H'*					
Site	1	609.302	609.302	63.512	<0.0001
Date	6	313.416	52.236	5.444	<0.001
Site × Date	6	284.858	47.476	4.948	<0.0001
Residual	171	1640.477	9.593		
Simpson's reciprocal *D*					
Site	1	448.441	448.441	47.967	<0.0001
Date	6	306.274	51.046	5.013	<0.0001
Site × Date	6	559.163	93.194	9.152	<0.001
Residual	171	1741.269	10.183		
Pielou's evenness					
Site	1	0.371	0.371	86.980	<0.0001
Date	6	0.448	0.074	17.512	<0.0001
Site × Date	6	0.113	0.019	4.423	<0.001
Residual	171	0.729	0.004		

Table 3. Summary of 2-way ANOVA of 20 commonest species. p-values provided for site, date and interaction effects (ns: not significant at 5% level). Densities provided are averages from all samples collected throughout the experiment. Where significant ($p < 0.05$) interactions were found, the change indicated represents change in abundance (relative to the reference site) associated with the disturbance of the treatment site (+ve: increase in abundance following disturbance; −ve: decrease in abundance following disturbance; ?: change variable and unclear). % change: interaction change at which an effect would be detected at 90% probability. Those species showing consistent effects, which may therefore be considered indicator species for physical disturbance in this habitat, have been highlighted in bold type

Species	Density (m^{-2})	Phylum	Site	Date	Interaction	Change	% change
Chaetozone setosa	79.06	Annelida	<0.0001	<0.0001	<0.05	+ve	61
Mediomastus fragilis	68.24	Annelida	<0.0001	<0.0001	<0.05	+ve	105
Caulleriella zetlandica	47.54	Annelida	<0.0001	<0.0001	<0.0001	+ve	61
Pseudopolydora paucibranchiata	39.45	Annelida	ns	<0.0001	<0.0001	+ve	117
Abra alba	34.62	Mollusca	ns	<0.0001	<0.05	?	50
Lagis koreni	23.11	Annelida	<0.0001	<0.0001	ns		73
Melinna palmata	17.96	Annelida	ns	<0.0001	<0.001	+ve	41
Thyasira flexuosa	15.36	Mollusca	ns	<0.0001	ns		63
Scalibregma inflatum	12.06	Annelida	ns	<0.0001	<0.05	?	85
Nucula nitidosa	11.66	Mollusca	<0.005	<0.001	<0.005	−ve	71
Scolopolos armiger	10.19	Annelida	<0.0001	<0.05	<0.01	−ve	56
Pholoe inornata	9.64	Annelida	ns	<0.0001	ns		70
Nephtys cirrosa	9.42	Annelida	<0.0001	<0.0001	<0.001	−ve	48
Terebellides stroemi	9.07	Annelida	<0.01	<0.0001	<0.005	−ve	52
Nuculoma tenuis	6.45	Mollusca	<0.005	<0.0001	ns		72
Corbula gibba	6.03	Mollusca	<0.0001	<0.0001	<0.001	−ve	45
Nemertea sp.	5.75	Nemertea	<0.0001	<0.0001	ns		75
Aphelochaeta marioni	5.36	Annelida	ns	<0.0001	<0.05	?	51
Abra nitida	5.18	Mollusca	ns	<0.01	ns		68
Goniada maculata	5.11	Annelida	<0.05	<0.001	<0.05	−ve	27

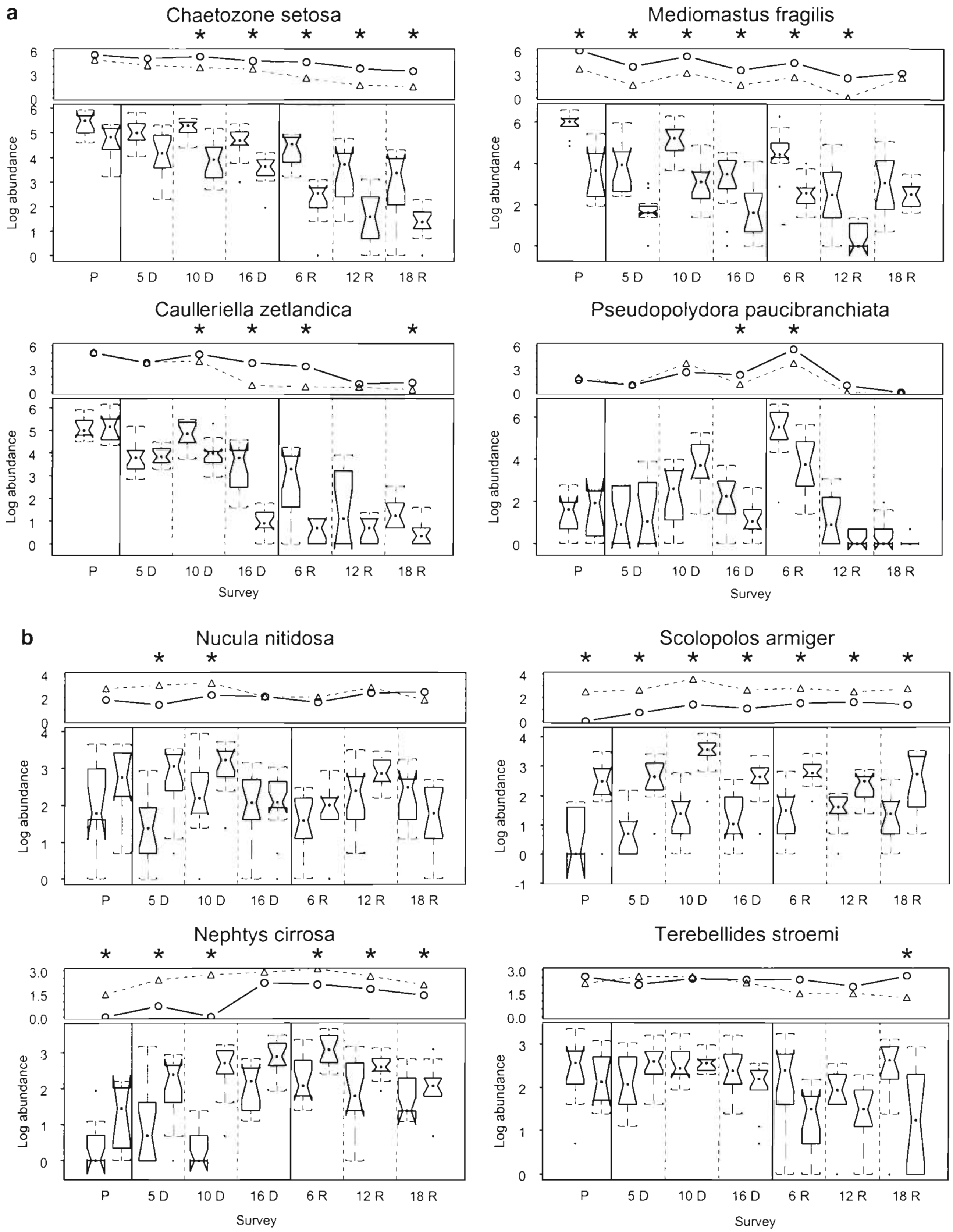

Fig. 5. Box plots and time series for the median values of abundance of 4 infaunal species showing (a) an increase and (b) a decrease in abundance in response to physical disturbance. Further details as for Fig. 4

appear more scattered in the 12 mo survey, there was more overlap between the 2 areas than on the previous survey, a trend that continued in the final survey (Fig. 6b). These subjective impressions were confirmed by 2-way nested analysis of similarities (ANOSIM; Clarke & Green 1988), with both date and treatment having significant effects ($p < 0.001$). Pairwise analysis of similarities (Clarke & Green 1988) with Bonferroni adjusted probabilities for multiple comparisons showed that while the communities were not significantly different before the experiment started, both sites differed significantly over time and were significantly different after 5 mo of disturbance, remaining so throughout the remainder of the experiment.

A SIMPER test (Clarke 1993) was used to identify which species contributed most to the similarity or dissimilarity between the 2 sites. The results were very similar to those described for the analysis of individual species abundances using 2-way ANOVA, with the same species responsible for differences between the communities of the 2 areas between surveys.

ABC curves (Warwick 1986) are shown for the reference and treatment areas for selected surveys in Fig. 7. This figure plots cumulative dominance curves for abundance and biomass on the same graphs, allowing comparison of the forms of these curves. In undisturbed communities the biomass curve would be expected to lie above the abundance curve throughout its length, with the reverse for grossly disturbed communities (Warwick 1986). In moderately disturbed areas the 2 curves are closely coincident and may cross each other 1 or more times.

Adopting the ABC criterion for a disturbed community, it can be seen that prior to the application of the experimental treatment both sites were moderately disturbed, possibly due to some degree of carbon enrichment or metal contamination (Haig 1986, Pearson et al. 1986). While the reference site was in an undisturbed state by the 6 mo disturbance survey, the treatment site remained in a moderately disturbed condition throughout the period of experimental trawling (Fig. 7), only becoming undisturbed after 12 mo of recovery (plot not shown). Both sites showed evidence of a seasonal pattern in the W statistic (Fig. 8; a measure of the difference between the abundance and biomass lines on an ABC plot, standardised to a common scale; Clarke 1990), with values being higher in the spring (May) than the autumn (October-November), probably related to the recruitment of small-bodied individuals (e.g. *Mediomastus fragilis*) during the summer. Two-way ANOVA of the W statistic showed significant site, date ($p < 0.0001$) and interaction ($p < 0.01$) terms. While the values of the W statistic were not significantly dif-

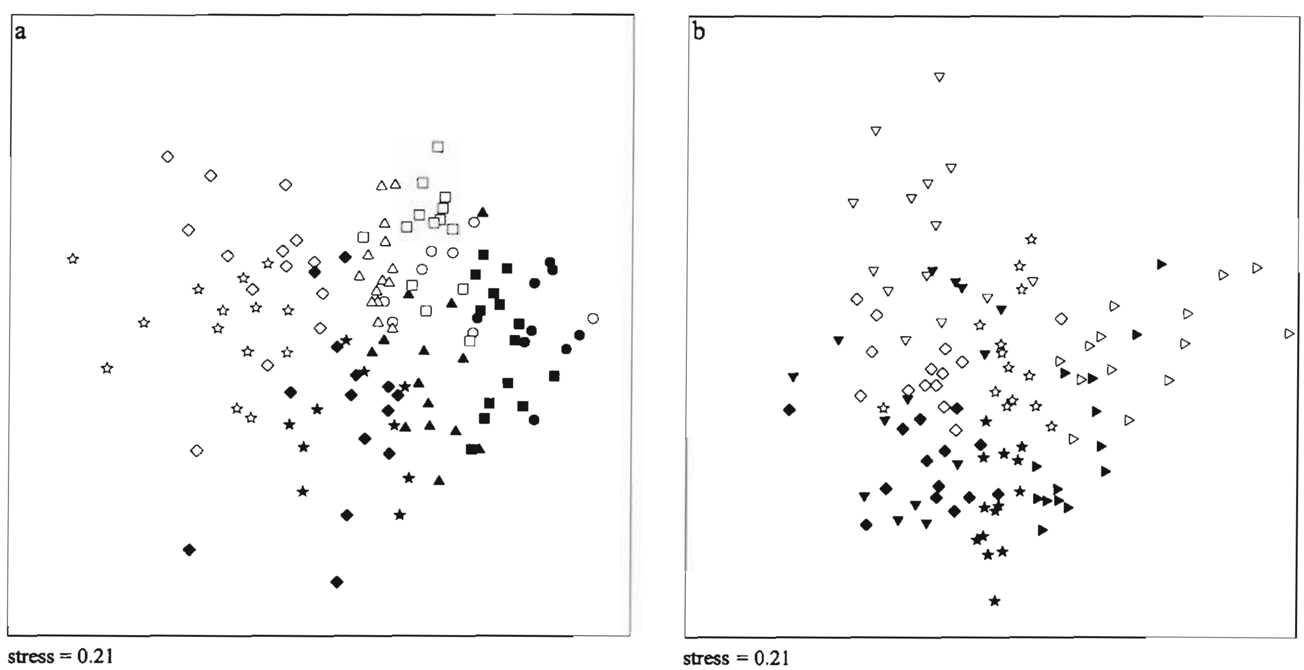

Fig. 6. MDS plots of infaunal data for reference (open symbols) and treatment (closed symbols) areas from (a) preliminary to 6 mo recovery survey and (b) 16 mo disturbance to 18 mo recovery survey. (○) Preliminary survey; (△) 5 mo of disturbance; (□) 10 mo of disturbance; (◇) 16 mo of disturbance; (☆) 6 mo of recovery; (▽) 12 mo of recovery; (▷) 18 mo of recovery

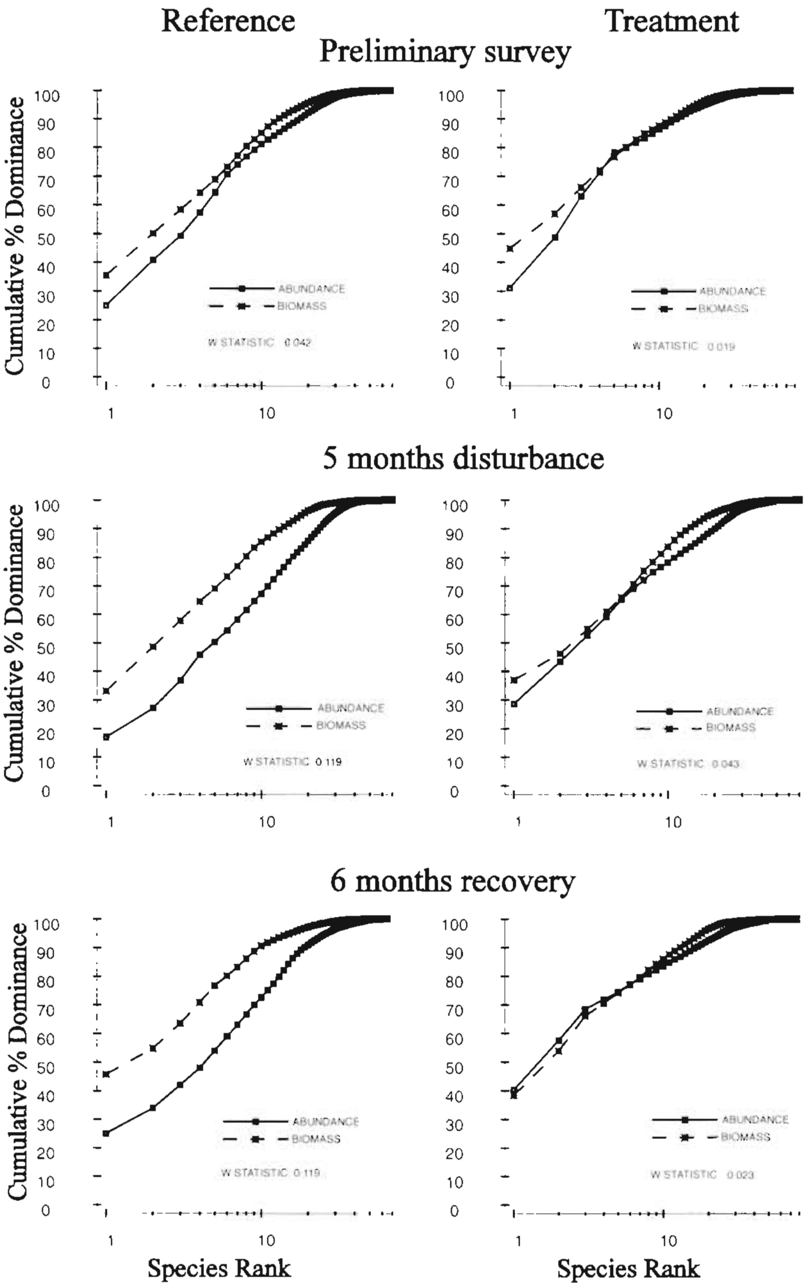

Fig. 7. ABC curves (Warwick 1986) for selected surveys

ferent between sites in the preliminary survey, the statistic was significantly greater at the reference site after 5 mo of disturbance (i.e. the ABC curve for the treatment site indicated greater disturbance than that for the reference area) and remained so until after 18 mo of recovery (Fig. 8). Therefore, while the treatment site could be considered undisturbed after 12 mo of recovery on the basis of ABC analysis, it only reached a similar condition to the reference site after 18 mo.

Average densities of epifauna recorded in the loch from TV surveys were low (Table 4). Two-way ANOVA of number of species and total number of individuals m^{-2} identified significant date effects, but neither showed a significant interaction, and there was therefore no identifiable treatment effect (Table 5). Interaction effect changes of 19 and 11%, respectively, would have been detected with a probability of 90%.

While some species showed no significant site:date interaction, and therefore no identifiable treatment effect, the brittle star *Ophiura* sp. appeared to increase with disturbance, while long rough dab *Hippoglossoides platessoides*, the anemone *Metridium senile* and the whelk *Buccinum undatum* each declined in density relative to the reference area (Table 6). These effects were noted during the 16 mo disturbance survey and persisted for 6 mo into the recovery period for *B. undatum* (Fig. 9).

DISCUSSION

The main physical effect of our trawling appears to be the trenches left in the sediment by the trawl doors. This differs from beam trawls and scallop dredges, which flatten seabed features (Currie & Parry 1996, Kaiser & Spencer 1996a), although beam trawls also leave trenches in softer sediment. Both the Side-scan and RoxAnn results indicate clear physical effects while trawling continued, but while the RoxAnn data indicated recovery after 6 mo, the Side-scan results suggest that over 18 mo was required before the physical characteristics of the sites became indistinguishable. The difference was probably due to the frequencies of the transducers used. While the echo-sounder (RoxAnn) transducer had a signal (50 kHz) that would penetrate into the seabed, that of the Side-scan (120 kHz) would not, and would therefore be more sensitive to surface features. The features produced are unlikely to be as large or long-lasting in less sheltered areas with coarser sediments (see for example Currie & Parry 1996), unless an interaction effect between resident biota influences sediment stability. The disturbance was not detected to have any effect on sediment parti-

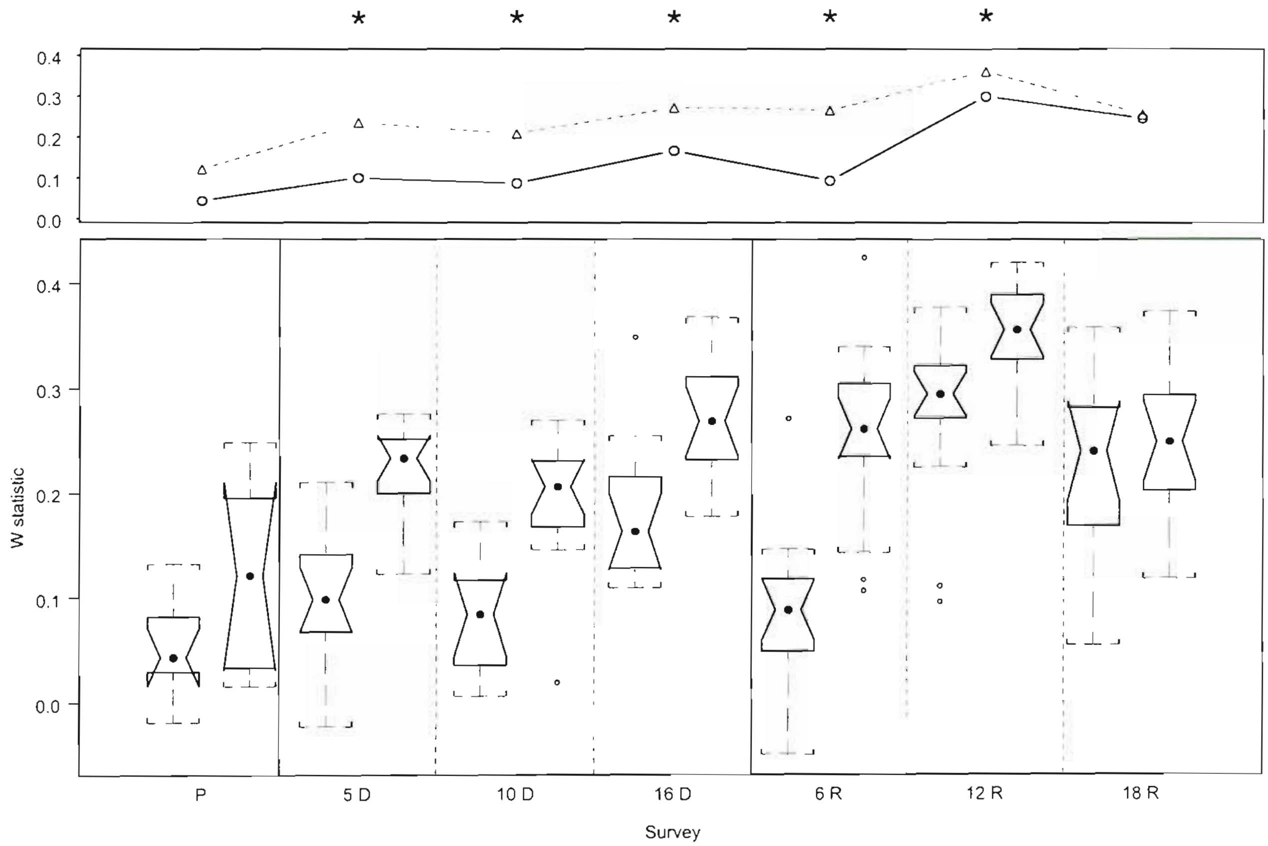

Fig. 8. Box plots and time series for the median values of the *W* statistic for each site through the experiment. Further details as for Fig. 4

cle size or organic carbon, although power was high for these parameters.

The fauna of the loch was similar to other inner sea lochs of the Clyde (Pearson et al. 1986), with the species present suggesting some degree of carbon enrichment (see also ABC curves in Fig. 7). In the preliminary survey, opportunistic species contributed most to the inter-site similarity, thus also suggesting some degree of disturbance.

With respect to broad taxonomic categories, the proportion of individuals made up by polychaetes was consistently higher in the treatment area, while the proportion made up by molluscs was consistently lower, although the experimental disturbance had no significant effect on these proportions. Trawling disturbance did, however, lead to an increase in the number of species and individuals relative to the reference area while reducing diversity and evenness (Fig. 4a, b). The fact that the measures of diversity decreased while the number of individuals and species increased suggests that there was a disproportionate increase in the abundance of a few dominant species in the treatment area — a response typically predicted for a disturbed area (Warwick 1986). The time scales over which the different effects became obvious differed, suggesting varying levels of sensitivity to trawling disturbance. The measures of diversity were the most sensitive to the initial changes in the community, while an effect on species richness was detected later but lasted longer into the recovery period.

The main species which showed a consistent increase in abundance in association with disturbance (*Cheatozone setosa* and *Caulleriella zetlandica*) belong to the cirratulid family and are considered opportunistic in nature. The time scales over which the species showed significant differences varied, with *C. setosa* remaining more abundant in the treatment area beyond the end of the experiment, while *C. zetlandica* showed less difference between sites after 12 mo of recovery (Fig. 5a). The spionid *Pseudopolydora paucibranchiata* increased in density immediately after the disturbance finished (Fig. 5a), suggesting that although it is less able to take advantage while trawling was continuing, this species is an opportunist and can rapidly increase in numbers when trawling ceases.

Reductions in density in association with disturbance were less obvious, but some species could be identified as sensitive to physical disturbance in this habitat. The bivalves *Nucula nitidosa* and *Corbula gibba* both

declined in abundance relative to the reference area following disturbance. Suspension feeding bivalves, such as *C. gibba*, are generally unable to escape burial of more than 5 cm (Maurer et al. 1981) and are also sensitive to the high rates of sedimentation (Howell & Shelton 1970) likely to occur following intensive trawling. Interestingly, *Corbula coxi* has also been found to be sensitive to fishing disturbance (Currie & Parry 1996). The polychaetes *Scolopolos armiger*, *Nephtys cirrosa* and *Terebellides stroemi* also decreased in density following disturbance. *Scolopolos fragilis* has been shown to be very sensitive to burial (Maurer et al. 1982)—a similar situation may also occur for *S. armiger*. Larger-bodied species such as *N. cirrosa* and *T. stroemi* would be expected to be adversely affected by physical disturbance (either through direct damage or predation following disturbance). Howell & Shelton (1970) also found that *Nephtys hombergi* is sensitive to high sedimentation rates of fine clay materials, and this may also be the case for *N. cirrosa*.

Multivariate analysis of the community data showed that the 2 sites became significantly different after only 5 mo of disturbance, remaining so throughout the experiment. An increase in abundance of opportunistic species was mainly responsible for the differences in the communities. The *W* statistic showed that the sites were different after only 5 mo of disturbance, and while the treatment site could be considered undisturbed after 12 mo of recovery on the basis of ABC criterion, it only reached a similar condition to the reference site after 18 mo.

For epifaunal species, no long-term effects on the total number of species or individuals were detected, but individual species did show effects, notably an increase in the density of *Ophiura* sp. and a decrease in the density of *Hippoglossoides platessoides*, *Metridium senile* and *Buccinum undatum*. Power was high for both the summary parameters and individual species tests, but underwater visibility was very poor, and TV surveys may not be the best way to assess epifaunal densities at such sites. It has been suggested that increases in echinoderm populations in the North Sea are associated with fishing disturbance (Aronson 1990, Lindley et al. 1995). It is unclear why the density of long rough dab *H. platessoides* decreased in association with disturbance, but the plumose anemone was probably damaged or killed by physical impact with the fishing gear, thus reducing its density in disturbed areas. No effect was detected for the other common

Table 4. Epifaunal species recorded from Agassiz trawl samples (preliminary survey) and TV surveys. Densities (averages from all TV surveys, both sites) are provided for the species commonly identified during TV surveys

Species	Phylum	Density (m^{-2})
Asterias rubens	Echinodermata	0.071
Virgularia mirabilis	Cnidaria	0.054
Hippoglossoides platessoides	Pisces	0.020
Liocarcinus depurator	Crustacea	0.014
Ophiura ophiura	Echinodermata	0.013[a]
Ophiura affinis	Echinodermata	
Metridium senile	Cnidaria	0.009
Pagurus bernhardus	Crustacea	0.009
Buccinum undatum	Mollusca	0.007
Callionymus lyra	Pisces	0.007[b]
Gobius niger	Pisces	
Taurulus bulbais	Pisces	
Pecten maximus	Mollusca	
Aporrhais pespelicani	Mollusca	
Aphrodite aculeata	Annelida	
Cerianthus lloydi	Cnidaria	
Carcinus maenas	Crustacea	
Hyas araneus	Crustacea	
Palaemon serratus	Crustacea	
Crangon allmani	Crustacea	
Echina esculentus	Echinodermata	

[a]For both *Ophiura* sp. combined, as it was not possible to differentiate the two from the TV data
[b]For all fish species, other than *Hippoglossoides platessoides*, combined

Table 5. Analysis of variance table for the effects of site and date on log(x + 1) transformed counts of total number of species and total number of individuals from TV surveys

	df	SS	MS	*F*	p
Number of species					
Site	1	0.069	0.069	3.72	0.064
Date	6	0.301	0.050	2.70	<0.05
Site × Date	6	0.115	0.019	1.03	0.424
Residual	28	0.502	0.018		
Number of individuals					
Site	1	0.001	0.001	0.15	0.705
Date	6	0.186	0.031	4.88	<0.01
Site × Date	6	0.028	0.005	0.73	0.629
Residual	28	0.171	0.006		

Table 6. Summary of 2-way ANOVA of density from TV survey in relation to site and date for commonest epifaunal species. p-values are provided for site, date and interaction effects (ns: not significant at 5% level). % change: interaction change at which an effect would be detected at 90% probability. Densities provided are averages from surveys collected throughout the experiment. For further details see Table 3

Species	Density (m^{-2})	Phylum	Site	Date	Interaction	Change	% change
Asterias rubens	0.071	Echinodermata	ns	<0.05	ns		5
Virgularia mirabilis	0.054	Cnidaria	<0.05	<0.01	ns		5
Hippoglossoides platessoides	0.020	Pisces	ns	<0.01	<0.01	-ve	2
Liocarcinus depurator	0.014	Crustacea	ns	ns	ns		2
***Ophiura* sp.**	0.013	Echinodermata	<0.01	<0.001	<0.01	+ve	2
Metridium senile	0.009	Cnidaria	<0.001	<0.001	<0.001	-ve	0.5
Pagurus bernhardus	0.009	Crustacea	ns	ns	ns		3
Buccinum undatum	0.007	Mollusca	<0.01	<0.05	<0.05	-ve	1
Other fish	0.007	Pisces	ns	<0.01	ns		1

cnidarian found at the site, *Virgularia mirabilis*, perhaps because this species is able to rapidly withdraw into the mud, therefore avoiding being damaged as a trawl passes. A scavenging species such as *B. undatum* might be expected to benefit from fishing disturbance, through increased food availability. However, recent studies suggest that this species is sensitive to the physical disturbance associated with beam trawling (M. Bergman, NIOZ, pers. comm.). Kaiser & Spencer (1994) found that benthic disturbance by fishing gear caused an increase in the density of epifaunal scavengers, in response to an increase in food availability in the form of damaged and disturbed organisms. Such responses to disturbance are generally short term in nature (Hall et al. 1994), however, and may be dependent on tidal conditions (Hall et al. 1996).

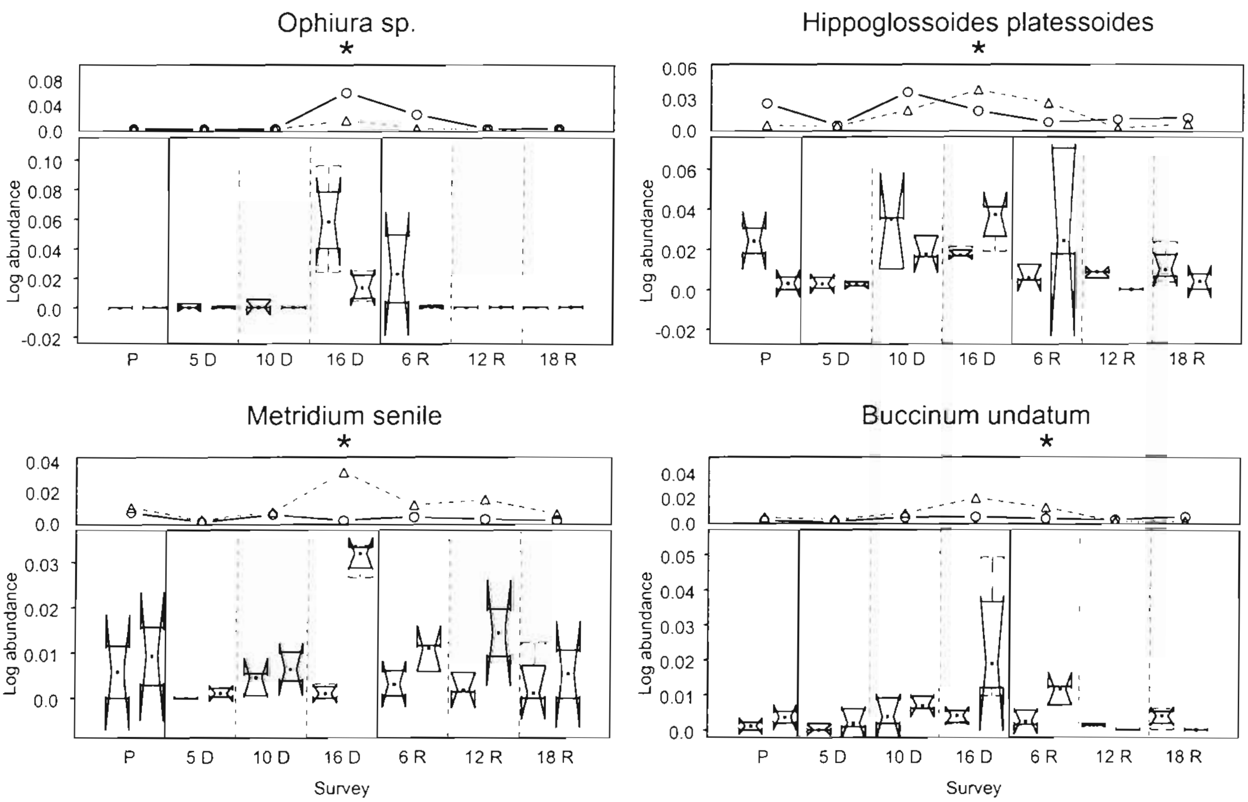

Fig. 9. Box plots and time series for the median values of abundance of epifaunal species showing a change in abundance in response to physical disturbance. Further details as for Fig. 4

Taken overall, effects on epifauna at this site appear to have been persistent during the period of fishing, but recovery was relatively rapid. For the most part, densities in the treatment area were indistinguishable from the reference area 6 mo after fishing ceased. It should be borne in mind, however, that the epifaunal species assemblage in Loch Gareloch was relatively sparse in the first place, with few erect sessile species such as sponges or corals which are especially susceptible to fishing disturbance. Since they were not (and presumably never have been) present at this site we can draw no conclusions regarding such communities.

As noted earlier, the experimental design we had to adopt (i.e. a single treatment and reference area) is only suitable for demonstrating differences between locations (Hurlbert 1984). Nevertheless, we argue that, by sampling at repeated points through time, during a period of impact and recovery, we have examined the effects of disturbance, and the conclusions we draw for this site are likely to be of relevance to other fine muddy habitat communities. Had the gear been equipped with a net, then greater effects on epifauna might be expected. Large numbers of epifaunal species would be removed in the catches, which would immediately deplete the local populations of less mobile and sedentary species, and increase the time required for recovery. If the catches were also able to significantly deplete the populations of mobile scavenger species (an event possible in the relatively enclosed Loch Gareloch, but unlikely in the open sea; Kaiser & Spencer 1996b), then there may also have been knock-on effects on the infauna, which would be subject to less predation following the disturbances, and therefore show less effects due to fishing disturbance.

We have shown that experimental trawling disturbance had clear long-term effects on the topography of the seabed and the infaunal community at this site, and that, while physical effects were almost indistinguishable after 18 mo of recovery, community effects (measured by both univariate and multivariate techniques) extended beyond the life of the experiment. Similar effects would probably be observed at other sheltered sites with fine silt sediments. Such long recovery times suggest that even fishing during a restricted period of the year may be sufficient to maintain a community in an altered state.

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