

The interaction between physical disturbance and organic enrichment: An important element in structuring benthic communities

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Abstract

The interaction between physical disturbance and organic enrichment, with respect to its effect on the diversity and community structure of a macroinfaunal assemblage, has been examined in a benthic mesocosm experiment. The experiment was conducted at the Solbergstrand mesocosm (Norwegian Institute for Water Research) using subtidal sediment collected from Bjørnhordenbukta, a small sheltered bay in Oslofjorden. Ninety-eight areas of homogenized sediment were subjected to one of seven levels of organic enrichment, combined with one of seven different frequencies of physical disturbance, each replicated once. This structured matrix of physical disturbance and organic enrichment treatments demonstrated the combined effects of these factors to be nonadditive. Diversity was lower than expected when low frequencies of physical disturbance acted in conjunction with high levels of organic enrichment or when high frequencies of physical disturbance were combined with low levels of organic enrichment. Diversity was higher than expected when both disturbance and enrichment were either high or low. The implications of this interaction between physical disturbance and organic enrichment for the application of the dynamic equilibrium model (Huston 1979) to sediment communities are discussed. Multivariate analysis also showed community structure to be significantly affected by physical disturbance, organic enrichment, and interactions between the two. It is concluded that strong interactions between physical disturbance and organic enrichment, coupled with both small- and large-scale variability in these factors, could promote heterogeneity and diversity in benthic infaunal assemblages. However, this remains to be tested in field conditions. Additionally, interactions between physical disturbance and organic enrichment may have important implications for matters of coastal zone management.

Marine benthic infaunal assemblages are subjected to a variety of physical disturbance events, and their response to such events has been studied extensively. These studies have ranged from the large-scale effects of trawling (e.g., Tuck et al. 1998) and storm events (e.g., Posey et al. 1996) to the small-scale disturbances caused by mobile bioturbating organisms, both epifaunal (e.g., Hall et al. 1991; Thrush et al. 1991) and infaunal (e.g., Flach 1992; Widdicombe and Austen 1998). The importance of different scales of physical disturbance was discussed by Zajac et al. (1998) who, along

with others (e.g., Levin and Paine 1974; Hall 1994; Levin 1994), highlighted the importance of cycles of disturbance and recovery in maintaining heterogeneity in soft sediment environments and thereby setting community structure. The importance of these cycles was first suggested by Johnson (1970, 1973), who concluded that “the continual occurrence of small-scale disturbances can account for part of the spatial and temporal variations of diversity within benthic communities.”

Much of the extensive literature concerned with how marine benthic communities respond to organic enrichment has concentrated on the effects of anthropogenic inputs associated with freshwater runoff (e.g., Beukema 1991), aquaculture (e.g., Ritz et al. 1989), and sewage disposal (e.g., Hall et al. 1997). These studies of anthropogenic eutrophication, together with those examining naturally occurring organic enrichment events (e.g., Oug et al. 1991), have served to strengthen the validity of the community response model of Pearson and Rosenberg (1978). Based on surveys of macrobenthic communities along gradients of organic enrichment, this model predicts a decline of suspension feeders and an increase in deposit feeders as organic input to the sediment increases, irrespective of the type of organic material responsible for the enrichment. Other models (e.g., Rhoads et al. 1978) predicted a community response to physical disturbance similar to that described for organic enrichment.

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Such models suggest that communities along a physical disturbance or organic enrichment gradient display serial changes in structure as the intensity or level of the perturbation changes. While these investigations into the effects of either physical disturbance or organic enrichment are extensive, they have not addressed the possibility of interactions between these two factors when acting on an assemblage simultaneously. Such interactions may have substantial implications for predictive models.

Organic enrichment has been shown to have a significant effect on species diversity, a particular aspect of community structure. The relationship between productivity, or "energy in the system" (Wright 1983), and diversity was described by Grime (1973*a,b*), who presented the intermediate productivity hypothesis (IPH). This hypothesis predicted maximum species diversity occurred at some intermediate level of productivity, at which competition for food is reduced and the coexistence of potentially competing species was promoted. Grime's (1973*a,b*) definition of productivity was a combination of light availability and the level of soil nutrients supplied to the herbaceous plants communities he studied. Using such a definition it is not unreasonable to view the supply of organic material to marine benthic communities as a resource that could influence species diversity in a manner predicted by the IPH. A recent field study assessing the impacts of terrestrial runoff on macrobenthic communities supported the IPH as it demonstrated that maximum diversity (species richness) corresponded to intermediate levels of enrichment (Frouin 2000).

A relationship similar to that for diversity and organic enrichment has been observed between diversity and physical disturbance, leading Connell (1978) to propose the intermediate disturbance hypothesis (IDH). This hypothesis identifies the severity and frequency of disturbance as key elements in setting community diversity. Similar to the IPH, the IDH predicts maximum species diversity occurs at some intermediate level of disturbance, at which competitive exclusion is reduced. This hypothesis was originally erected from studies of terrestrial communities, and subsequent evidence for it being applicable in the marine environment has come, traditionally, from rocky intertidal (e.g., Paine 1966) and coral reefs studies (e.g., Connell and Keough 1985). For soft sediment communities, direct evidence for competitive exclusion within communities of soft sediments has, to date, been scarce, which leads to a reluctance in accepting the IDH as a mechanism for diversity maintenance in this habitat. One study that did claim to provide such evidence was that of Kukert and Smith (1992), which used artificial mounds to explore macrofaunal community response to burial disturbance in the Santa Catalina Basin. These authors concluded that the changes in diversity they observed were "a consequence of reduced pressure from competitive dominants occurring during community succession following burial disturbance." In addition to this evidence, previous field observations of epibenthic agglutinating foraminiferans, also in the Santa Catalina Basin (Levin et al. 1991) and recent laboratory-based experiments on the effects of bioturbation on meiofaunal and macrofaunal communities (Austen et al. 1998; Widdicombe and Austen 1999) have elicited community responses that were in agreement with the IDH.

Such studies would suggest that there is justification in considering the IDH as a potential explanation of diversity maintenance within soft sediment communities in addition to the traditionally accepted habitats of coral reefs and the rocky intertidal.

It was evident to Huston (1979) that both the IPH (Grime 1973*a,b*) and the IDH (Connell 1978) relied on competitive displacement. By combining these two hypotheses, Huston (1979) proposed the dynamic equilibrium model. This model assumed diversity represented a balance between growth rates (productivity/organic enrichment) and disturbance, with maximum diversity being observed when an assemblage received intermediate levels of both productivity and disturbance. Empirical support for the dynamic equilibrium model is hard to come by since the necessary, multifactorial experiments are intrinsically more difficult to conduct than experiments that manipulate only a single factor. However, much circumstantial evidence does exist from field surveys of interacting gradients of disturbance and rate of displacement (see Huston 1994). Additionally, several models of plant competition and succession (e.g., Botkin et al. 1972; Caswell and Cohen 1991) have been used to conduct simulation experiments, the results of which closely agreed with the predictions of the dynamic equilibrium model.

While investigations into the effects of either physical disturbance or organic enrichment are extensive, they have not addressed the possibility of interactions between disturbance and organic enrichment acting simultaneously on an assemblage. Such interactions may have substantial implications for predictive models, such as the dynamic equilibrium model (Huston 1979). Using an experimental approach, this paper explores the response of a benthic macrofaunal community to the combined influence of both physical disturbance and organic enrichment. We have attempted to test the generality of the IDH, IPH, and dynamic equilibrium models, and their application to the marine environment has been discussed. We have examined the hypothesis that the effects of organic enrichment and physical disturbance on the structure and diversity of a macrobenthic community are additive.

Methods

Experimental design—The experiment was carried out in the mesocosm facility of the NIVA marine research station Solbergstrand, Oslofjrd, Norway. The mesocosm was described in detail by Berge et al. (1986). On 10 May 1996, muddy sand was collected by Day grab from Bjrhodenbukta, a sheltered bay in the inner part of Oslofjrd. On the same day, the sediment was placed in large (1 m²) containers where it was homogenized and used to fill 98 plastic buckets (26-cm diameter) to a depth of 20 cm. The buckets of sediment were then placed in a 5 m × 7 m indoor, epoxy resin coated concrete basin, at a constant water depth of 100 cm. The water depth was maintained using an open circulation seawater supply drawn from 60-m depth from the fjrd and allowing it to run to waste. A consequence of this continuous supply was that a small degree of larval supply was possible. The sediment in the buckets was allowed to consolidate for

Table 1. Results from ANOVA (three factor mixed model) analysis of abundance data (number of individuals/treatment) for the 16 numerically dominant taxa (disturbance and enrichment are fixed factors, the position of replicates in either block 1 or 2 is a random factor). Bold values indicate significant differences, $p < 0.05$.

Source	DF	SS	MS	F	P
<i>Heteromastus filiformis</i>					
Disturbance	6	523058	87176	1.77	0.252
Enrichment	6	231668	38611	1.03	0.484
Disturbance \times enrichment	36	739951	20554	0.63	0.915
<i>Chaetozone setosa</i>					
Disturbance	6	12353	2059	9.89	0.007
Enrichment	6	27043	4507	8.33	0.010
Disturbance \times enrichment	36	24988	694	2.00	0.020
<i>Paraonis fulgens</i>					
Disturbance	6	5439	906	8.53	0.010
Enrichment	6	4652	775	6.55	0.019
Disturbance \times enrichment	36	4952	138	0.93	0.589
<i>Nuculoma tenuis</i>					
Disturbance	6	653	109	7.84	0.012
Enrichment	6	1277	213	3.04	0.101
Disturbance \times enrichment	36	1673	46	1.31	0.213
<i>Cossura longicirrata</i>					
Disturbance	6	3601	600	16.00	0.002
Enrichment	6	3339	556	7.79	0.012
Disturbance \times enrichment	36	5218	145	0.96	0.547
<i>Pseudopolydora pauchibranchiata</i>					
Disturbance	6	1865	311	11.75	0.004
Enrichment	6	676	113	1.12	0.448
Disturbance \times enrichment	36	3077	85	0.91	0.609
<i>Goniada maculata</i>					
Disturbance	6	23	4	0.24	0.946
Enrichment	6	500	83	8.20	0.011
Disturbance \times enrichment	36	366	10	1.66	0.066
<i>Nemertea indet.</i>					
Disturbance	6	118	20	9.25	0.008
Enrichment	6	158	26	5.42	0.029
Disturbance \times enrichment	36	386	11	1.08	0.404

9 weeks before any experimental manipulation began. This enabled the reestablishment of oxygen and nutrient gradients and provided a settlement period when infaunal organisms could regain their spatial positions within the sediment before the experimental manipulations began.

Buckets were held firmly within a wooden frame and arranged in two 7 by 7 blocks of 49 buckets. From 12 July 1996, for a 12-week period, each bucket within each block was subjected to one of seven levels of organic enrichment, combined with one of seven different frequencies of physical disturbance. Thus, there was a structured matrix of 49 treatment combinations that was duplicated between blocks. Greco-latin squares were used in the experimental design so that each row within each block contained one of each disturbance intensity and one of each organic enrichment level. Additionally, the arrangement of treatments within each of the two blocks was different.

Organic enrichment was administered at the start of the experiment by a single application of powdered, dried *Ascophyllum nodosum* (L.) Le Jolis (product A120 from Algae Products A/S; maximum particle diameter 120 μm). The powdered *A. nodosum* contained 31.5% carbon and 0.9% nitrogen. After the water level in the mesocosm basin had been lowered to below the edge of the buckets, *A. nodosum*

was spread evenly across the sediment surface at seven treatment levels (P0 to P6) equivalent to 0, 12.5, 25, 50, 100, 200, and 400 g carbon m^{-2} , respectively. In inshore waters, the rate of deposition of organic matter is generally in the region of 25–75 g $\text{cm}^{-2} \text{yr}^{-1}$ (Gee et al. 1985 and references therein). Therefore, it was assumed the quantities of organic enrichment used in the current experiment represented a range of values from very low to gross enrichment. The brown alga *Ascophyllum nodosum* was chosen as it is a naturally occurring marine product and has been used successfully as a source of labile carbon for organic enrichment experiments by previous authors (e.g., Gee et al. 1985; Schratzberger and Warwick 1998).

Physical disturbance of a consistent duration and intensity was administered with a mechanical stirrer that raked the sediment surface to a depth of 2 cm. A plastic, circular disc (250-mm diameter), covered with 95 stainless steel nails (4-mm diameter), each protruding approximately 20 mm from the disc surface, was lowered onto the sediment surface and rotated at a constant speed (68 rpm). The nails on the disc were orientated at different angles, which prevented the disturbance being concentrated in certain areas and ensured a uniform disturbance across the entire sediment surface. Disturbances lasted for exactly 24 s, with a constant number of

Table 1. Continued.

Source	DF	SS	MS	F	P
<i>Diplocirrus glaucus</i>					
Disturbance	6	93	16	4.44	0.046
Enrichment	6	162	27	13.55	0.003
Disturbance × enrichment	36	322	9	3.00	0.001
<i>c. f. Syllis cornuta</i>					
Disturbance	6	45	8	2.34	0.162
Enrichment	6	24	4	1.32	0.373
Disturbance × enrichment	36	116	3	1.10	0.391
<i>Pholoe minuta</i>					
Disturbance	6	82	14	9.10	0.008
Enrichment	6	53	9	5.56	0.028
Disturbance × enrichment	36	110	3	1.36	0.178
<i>Schistomeringos caecus</i>					
Disturbance	6	51	8	3.81	0.064
Enrichment	6	45	7	1.52	0.313
Disturbance × enrichment	36	139	4	0.95	0.565
<i>Lumbrineris tetura</i>					
Disturbance	6	18	3	1.84	0.239
Enrichment	6	30	5	1.57	0.298
Disturbance × enrichment	36	92	3	1.18	0.310
<i>Anobothrus gracilis</i>					
Disturbance	6	311	52	28.82	0.001
Enrichment	6	52	9	1.92	0.224
Disturbance × enrichment	36	212	6	1.47	0.127
<i>Lumbrineris fragilis</i>					
Disturbance	6	24	4	1.63	0.284
Enrichment	6	73	12	12.03	0.004
Disturbance × enrichment	36	76	2	1.69	0.060
<i>Eteone flava</i>					
Disturbance	6	4	1	0.47	0.808
Enrichment	6	8	1	1.08	0.198
Disturbance × enrichment	36	40	1	1.46	0.132

revolutions for each disturbance event. Suspension of the mechanical stirrer from a fixed height-moveable gantry above the mesocosm basin ensured that a constant pressure and depth of disturbance was applied to all treatments. Prior to the disturbance being administered, the water level in the basin was lowered to below the edge of the buckets. This prevented loss of any fine material during periods of disturbance. After allowing approximately 1 h for any resuspended material within the disturbed buckets to settle out, the water level in the basin was raised. The physical disturbance frequencies were no disturbance (D0), once every 4 weeks (D1), once every 2 weeks (D2), once a week (D3), twice a week (D4), three times a week (D5), and every day (D6). Although more rapidly and regularly administered than in natural situations, this disturbance of the upper sediment layers may be considered as analogous to the sediment turnover caused by the movement and feeding behavior of large infaunal, deposit feeding species (e.g., the heart urchin *Brissoopsis lyrifera*).

At the end of the 12-week experimental period, the sediment in each bucket was sieved over a 500- μ m mesh. The residue was fixed in a 10% formaldehyde solution and was sorted under a binocular microscope. All animals were extracted and identified to the lowest possible taxonomic level. Environmental conditions remained constant throughout the

experiment: temperature was $7 \pm 1^\circ\text{C}$ and salinity was 34.5 ± 0.5 psu.

Data analysis—Measures of α diversity were calculated; number of species, Margalef's species richness, Pielou's evenness, and Shannon-Wiener (\log_e). Global treatment effects and pairwise interaction values for these measures were identified using a three-factor mixed model ANOVA computed using Systat version 7.0. Visual interpretation of residual plots was used to confirm that the data complied with the assumptions of the ANOVA model, e.g., homogeneity of variance. SURFER version 5.02 was used to generate contour plots for number of species using standard krigging and a low level of smoothing.

Multivariate data analyses followed the methods described by Clarke (1993) using the PRIMER version 4.0. software package (Clarke and Warwick 1994). Analysis was carried out on both untransformed and $\sqrt{\sqrt{\quad}}$ transformed data using the Bray-Curtis similarity measure to determine the effects of treatments on different components of the community. Analysis of untransformed data is sensitive to changes in the abundance of the dominant species, while analysis of $\sqrt{\sqrt{\quad}}$ transformed data detects effects on community structure generally, including changes in abundance of the lower abundance and rare species, without being unduly influenced by

dominant, high-abundance species. Two-way crossed ANOSIM (analysis of similarities) was carried out to test for treatment effects. The ANOSIM test for multivariate data is equivalent to an ANOVA test for univariate data, except that ANOSIM does not allow testing for interaction effects. Multidimensional scaling (MDS) was used to visualize patterns of community change (1) in response to physical disturbance at the seven different levels of organic enrichment and (2) in response to organic enrichment at the seven different levels of disturbance. The significance of differences between these patterns of response was tested using RELATE (Clarke et al. 1993) by calculation of the Spearman rank correlations (ρ) between two matrices and in this case between each pair of faunal similarity matrices. RELATE was then used to assess how closely patterns of response correlated to perfect seriation, by calculating the strength of correlation between the observed rank dissimilarities for the experimental biotic data with an artificially constructed rank distance matrix simulating perfect seriation (rank 0 between replicates, rank 1 between adjacent treatments etc., up to rank 6 between extreme treatments). The ρ values from this analysis (Spearman rank correlations between the biotic dissimilarity and the perfect seriation distance matrices) enabled the direct comparison of seriation strength between patterns produced at different disturbance frequencies or organic enrichment levels (Clarke, pers. comm.).

Results

Patterns in species abundance—A total of 81 taxa were represented within the mesocosm community, with the 16 numerically dominant taxa being *Heteromastus filiformis*, *Chaetozone setosa*, *Paraonis fulgens*, *Nuculoma tenuis*, *Cossura longocirrata*, *Pseudopolydora pauchibranchiata*, *Goniada maculata*, *Nemertea* indet., *Diplocirrus glaucus*, c.f. *Syllis cornuta*, *Pholoe minuta*, *Schistomeringos caecus*, *Lumbrineris tetura*, *Anobothrus gracilis*, *Lumbrineris fragilis*, and *Eteone flava* (listed in order of decreasing abundance). Of these, the abundance of six taxa was shown to be significantly affected by both physical disturbance and organic enrichment (Table 1). In ANOVAs that investigate multiple comparisons there is a possibility that, if enough tests are performed, significant values will be encountered even if the null hypothesis of no effects was true throughout. To counteract this possibility it is customary to apply a correction that reduces the p value at which a test is considered significant in line with the number of tests performed. Unfortunately, in tests such as that presented in this paper, which rely on a large number of multiple tests, in this case 48, such corrections reduce the p value to such an extent as to make the tests worthless. However, in a total of 48 tests, assuming a model of 5% of error, the number of falsely significant results is still quite small, with only three tests potentially appearing significant even if the null hypothesis

of no effects was true throughout. In Table 1 there were 19 such significant values and the probability of seeing this many significant values by chance, calculated on a single binomial model, is approximately zero. Consequently, a p value of 0.05 was maintained as to indicate situations where significant effects were likely to be occurring, although the reader should be mindful of the possibility that a small number of these significant results may have occurred by chance. For *Nemertea* indet. and the polychaetes *Paraonis fulgens*, *Phole minuta*, and *Cossura longocirrata* there was no interaction between the effects of disturbance and enrichment on the abundance of these taxa (Table 1). A significant interaction term indicated the effects of disturbance and enrichment on the abundance of the polychaetes *Diplocirrus glaucus* and *Chaetozone setosa* were not independent. Three species, the bivalve *Nuculoma tenuis* and the tube building polychaetes *Pseudopolydora pauchibranchiata* and *Anobothrus gracilis*, were significantly affected by disturbance alone, whereas a further two species, the large bodied, mobile polychaetes *Goniada maculata* and *Lumbrineris fragilis*, were affected by enrichment but not by disturbance. Graphical representation of the effects of physical disturbance and organic enrichment on the abundance of these 11 taxa is given in Fig. 1. Where effects were significant there was a general trend for abundance to be lowest where physical disturbance was most frequent. However, changes in abundance in response to different levels of organic enrichment were less clear. The abundance of most species was lowest at the highest levels of enrichment, but, the lowest levels of enrichment did not always correspond to the highest levels of abundance. For example, the abundance of *Nemertea* was highest in treatments receiving intermediate levels of enrichment. No significant effect of either disturbance or enrichment was demonstrated for the remaining five polychaete species; *Heteromastus filiformis*, c.f. *Syllis cornuta*, *Schistomeringos caecus*, *Lumbrineris tetura*, and *Eteone flava*.

At the end of the experiment, the structure and diversity of the mesocosm community from treatments that had received no enrichment and no physical disturbance was comparable to the naturally occurring community present at the collection site, Bjørnhordenbukta (see Valderhaug and Gray 1984). Abundance in treatments ranged from seven to 1194 individuals, and the number of taxa per treatment ranged from one to 36.

Patterns in diversity—All diversity measures were significantly affected by organic enrichment, but only number of species were significantly affected by physical disturbance (Table 2). Significant interaction effects between physical disturbance and organic enrichment for three diversity measures, number of species, species richness, and Shannon-Wiener index, were demonstrated by the three-factor mixed model ANOVA (Table 2). This indicated that the effects of physical disturbance and organic enrichment, on these three

Fig. 1. Contour plots demonstrating the abundance (number of individuals/treatment) of 11 numerically dominant species at different combinations of disturbance intensities and organic enrichment levels.

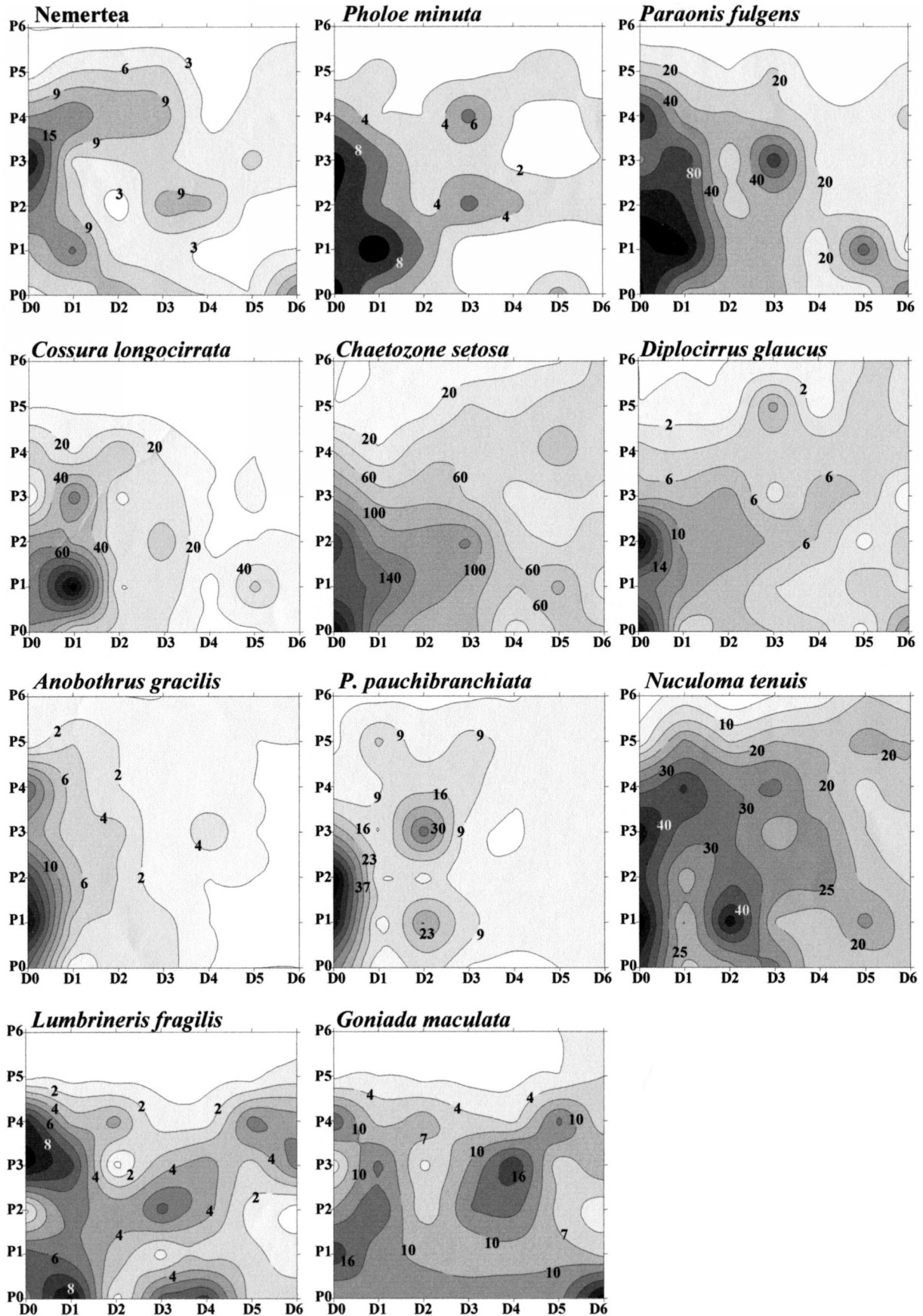


Table 2. Results from ANOVA (three factor mixed model) analysis of community structure measures (disturbance and enrichment are fixed factors, the position of replicates in either block 1 or 2 is a random factor). Bold values indicate significant differences, $p < 0.05$.

Source	DF	SS	MS	F	P
<i>Number of species</i>					
Disturbance	6	415.27	69.21	5.45	0.001
Enrichment	6	2701.41	450.23	35.44	0.001
Disturbance × enrichment	36	1313.16	36.48	2.87	0.001
<i>Number of individuals</i>					
Disturbance	6	1137535	189589	3.27	0.087
Enrichment	6	803951	133992	2.34	0.162
Disturbance × enrichment	36	1113402	30928	0.69	0.868
<i>Species richness (Margalef)</i>					
Disturbance	6	4.2444	0.7074	1.98	0.213
Enrichment	6	61.1578	10.1930	34.37	0.001
Disturbance × enrichment	36	32.2220	0.8951	3.23	0.001
<i>Shannon-Wiener diversity</i>					
Disturbance	6	1.01673	0.16946	1.23	0.405
Enrichment	6	7.60262	1.26710	22.19	0.001
Disturbance × enrichment	36	6.39821	0.17773	2.55	0.003
<i>Pielou's evenness</i>					
Disturbance	6	0.21273	0.03456	1.43	0.339
Enrichment	6	0.23660	0.03943	4.46	0.046
Disturbance × enrichment	36	0.56878	0.01580	1.10	0.392

diversity measures, were nonadditive. The contour plots in Fig. 2 demonstrate the response of the four diversity indices (number of species, species richness, Shannon-Wiener, and Pielou's evenness) to increasing levels of organic enrichment and physical disturbance. It would appear that, as the richness (number of species) becomes less important and the distribution of individuals within each species (evenness) becomes more important in the calculation of the indices, the effect of increasing the frequency of physical disturbance appears to lessen compared with the effect of increasing the amount of organic enrichment (Fig. 2, Table 2).

The rate at which diversity decreases appears to be greater in response to changes in organic enrichment than in response to increased physical disturbance (Fig. 2). The pattern observed in Fig. 2 can be seen as a subset of the pattern described by Huston (1979), with the areas of Huston's model corresponding to lower physical disturbance and lower organic enrichment not being represented in Fig. 2.

The ANOVA interaction values between the effects of physical disturbance and organic enrichment on the number of species, species richness, and Shannon-Wiener (Table 3) highlight where the effects of physical disturbance and organic enrichment act on a community either synergistically or antagonistically. In areas of no physical disturbance but high levels of organic enrichment, the diversity was lower than would be expected. However, in areas of high experimental disturbance and high levels of organic enrichment, diversity was higher than would be expected if these two factors were acting independently on the community. The interaction values demonstrate that, when acting simultaneously on a community, physical disturbance and organic enrichment can act either synergistically or antagonistically depending on the magnitudes of each factor.

An ameliorating effect, on species diversity, of physical disturbance in areas of high organic enrichment is identified

in Table 3 and demonstrated in Fig. 2. At high levels of organic enrichment (P5 and P6) increasing the physical disturbance frequency resulted in higher diversity, while in areas of low organic enrichment (P0, P1, and P2) increasing physical disturbance caused diversity to decrease. In areas of midlevel organic enrichment (P3 and P4), diversity remained relatively constant over a range of low to midfrequencies of physical disturbance (D3). In areas of low physical disturbance frequency (D0 and D1) diversity is highest in treatments with little or no organic enrichment (P0 and P1). At midfrequencies of physical disturbance (D2–D4), maximum diversity was observed in midlevel organic enrichment treatments (P2–P4). While at high physical disturbance frequencies, changes in the level of organic enrichment had little effect on diversity. The overall trend was for the level of organic enrichment at which diversity was highest to increase as the frequency of physical disturbance increased (Fig. 3). Where one type of disturbance factor was low (physical disturbance or organic enrichment) diversity decreased as the intensity of the other factor increased. However, this decrease was greatest in the combination of low physical disturbance with increasing organic enrichment (Fig. 3). This suggested that the spread of treatments chosen for organic enrichment was broader than that of the treatments chosen for physical disturbance.

Patterns in community structure—Global tests using two-way crossed ANOSIM showed significant treatment effects for both physical disturbance (untransformed; $R = 0.174$, $p = 0.001$; $\sqrt{\sqrt{}}$ transformed; $R = 0.266$, $p = 0.000$) and organic enrichment (untransformed; $R = 0.121$, $p = 0.003$; $\sqrt{\sqrt{}}$ transformed; $R = 0.180$, $p = 0.001$).

Faunal composition of the test community varied in response to different intensities of physical disturbance or amounts of organic enrichment. These differences in com-

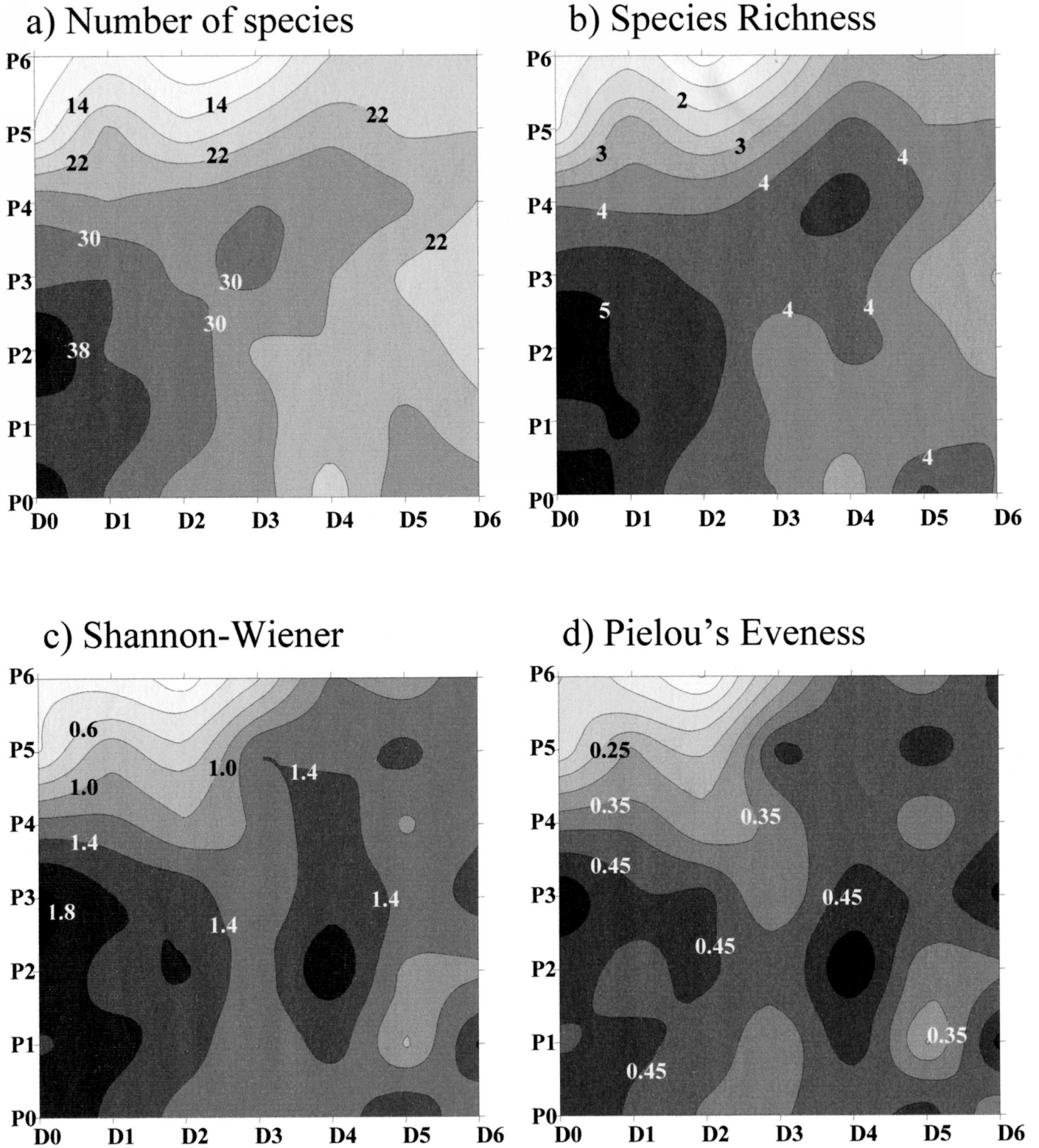


Fig. 2. Contour plots demonstrating diversity (number of species, Margalef's species richness, Shannon-Wiener, Pielou's evenness) at different combinations of disturbance intensities and organic enrichment levels. (P0–P6 = organic enrichment; D0–D6 = physical disturbance).

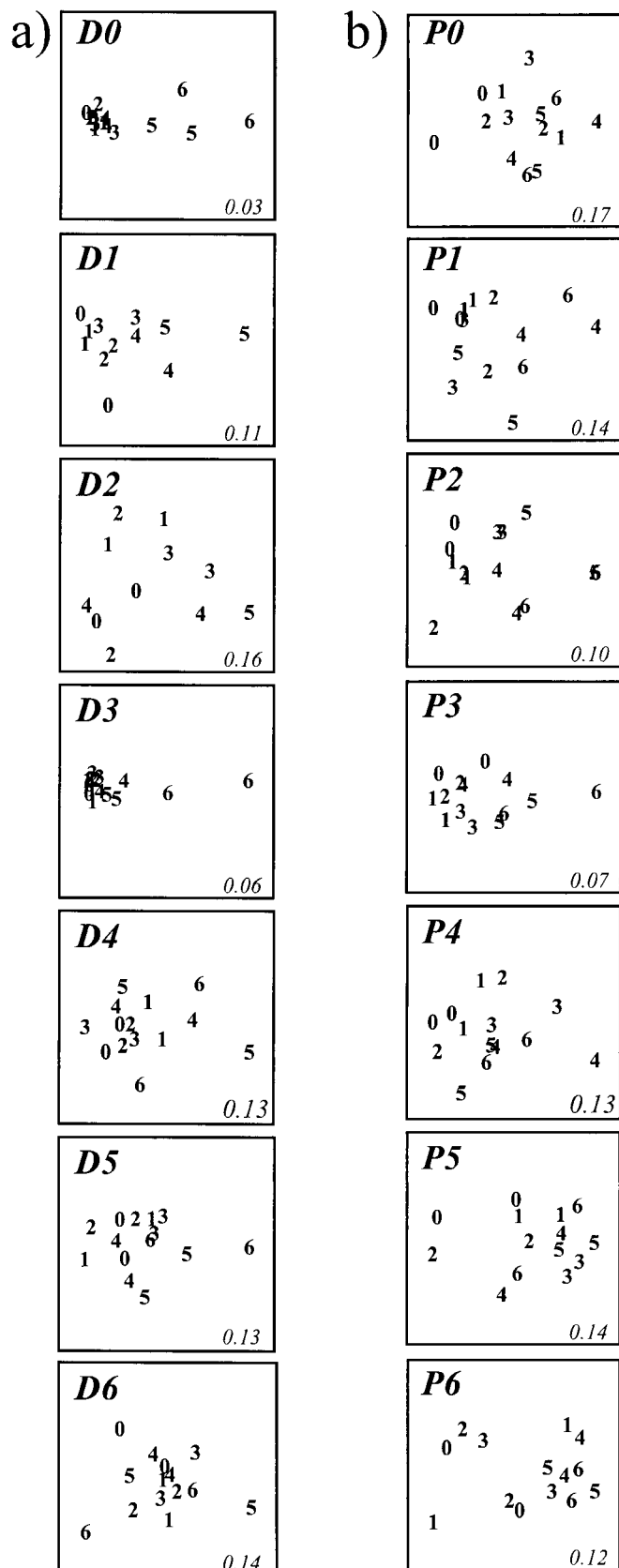


Fig. 3. Nonmetric multidimensional scaling (MDS) ordinations of macrofaunal abundance on $\sqrt{\sqrt{}}$ transformed data comparing (a)

Table 3. Interaction terms from ANOVA showing pair-wise comparisons of disturbance and organic enrichment treatment levels.

	D0	D1	D2	D3	D4	D5	D6
(a) Number of species							
P0	6.6	-0.9	-0.5	-0.8	-5.7	0.0	1.2
P1	1.9	5.4	2.3	-1.5	-4.4	-1.2	-2.5
P2	8.1	0.6	2.0	-2.3	0.3	-3.5	-5.3
P3	-0.2	1.8	2.2	3.4	0.0	-3.3	-4.0
P4	0.8	-3.7	0.7	1.4	0.5	0.2	-0.1
P5	-9.6	0.4	-3.2	2.0	4.1	2.8	3.5
P6	-7.6	-3.6	-3.7	-2.0	5.1	4.8	7.0
(b) Margalef's species richness							
P0	0.9	-0.1	-0.1	-0.1	-1.0	0.2	0.0
P1	0.2	0.8	0.4	-0.3	-0.6	-0.4	-0.0
P2	1.1	0.0	0.6	-0.5	0.2	-0.5	-0.9
P3	0.2	0.2	0.5	0.4	-0.1	-0.6	-0.6
P4	0.2	-0.5	0.0	0.3	0.1	-0.1	-0.0
P5	-1.5	0.1	-0.6	0.5	0.6	0.6	0.4
P6	-1.1	-0.5	-0.8	-0.3	0.8	0.7	1.1
(c) Shannon-Wiener (\log_e)							
P0	0.3	-0.0	0.0	-0.1	-0.4	0.2	-0.1
P1	0.1	0.3	0.2	-0.1	-0.1	-0.3	0.1
P2	0.3	-0.1	0.4	-0.1	0.2	-0.3	-0.4
P3	0.3	0.0	0.3	-0.2	-0.1	-0.2	-0.2
P4	0.1	0.0	-0.1	0.1	-0.0	-0.2	0.0
P5	-0.7	-0.1	-0.3	0.5	0.1	0.4	0.1
P6	-0.4	-0.1	-0.4	-0.2	0.3	0.4	0.5

community structure constituted a “community response pattern” to either of the two experimental variables and these patterns are represented two-dimensionally as MDS ordinations (Fig. 3). As an approach to identifying interaction between the effects of physical disturbance and organic enrichment on multivariate aspects of community structure, RELATE was used to test whether the “community response patterns” to organic enrichment were influenced by changing the intensity of physical disturbance (Table 4), or whether the “community response patterns” to physical disturbance were influenced by changing the level of organic enrichment.

When using $\sqrt{\sqrt{}}$ transformed data in the RELATE analysis, there were a high number of significant correlations between the “community response patterns” of the different physically disturbed treatments, each subjected to the same range of organic enrichment (Table 4). This showed that, for lower abundance and rarer species, the response to organic enrichment was generally consistent regardless of the physical disturbance frequency. However, when using untransformed data in the RELATE analysis, fewer significant cor-

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the effect of organic enrichment on community response between areas subjected to different physical disturbance frequencies and (b) the effect of physical disturbance on community response between areas subjected to different organic enrichment levels. (Not all enrichment data are included in MDS for D1 and D2—see text for details.) Stress values in italics. (0 = low physical disturbance/organic enrichment; 6 = high physical disturbance/organic enrichment)

Table 4. Pairwise comparisons of the multivariate community structure generated by a gradient of organic enrichment in single disturbance regimes using RELATE on (a) untransformed and (b) $\sqrt{\sqrt{\quad}}$ transformed data and Bray-Curtis similarities. Bold values indicate significant correlations in the community structure in the treatments compared, $p < 0.05$. Results represented as ρ -values with p -values for a test of “no relationship” in parentheses.

	D0	D1	D2	D3	D4	D5	D6
(a) Untransformed data							
D1	0.33 (0.06)						
D2	0.62 (0.00)	0.36 (0.05)					
D3	0.70 (0.00)	0.32 (0.05)	0.64 (0.00)				
D4	0.35 (0.02)	-0.04 (0.57)	0.24 (0.09)	0.23 (0.08)			
D5	0.15 (0.22)	-0.03 (0.49)	0.24 (0.13)	0.22 (0.14)	-0.06 (0.60)		
D6	-0.14 (0.82)	-0.05 (0.56)	-0.33 (1.00)	-0.24 (0.97)	-0.14 (0.79)	-0.23 (0.94)	
(b) $\sqrt{\sqrt{\quad}}$ transformed data							
D1	0.64 (0.00)						
D2	0.85 (0.00)	0.65 (0.00)					
D3	0.60 (0.01)	0.52 (0.01)	0.61 (0.00)				
D4	0.44 (0.02)	0.39 (0.03)	0.45 (0.02)	0.16 (0.20)			
D5	0.50 (0.01)	0.09 (0.29)	0.44 (0.02)	0.36 (0.04)	0.02 (0.43)		
D6	0.21 (0.15)	0.46 (0.02)	0.23 (0.12)	-0.09 (0.62)	0.36 (0.04)	-0.17 (0.83)	

relations were observed (Table 4). This suggested that changes in the relative abundance of numerically dominant species, in response to organic enrichment, were affected by different physical disturbance frequencies.

When using both untransformed and $\sqrt{\sqrt{\quad}}$ transformed data, very few significant correlations were observed between the “community response patterns” of different organically enriched treatments, each subjected to the same range of physical disturbance frequencies. Pairwise comparisons using RELATE showed only one significant correlation when using untransformed data (P0 vs. P5) and two significant correlations when using $\sqrt{\sqrt{\quad}}$ transformed data (P2 vs. P3 and P1 vs. P4). This suggests that the response to physical disturbance of both the numerically dominant species and of the low abundance and rare species was affected by the amount of organic material received.

To examine the pattern of community response to either organic enrichment or physical disturbance in more detail, the ordinations of community structure in Fig. 3 were compared with a pattern that observed perfect seriation. RELATE was used to test for significant correlations (Table 5). At low physical disturbance frequencies (D0–D3), the community response to increasing levels of organic enrichment was serial, with communities being most similar to each other when the differences between their respective levels of organic enrichment are small. At high physical disturbance frequencies (D4–D6), seriation breaks down (Table 5a). A

serial response to physical disturbance was shown mostly in midorganic enrichment treatments (P2 and P3) (Table 5b). Additional serial response was observed in P0 and P5 for untransformed data and in P6 for $\sqrt{\sqrt{\quad}}$ transformed data.

In two of the ordinations presented in Fig. 3 (D1 and D2) some of the highest organic enrichment levels were omitted from the ordinations. The community structure in these treatments was very different to that in the other treatments compared; consequently, the latter were tightly clustered in the MDS. By omitting the high enrichment data it was possible to visualize the patterns contained within the remaining data more clearly. For calculation of seriation values all data were included.

Discussion

The results of this experiment were consistent with those predicted by the dynamic equilibrium model (Huston 1979), and, therefore, this model may serve as a basis of an explanation for the relationship between diversity, physical disturbance, and organic enrichment.

The discrepancy between the predicted surface plot of the dynamic equilibrium model (Huston 1979) and the plots generated from actual data (Fig. 2a,b) may be due to a number of factors, acting singularly or in combination. First, any sediment collected from the field that contains a viable fauna will have a preexisting level of organic material. Conse-

Table 5. R -values from RELATE test of seriation. Bold values indicate significant correlations between community responses observed in actual data and a similarity matrix observing perfect seriation, $p < 0.05$.

(a) Community response to changes in organic enrichment level at different frequencies of physical disturbance							
Disturbance frequency	D0	D1	D2	D3	D4	D5	D6
Untransformed data	0.377	0.257	0.215	0.403	-0.024	0.006	0.025
$\sqrt{\sqrt{\quad}}$ transformed data	0.475	0.467	0.400	0.387	0.148	0.108	0.045
(b) Community response to changes in physical disturbance frequency at different levels of organic enrichment							
Organic enrichment level	P0	P1	P2	P3	P4	P5	P6
Untransformed data	0.378	0.119	0.384	0.329	0.102	0.341	-0.018
$\sqrt{\sqrt{\quad}}$ transformed data	0.152	0.190	0.364	0.449	0.014	0.100	0.230

quently, it is not possible to produce treatments with no organic material, and this will, therefore, truncate the response surface of Huston's model. Similarly, the removal of the sediment from the field and its collection in the treatment buckets will result in some physical disturbance of the sediment and resident fauna. Therefore, the reestablished assemblage was a nonequilibrium abstraction of the natural one and was in a state of recovery from this disturbance at the start of the experiment, 9 weeks later. Physical disturbance would also be introduced by the bioturbation generated by organisms already present within the sediment. This bioturbation, together with disturbance due to collection, meant it was not possible to produce treatments with no physical disturbance, and this will truncate the response surface of Huston's model. The response surface observed for number of species in Fig. 2 may, therefore, be seen as a subset of the predicted response surface presented by Huston's model, with the areas of his model corresponding to zero/low disturbance and organic enrichment absent from the response surface in Fig. 2.

An additional discrepancy between Huston's model and the response surface in Fig. 2a may have resulted from the pragmatic way in which the treatment levels were chosen. Axes units were not assigned to Huston's conceptual model and it is, therefore, difficult to determine the appropriate scale and spread for each of the two factors. The spread of treatments chosen for both organic enrichment and physical disturbance represented a subset of a larger disturbance or enrichment gradient. Although their relative positions were determined, the exact position of experimental treatments on the larger gradients was unknown. Therefore, when describing the frequency of physical disturbance, terms such as "high" or "low" are relative to other treatments rather than to field disturbances or the disturbance effects of organic enrichment. The levels used for organic enrichment were justified in the methods and were expected to correspond to naturally occurring high and low levels of enrichment. Additionally, diversity appeared to decrease more rapidly in response to increased organic enrichment than to increased physical disturbance. This may also have resulted from the pragmatic way in which treatment levels were selected. Prior to this experiment, it was impossible to know what frequency of disturbance equated to any specified amount of organic enrichment in terms of impact on the macrobenthic community. The relative rates at which changes in disturbance and enrichment altered diversity were also unknown. Therefore, the severity of the gradient between low (P0) and high (P6) organic enrichment treatments may have been greater than that of the gradient between low (D0) and high (D6) physical disturbance treatments.

In addition to supporting the predictions of the dynamic equilibrium model, this paper has also shown that the effects of physical disturbance and organic enrichment do not act on diversity independently. Diversity was lower than expected assuming an additive model when low frequencies of physical disturbance acted in conjunction with high levels of organic enrichment or when high frequencies of physical disturbance were combined with low levels of organic enrichment. Diversity was higher than expected when both disturbance and enrichment were either high or low.

The interaction between physical disturbance and organic

enrichment may have several causes. Physical disturbance may increase the depth of oxygen penetration in enriched sediments, supplying the increased oxygen demand of microbial decomposers as the additional organic material is processed. This will reduce the impact of oxygen depletion on species of macrofauna sensitive to low oxygen levels, while also stimulating the activity of aerobic microbial decomposers and accelerating carbon processing. Hulthe et al. (1998) observed that fresh material degrades at the same rate in oxic and anoxic conditions, but old buried material degrades 3.6 times faster in oxic conditions than in anoxic conditions. Physical disturbance may bury fresh material for anoxic degradation and expose old buried material to oxic conditions, thus enhancing organic carbon oxidation in marine sediments. Alternate exposure of material to the activities of both oxic and anoxic microorganisms through physical disturbance will result in greater carbon degradation than when material is subjected to a constant oxic or anoxic regime (Aller 1994). The idea that physical disturbance prevents oxygen depletion may be part of the reason why the presence of *Beggiatoa* sp. mats were limited to treatments with high organic enrichment and little or no disturbance. The presence of this bacterial mat has been associated with eutrophic conditions and severe oxygen depletion (Sampou and Oviatt 1991), and its presence in grossly enriched treatments was expected. Consequently, the absence of *Beggiatoa* sp. from the high organic treatments that had received some physical disturbance may have been as a result of increased sediment oxygenation. What is more likely, however, is that a combination of increased sediment oxygenation and the physical disruption of these mats as a result of the disturbance prevented their formation in physically disturbed areas. In field conditions, it has been shown that interactions between physical disturbance and organic enrichment occur when physical disturbance of the sediment surface causes the resuspension of the organic material and results in the removal of that material via lateral water movements (e.g., Guidi-Guilvard and Buscail 1995). In the current study, this final mechanism would have had minimal effect because, after disturbance had been administered, disturbed sediment was allowed to settle before the water level was raised and the treatments exposed to lateral water movement. Consequently, the results from the current study would suggest that lateral removal of organic material is not the only mechanism by which physical disturbance ameliorates the effects of organic enrichment. Processes such as increased sediment oxygenation are also important. Previous studies using field experiments and observations have prompted authors to advocate the use of both direct sediment disturbance (e.g., ploughing) and the addition of bioturbating species as methods for "reconditioning" organically polluted sediments (e.g., Chareonpanich et al. 1994). By showing that, in a laboratory experiment, sediment disturbance can offset the damaging effects of high levels of organic material deposited on the benthos, this paper supports the conclusions of these authors.

Examining the combined effects of physical disturbance and organic enrichment on the abundance of the numerically dominant species revealed differences in the way species respond to physical disturbance and organic enrichment. As

was predicted by Brenchley (1981), tube building species such as *Anobothrus gracilis* and *Pseudopolydora pauchibranchiata* were shown to be extremely sensitive to increases in the frequency of physical disturbance. This sensitivity is assumed to be a result of either damage to individuals or the failure of organism to regain/maintain their position within the sediment during or after disturbance. *Lumbrineris fragilis* and *Goniada maculata* are large, mobile species and showed no such intolerance to physical disturbance. However, their abundance was significantly reduced in areas receiving the highest levels of organic enrichment. These results concurred with the conclusions of Pearson and Rosenberg (1978) in that *A. gracilis* and *P. pauchibranchiata* were typical of "transitory" or "second order progressive" species. It is likely that the low levels of oxygen, characteristic of extremely enriched environments, prevented larger species, with relatively small body surface to volume ratios and no specialized respiratory apparatus, from persisting in these areas. A second species of *Lumbrineris* was recorded in the current study. *Lumbrineris tetura* was generally smaller than *Lumbrineris fragilis*, and this size difference may explain why the abundance of the former was not significantly reduced by increased organic enrichment. In general, it seems that an organism's tolerance to physical disturbance is influenced by its level of mobility, while tolerance to the deoxygenation associated with organic enrichment is influenced by an organism's body surface to volume ratio. It may be assumed, therefore, that species of limited mobility and with no specialized branchial structures would be significantly affected by increases in both physical disturbance and organic enrichment. In the current study, the abundance of three taxa fitting these criteria was shown to do just that, with the abundance of *Nemertea*, *Pholoe minuta*, and *Cossura longocirrata* decreased in response to an increase in both disturbance and enrichment. Two species that also demonstrated significant changes in abundance in response to both disturbance and enrichment were the polychaetes *Chaetozone setosa* and *Diplocirrus glaucus*; however, statistical analysis demonstrated a significant interaction between the two factors. In treatments combining high levels of both enrichment and disturbance, their abundance was higher than would have been expected if both factors had been acting independently. *Chaetozone setosa* possess many long, thin branchial filaments, while *Diplocirrus glaucus* has eight stout branchial filaments in addition to a papilled body surface. It is possible that these species used their breathing apparatus/adaptations to capitalize on any oxygenation resulting from increased physical disturbance. However, no such interaction between disturbance and enrichment was observed for the abundance of *Paraonis fulgens*, despite its possessing 22 pairs of small digitate gills. It may have been that *P. fulgens* was more susceptible to damage from physical disturbance than either *C. setosa* or *D. glaucus*. Alternatively, as the gills of *P. fulgens* have a smaller surface area to volume ratio than those of *C. setosa* or *D. glaucus*, the branchial apparatus of *P. fulgens* may have been insufficient to benefit fully from the possible increase in oxygen due to increased physical disturbance.

The effects of increasing levels of physical disturbance on the community structure of samples treated with organic ma-

terial were also complex. When organic enrichment levels were either high or low, increasing the frequency of disturbance did not have a predictable, serial effect. Serial changes in community structure as an effect of increasing physical disturbance were only observed at intermediate (25 and 50 g cm⁻²) organic enrichment levels. In the field the supply of organic material to coastal sediments is highly variable, both temporally and spatially. Additionally, there are many sources of organic material, some from large-scale inputs (e.g., algal blooms, benthic primary production, terrigenous material from riverine input) and some that operate at smaller, more localized scales (e.g., fish/mammal carcasses, macroalgal detritus). The results presented in this paper illustrate the importance of considering this natural variability in the supply of organic material when predicting or assessing the effect of physical disturbance on benthic communities. Coastal zone management often requires monitoring of the effects of both physical disturbance, e.g., demersal fishing and dredging, and organic enrichment, e.g., fish farm waste. The results presented here emphasize that these monitoring efforts should not address single disturbance types in isolation but should consider all environmental conditions that may alleviate or exacerbate any community response.

Localized forms of physical disturbance are common in fine sediments and occur at a range of scales and frequencies. Large-scale disturbances (e.g., natural events such as storms or anthropogenic impacts such as trawling or dredging) cover large areas but may be relatively infrequent, allowing extended periods of recovery between disturbances. On a smaller scale, bioturbation by large macrofaunal organisms have been shown to have a considerable effect on both the associated macrofaunal and meiofaunal communities (e.g., Austen et al. 1998; Widdicombe and Austen 1999). In areas sheltered from large-scale hydrodynamic disturbances, the seasonal and spatial patchiness in the distribution of bioturbating macrofauna may increase the heterogeneity within an otherwise homogeneous area, in accordance with the spatial-temporal mosaic theory (Grassle and Morse-Porteous 1987). In addition, the interactive effects observed in this study suggest that the frequency of physical disturbance caused during bioturbation will both structure the fauna and affect the manner in which that fauna responds to changes in organic enrichment. Consequently, such bioturbation induced community heterogeneity will be exacerbated by variability in the supply of organic material. Variable nutrient input and hydrodynamic features, such as internal waves (Lennert-Cody and Franks 1999) may act to concentrate planktonic organisms, resulting in a patchy supply of organic material to the benthos. Additionally, physical structures caused by macrobenthic organisms, e.g., feeding pits, tubes, expulsion mounds, can act to increase variability by further concentrating or dissipating organic material (Yager et al. 1993).

This study has demonstrated experimentally a relationship between physical disturbance, organic enrichment, and diversity in marine benthic communities, consistent with the dynamic equilibrium model. It has also shown that the effects of physical disturbance and organic enrichment do not act independently on the abundance of some species, benthic community structure, and diversity. However, in order to ful-

ly accept the generality of these conclusions, it is imperative that further evidence demonstrating the effects of physical disturbance and organic enrichment on benthic infaunal communities is obtained from naturally occurring field situations. Until such validation is available, the results presented here should be used with an awareness for the potential limitations of mesocosm experimental approaches, particularly when applied to community processes. In particular, recovery after disturbance plays an important role in setting levels of diversity in benthic communities (e.g., Grassle and Morse-Porteous 1987). Owing to restricted immigration, the importance of this process within mesocosm systems is reduced, while the influence of an individual organisms' tolerance to a particular perturbation is increased. The main consequence of this is to increase the scale at which the experiment is relevant with small-scale disturbances in mesocosm systems being analogous to much larger events in the field (Widdicombe 2001). An additional artifact is the inability of some taxa to persist within mesocosms. The benthic assemblages maintained within the Solbergstrand mesocosm have been shown to have higher faunal densities and lower species diversities than locally occurring field communities (Widdicombe 2001) with the majority of the taxa missing from the mesocosm being crustaceans. However, community structure analysis has demonstrated that the polychaete assemblage was a good approximation of that recorded in the field. With the majority of the conclusions drawn from the current study having been concentrated on the responses of polychaete fauna, it may be assumed that the results presented here are robust and have relevance to field situations.

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