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Comparison of the response of meio- and macrobenthos to disturbance and organic enrichment

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Abstract

The effects of the interaction between physical disturbance and organic enrichment with respect to various aspects of subtidal meiobenthic nematode community structure have been examined in a large-scale mesocosm experiment. The relationship between meiobenthic and macrobenthic community structure within this experiment has been explored. Meiofauna and macrofauna showed similar and strongly related responses. Highest diversity was observed in treatment combinations of low levels of disturbance and enrichment and this supports the "Dynamic Equilibrium Model" of Huston [Huston, M.A., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.]. Faunal community structure was more variable at treatment combinations of low levels of disturbance and high levels of organic enrichment. Physical disturbance subdued the effects of high levels of nutrient enrichment. The meio-macrobenthic comparison has been extended to other studies where both meiofaunal and macrofaunal responses have been determined. The response of meiobenthos is often, but not always, the same as that of macrobenthos. These inconsistencies can probably be explained by the constraints of the experimental design of the mesocosm, where macrobenthic recruitment is not possible, as well as the different ecology of these two faunal groups.
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1. Introduction

A study has demonstrated (Widdicombe and Austen, 1999) that macrobenthic communities respond to disturbance according to the "Intermediate Disturbance Hypothesis" (IDH) of Connell (1978). There is also some supporting evidence that macrobenthic communities respond to increased productivity according to the "Intermediate Productivity Hypothesis" of Grime (1973a,b). These hypotheses predict maximum diversity at intermediate levels of disturbance and productivity respectively. 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 between low and intermediate levels of both productivity and disturbance. There is little empirical support for the dynamic equilibrium model as the necessary, multi-factorial experiments are intrinsically more difficult to conduct than experiments which manipulate only a single factor. Recently, a mesocosm experiment demonstrated an interactive effect of physical disruption and organic enrichment on macrobenthic diversity and

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community structure (Widdicombe and Austen, 2001). The diversity response corresponded approximately to the dynamic equilibrium model.

Meiobenthic communities are less frequently studied than macrobenthic communities but there is increasing evidence that meiobenthos also conform to the IDH (Widdicombe and Austen, 2005). As well as being separated on the basis of size, meiobenthos and macrobenthos each have a series of distinctive ecological and evolutionary characteristics which suggest that the demarcation between the two groups is a meaningful one (Warwick, 1984). Meiobenthic fauna are motile and dispersal takes place probably throughout their lifetime but particularly as adults; they have direct development with no larval stage, generation time is generally less than one year and reproduction is semelparous with small broods; adults reach an asymptotic body size and finally, resource partitioning appears to be based on food particle selection (size, shape, quality) as there is discriminate use of particles based on trophic resources. Macrobenthic fauna are sedentary or motile; they mostly have a planktonic larval stage and high dispersal takes place in this phase of their life-cycle; reproduction is usually iteroparous with comparatively high numbers of egg and larval production; adults continue growth throughout their life and resource partitioning is based on spatial segregation and particle size selection although feeding is mostly non-selective. We might expect these contrasting components of the benthos to have different responses to disturbance. For example, meiofauna do not appear be as impacted as macrofauna by physical disturbance of the sediment in which they live (Warwick et al., 1990). Macrofauna do not appear to be able to re-establish as rapidly as meiofauna in such disturbed sediment. Equally, meiofauna are not able to recruit rapidly compared to macrofauna if there is large scale disturbance due to lack of dispersive meiofaunal life stages. We have carried out a series of previously published experiments to investigate the effects of organisms with different types of bioturbation activity on the structure of the associated subtidal meiobenthic nematode (Austen and Widdicombe, 1998; Austen et al., 1998), and macrobenthic communities (Widdicombe and Austen, 1998, 1999; Widdicombe et al., 2001). However formal statistical comparisons of the macrobenthic and meiobenthic nematode responses to these biotic disturbances have not yet been carried out.

In this paper we test the hypothesis that meiobenthic and macrobenthic communities respond in the same way to disturbance. We focus particularly on whether meiobenthic communities also conform to the dynamic equilibrium model. We do this by examining in detail whether meiobenthic nematodes respond to the interactive effects of physical disturbance and productivity within a mesocosm experiment and comparing their response with that of the macrobenthos from the same experiment. Finally, we compare macrobenthic and meiobenthic responses to biotic disturbances in previously published mesocosm experiments.

2. Methods

2.1. Productivity-disturbance experiment

Experimental methods have been published in detail in Widdicombe and Austen (2001) and are summarised here. The experiment was carried out in the mesocosm facility of the NIVA marine research station Solbergstrand, Oslofjord, Norway. On 10 May 1996, muddy sand was collected by Day grab from Bjørhodenbukta in Oslofjord, placed in large (1 m^2) containers where it was homogenised 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 × 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 sea water supply drawn from 60 m depth from the fjord 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 nine weeks before any experimental manipulation began. This allowed re-establishment of both chemical structure and recovery and re-establishment of fauna after the disturbance experienced during sediment collection.

Buckets were held firmly within a wooden frame and arranged in two 7 × 7 blocks of 49 buckets. Within each of the blocks, 49 treatments were allocated to the buckets consisting of one of 7 levels of organic enrichment combined with one of 7 different frequencies of physical disturbance administered over a 12 week period from 12 July 1996. 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.

Productivity was increased through organic enrichment administered at the start of the experiment by a single application of powdered, dried *Ascophyllum nodosum* (L.) Le Jol. (product A120 from Algea Products A/S, Kristiansund, Norway; maximum particle diameter 120 μm) at seven treatment levels (P0 to P6) equivalent to: 0, 12.5, 25, 50, 100, 200 and 400 g carbon m^{-2}, respectively.

Physical disturbance, of a consistent duration and intensity, was administered with a mechanical stirrer which raked the sediment surface to a depth of 2 cm for exactly

24 s with a constant number of revolutions (68 rpm) of the circular rake for each disturbance event (Fig. 1). Prior to the disturbance being administered, the water level in the basin was lowered to below the edge of the buckets and returned to normal levels approximately 1 h later. This prevented loss of any fine material during periods of disturbance. The physical disturbance frequencies were: no disturbance (D0), once every four weeks (D1), once every two 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 behaviour of large infaunal, deposit feeding species (e.g. the heart urchin *Brissopsis lyrifera*) or of disturbance caused by demersal fishing gear or a violent storm.

Environmental conditions remained constant throughout the experiment: temperature was 7 ± 1 °C and salinity was 34.5 ± 0.5 psu.

At the end of the 12 week experimental period, three meiofauna sediment cores were sampled randomly from each bucket using a 50 ml sawn-off syringe (internal diameter 2.6 cm) pushed into the sediment to a depth of 5 cm. The remainder of the sediment was sieved over a 0.5 mm mesh and the macrofauna from the residue were extracted, identified and enumerated. The macrobenthic analysis was published in Widdicombe and Austen (2001). Meiofaunal cores were combined and fixed in a 10% formaldehyde solution. Meiofauna were extracted from the sediment using flotation in Ludox TM colloidal silica (McIntyre and Warwick, 1984) with a 63 μm sieve. Samples were placed in 10% glycerol, evaporated to anhydrous glycerol, and then mounted on slides for microscopic identification and enumeration of all meiobenthic nematodes to lowest practical taxonomic level. For those genera where it is difficult to distinguish species among juvenile or female specimens, or where only female or juvenile specimens were observed, meiobenthic nematodes were identified only to genus level.

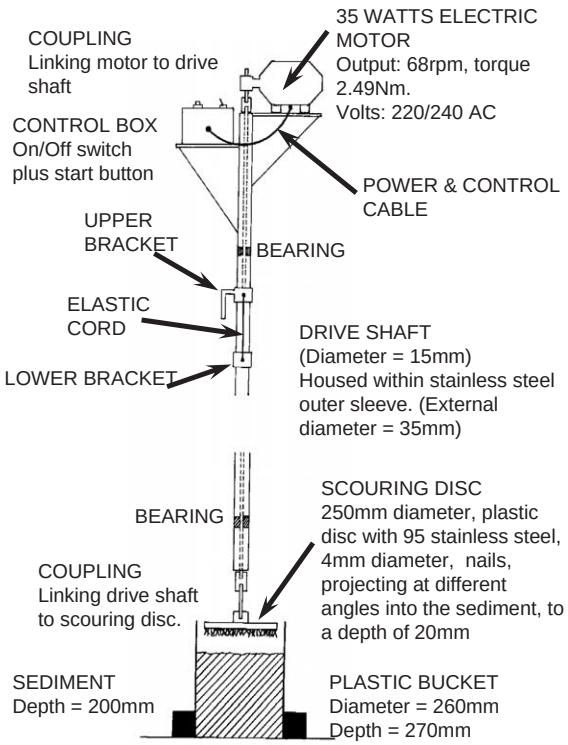

Fig. 1. Mechanical stirrer used to administer physical disturbance, of a consistent duration and intensity, in the productivity-disturbance experiment.

2.2. Biotic disturbance experiments

Experimental methods have been published in detail in Austen and Widdicombe (1998), Austen et al. (1998), Widdicombe and Austen (1998, 1999) and Widdicombe et al. (2001) and are summarised here. Within the same mesocosm system in Solbergstrand described above, four replicate boxes (1 m^2) were filled with fresh sediment collected using a Day grab from Bjørhodenbukta, Oslofjord. Boxes were then partitioned using mesh cages. Sediment and fauna were left for 9 days to allow the fauna and chemical gradients to start to re-establish after the disturbance created during the set-up. Different bioturbating macrobenthic species were added to the caged areas at low and high densities to create different types and intensities of biotic disturbance treatments. The species used were *Brissopsis lyrifera*, a sub-surface bulldozing, non-selective deposit feeding heart urchin, *Nuculoma tenuis*, a smaller sub-surface deposit feeding bivalve, and *Abra alba*, a sediment surface filter and deposit feeding bivalve. The mesh used allowed movement of meiobenthic nematodes, other meiofauna and small macrofauna between treatments and surrounding sediment but prevented the added species from escaping. The experiments were left for just under 20 weeks after which time macro and meiobenthos were sampled, extracted from the sediment and identified as above. The response of the fauna to the different types of disturbance was analysed in previously published papers (op. cit.) and in this particular study, the macrobenthic and meiobenthic responses have been compared.

2.3. Data analysis

Contour plots were used to examine the diversity response of meiobenthic nematodes to interactive effects of increasing productivity and physical disturbance. SURFER version 5.02 was used to generate contour plots for SΔ+ using standard krigging and a low level of smoothing. SΔ+ is a modified species richness measure that incorporates taxonomic relatedness between all species and was used as the diversity measure (Warwick and Clarke, 2001). It represents the sum of average taxonomic distance between all species and was determined using the PRIMER version 5.2 software package (Clarke and Warwick, 2001).

Multivariate data analysis followed methods described by Clarke and Warwick (2001) and Clarke (1993) using the PRIMER version 5.2 software package (Clarke and Warwick, 2001). In all statistical tests, a significance level of $p<0.05$ was used. Analysis was carried out using a range of data transformations to determine the effects of the treatments on different aspects of the community: (a) no transformation—sensitive to changes in the abundance of the dominant species, (b) √ transformation—detects effects on community structure generally without being unduly influenced by either dominant or rare species, (c) √√ transformation—sensitive to changes in abundance of the lower abundance and rare species. Similarity matrices for faunal data were constructed using the Bray Curtis similarity index based on faunal abundances. RELATE tests were used to compare faunal responses in the different experiments and among treatments. RELATE (Clarke et al., 1993) calculates the Spearman rank correlations (ρ) between two similarity matrices and in this case between each pair of faunal similarity matrices. The significance of this correlation is then tested by a randomisation/permutation test.

2.4. Effects of productivity and disturbance

Similarity matrices were constructed for subsets of all of the productivity treatments at each level of disturbance and for subsets of all of the disturbance treatments at each level of productivity. Using these matrices RELATE was used to compare the meiobenthic nematode community structure across the range of productivity treatments between each level of disturbance and then to compare the meiobenthic nematode community structure across the range of disturbance treatments between each level of productivity. RELATE was then used to asses how closely patterns of response correlated with 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, personal communication).

2.5. Multivariate comparison of macrobenthic and meiobenthic nematode community responses to disturbance

Pair-wise Bray–Curtis similarities (untransformed, root and fourth root transformed data) between mac-

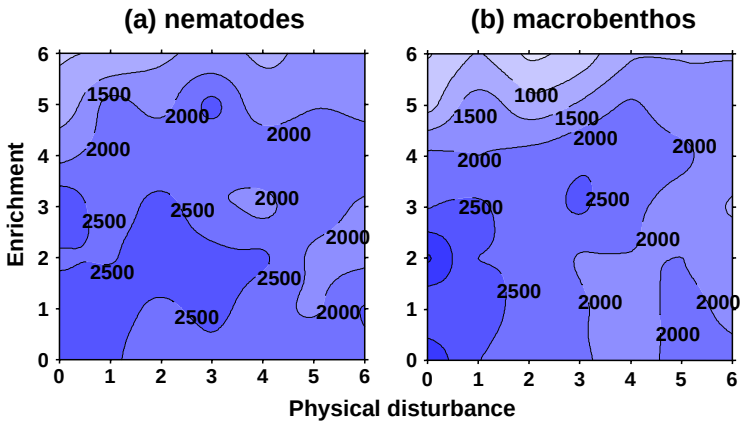

Fig. 2. Contour plots demonstrating diversity (SΔ+) at different combinations of disturbance intensities and organic enrichment levels. (P0–P6 = Organic Enrichment; D0–D6 = Physical Disturbance).

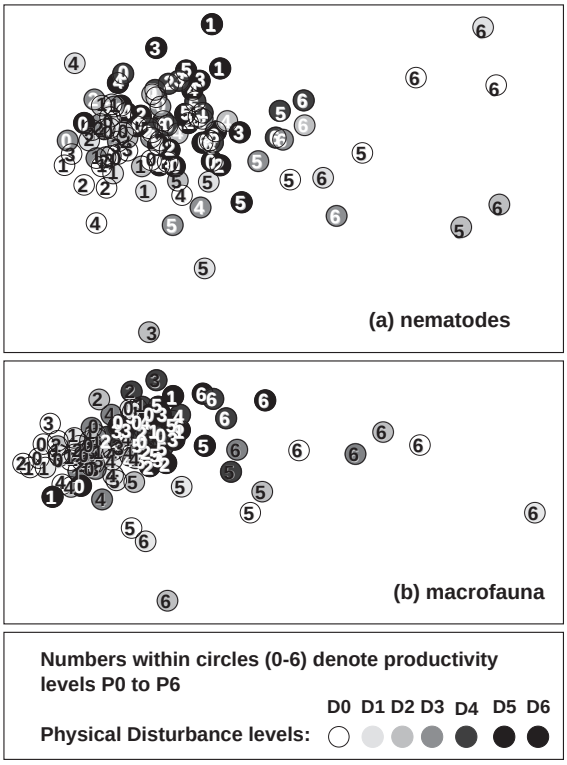

Fig. 3. Non-metric multidimensional scaling (MDS) ordination of root transformed faunal abundance data comparing the combined effects of different levels of organic enrichment and physical disturbance on community response of (a) meiobenthic nematodes and (b) macrobenthos. Stress values were 0.19 and 0.11, respectively. (0 = low physical disturbance/organic enrichment; 6 = high physical disturbance/organic enrichment).

robenthic samples were calculated and similarity matrices constructed. RELATE was used to compare these matrices with the equivalent matrices calculated from the meiobenthic nematode abundance data.

3. Results

3.1. Productivity-disturbance experiment

Highest levels of meiobenthic nematode diversity (SΔ+) were observed at levels of physical disturbance from D0 to D4 combined with organic enrichment levels from P0 to P3 (Fig. 2a). The contour plot was similar to that for macrobenthos (Fig. 2b) except that maximum diversity was generally at lower levels of disturbance (D0–D1).

In the MDS plots (Fig. 3) there is again a similar community response of the meiobenthos and macrobenthos. High physical disturbance treatments generally cluster quite closely regardless of the combined

Table 1
Results from RELATE analysis for correlation of meiobenthic nematode community structure within different treatments under a range of different data transformations

Untransformed data

	D0	D1	D2	D3	D4	D5
D1	**0.77**					
D2	**0.60**	**0.40**				
D3	**0.57**	**0.44**	**0.38**			
D4	**0.50**	**0.34**	**0.16**	**0.43**		
D5	−0.19	−0.13	−0.15	−0.03	−0.18	
D6	−0.29	−0.36	−0.19	−0.22	−0.19	0.00

	P0	P1	P2	P3	P4	P5
P1	**0.27**					
P2	−0.27	**0.29**				
P3	**0.29**	0.14	0.00			
P4	−0.01	0.20*	0.05	0.06		
P5	0.02	−0.25	0.05	−0.04	0.21*	
P6	−0.06	−0.06	0.03	0.23	0.17	**0.27**

√ transformed data

	D0	D1	D2	D3	D4	D5
D1	**0.81**					
D2	**0.72**	**0.58**				
D3	**0.70**	**0.55**	**0.55**			
D4	**0.46**	**0.43**	0.15	**0.44**		
D5	−0.04	−0.01	0.08	0.12	−0.14	
D6	−0.12	−0.32	−0.03	−0.16	−0.17	−0.025

	P0	P1	P2	P3	P4	P5
P1	0.26*					
P2	−0.24	0.04				
P3	−0.10	0.18	0.12			
P4	0.00	0.15	0.14	0.03		
P5	0.03	−0.14	−0.06	−0.09	**0.30**	
P6	0.06	0.14	−0.12	0.12	0.11	**0.44**

√ √ transformed data

	D0	D1	D2	D3	D4	D5
D1	**0.78**					
D2	**0.69**	**0.59**				
D3	**0.66**	**0.53**	**0.53**			
D4	**0.38**	**0.38**	0.04	**0.31**		
D5	0.15	0.01	0.12	0.15	−0.01	
D6	0.00	−0.18	0.01	−0.04	−0.10	0.06

	P0	P1	P2	P3	P4	P5
P1	0.09					
P2	0.02	−0.29				
P3	−0.11	0.07	0.23*			
P4	0.06	−0.03	0.15	−0.05		
P5	0.09	0.00	−0.11	−0.14	0.21*	
P6	0.09	0.25*	−0.22	−0.02	−0.02	**0.36**

Comparisons between disturbance treatments show whether the meiobenthic nematode community response to organic enrichment was the same within the different disturbance treatments. Comparisons between organic enrichment treatments show whether the meiobenthic nematode community response to disturbance was the same within the different organic enrichment treatments. Bold values indicate significant positive correlation at $p<0.05$, *denotes $p<0.1$.

productivity treatment, denoting high similarity in their benthic communities. Low and intermediate physical disturbance combined with high productivity treatments are much less similar to each other and also to all of the remaining treatments i.e. they are more variable.

At lower levels of disturbance (D0–D4) there were similar responses of the meiobenthic nematode community to the different levels of organic enrichment, regardless of data transformation (Table 1). The different meiobenthic nematode species, (rare, common, dominant) responded to enrichment in a similar way and this response was unaffected by low levels of disturbance. In contrast the effects of disturbance upon the enrichment treatments did not appear to be uniform (Table 1).

The effects of combinations of increasing organic enrichment and physical disturbance do not appear to be additive. At higher levels of physical disturbance disturbances (D4–D6), seriation breaks down (Table 2a). Seriation also breaks down at intermediate levels of organic enrichment (P4–P5).

3.2. Multivariate comparison of macrobenthic and meiobenthic nematode community responses to disturbance

In the productivity-disturbance experiment, macro and meiobenthic community responses to the experimental treatments were closely correlated regardless of whether the abundance data of either faunal group were transformed or not (Table 3a). In the biotic disturbance experiments there were some very significant correlations between the macrobenthic and meiobenthic nematode community responses but the results were not consistent. In the multispecies experiment with all three experimental bioturbating species (*Brissopsis*, *Nuculoma*, and *Abra*) used simultaneously in the same sediment boxes, there were very significant correlations,

Table 2
R-values from RELATE test of seriation

	Untransformed	√ transformed	√ √ transformed
a. Community response to changes in organic enrichment level at different frequencies of physical disturbance			
D0	**0.51**	**0.56**	**0.57**
D1	**0.36**	**0.40**	**0.40**
D2	**0.37**	**0.34**	**0.28**
D3	**0.43**	**0.46**	**0.45**
D4	0.18*	**0.27**	**0.26**
D5	−0.11	−0.06	0.01
D6	−0.13	−0.04	0.07
b. Community response to changes in physical disturbance frequency at different levels of organic enrichment			
P0	0.19*	**0.20**	**0.22**
P1	**0.22**	**0.21**	**0.20**
P2	**0.22**	**0.29**	**0.25**
P3	**0.32**	**0.29**	**0.23**
P4	**0.23**	0.16*	0.09
P5	0.17*	0.11	0.05
P6	**0.40**	**0.38**	**0.27**

Bold values indicate significant correlations between community responses observed in actual data and a similarity matrix observing perfect seriation ($p<0.05$), *denotes $p<0.1$.

Table 3
Results from RELATE analysis for correlation between macrobenthic and meiobenthic nematode community structure under a range of different data transformations

	Nematodes untransformed	Nematodes √ transformed	Nematodes √ √ transformed
(a) Productivity-disturbance experiment			
Macrofauna untransformed	**0.400**	**0.370**	**0.331**
Macrofauna √ transformed	**0.485**	**0.513**	**0.486**
Macrofauna √ √ transformed	**0.440**	**0.495**	**0.488**
(b) Multi species experiment with Brissopsis, Nuculoma and Abra treatments			
Macrofauna untransformed	0.056	0.101	0.114
Macrofauna √ transformed	**0.138**	**0.177**	**0.168**
Macrofauna √ √ transformed	**0.144**	**0.172**	**0.154**
(c) Brissopsis only experiment			
Macrofauna untransformed	0.007	0.061	0.094
Macrofauna √ transformed	0.078	0.055	0.024
Macrofauna √ √ transformed	0.084	0.004	0.004
(d) Multispecies experiment selecting Brissopsis and control samples only			
Macrofauna untransformed	0.167	0.128	0.072
Macrofauna √ transformed	0.106	0.096	0.065
Macrofauna √ √ transformed	0.054	0.055	0.046
(e) Multispecies experiment selecting Abra, Nuculoma and control samples only			
Macrofauna untransformed	0.052	0.104	0.126
Macrofauna √ transformed	**0.144**	**0.186**	**0.179**
Macrofauna √ √ transformed	**0.156**	**0.182**	**0.159**

Bold values indicate significant positive correlation at $p<0.05$.

but only if the macrobenthos data was transformed i.e. there was not a correlation with the dominant high abundance macrobenthic species (Table 3b). In the *Brissopsis* only experiment there was no correlation at all (Table 3c). Similarly, if only the *Brissopsis* treatments were analysed in the multi-species experiment there was no correlation (Table 3d). When just the communities in the *Nuculoma* and *Abra* treatments in the multispecies experiment were analysed, there were again significant correlations between the macrobenthic and meiobenthic nematode communities but again only if the macrobenthic data was transformed. The correlation coefficients (*R* values) were higher than when *Brissopsis* was included in the analyses, again indicating that only the faunal responses to biotic disturbance caused by the two bivalve species were correlated.

4. Discussion

Although studies exist on the separate effects of physical disturbance and of organic enrichment on meiobenthos, this is the first study, as far as we are aware, on the combined effects. Diversity of meiobenthic nematodes appears to respond to interactive physical and enrichment disturbance in a way that is approximately consistent with the predictions of the "Dynamic Equilibrium Model" (Huston, 1979). The contour or surface plots show that meiobenthic diversity was maximum at combinations of zero to medium experimental levels of physical disturbance and productivity presented in this experiment. The results from this experiment with both macrobenthos (Widdicombe and Austen, 2001) and now meiobenthic nematodes indicate that the Dynamic Equilibrium Model may serve as a basis of an explanation for the relationship between benthic diversity, physical disturbance and organic enrichment at least at local scales. There were small discrepancies between the predicted surface plot of the Dynamic Equilibrium Model (Huston, 1979) and the plots generated from actual data (Fig. 2a and b). The plots appeared to be truncated at the low physical disturbance and low productivity region of the model and can be visualised 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. As discussed in Widdicombe and Austen (2001), there are no scales on the axes of Huston's response surface of his model. It is impossible to determine if the relative scale of the two treatments administered in this experiment is of the same proportionate level as anticipated by Huston's model.

With respect to physical disturbance, the discrepancy between the observed surface plot and that predicted by the Dynamic Equilibrium Model was not as great for meiobenthic nematodes as it was for macrobenthos. The macrobenthic plot is truncated at very low levels of physical disturbance and maximum diversity for macrobenthos was actually in the zero physical disturbance treatment. This suggests that meiobenthos are less affected by physical disturbance than the macrobenthos. Meiobenthos may be less sensitive to changes in their position within the surface sediment or perhaps more readily able to re-establish their original position after brief periods of disturbance. This explanation has similarly been made by e.g. Austen et al. (1989), Warwick et al. (1990) and Gee et al. (1992) to interpret results from other comparisons of meiobenthic and macrobenthic community responses. Widdicombe and Austen (2001) proposed that tolerance to physical disturbance was greater in more motile macrobenthic organisms. Since the relative motility of adult meiobenthic nematodes is much lower than the more tolerant macrobenthic species, it is likely that tolerance to changing sedimentary environmental conditions is of greater importance for meiobenthos rather than the ability to move to a preferred position within the sediment. The improved surface sediment oxygenation caused by low levels of physical disturbance may have influenced meiobenthic community structure (Steyaert et al., 2003; Giere, 1993; Hendelberg and Jensen, 1993) but higher levels of physical disturbance cause sediment disruption that counteracts the positive oxygenating effects. Although the Dynamic Equilibrium Model may be applicable to both components of the benthos, the response surface and scales of disturbance at which it fits are not the same. The experiment suggests that both meio- and macrobenthos are equally sensitive to organic enrichment, but that macrobenthos are more sensitive to physical disturbance.

Some of the discrepancies from the predicted surface plot of the Dynamic Equilibrium Model may also be due to a number of experimental set-up factors, acting singularly or in combination. These have been discussed previously by Widdicombe and Austen (2001) with reference to the macrobenthos results. For example the sediment in Oslofjord that was used for the experiment already contained moderate to high levels of organic matter. During experimental set-up sediment was subjected to physical disturbance, and during the experimental phase there is likely to have been biotic disturbance or bioturbation caused by fauna living in the sediment in addition to the experimental physical disturbance. This bioturbation, together with disturbance due to sediment

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 of the meiobenthic nematode and macrobenthic communities to the productivity-disturbance experiment was highly correlated, regardless of which components of the fauna (rare, common, abundant or dominant) were being compared. For both macrobenthos and meiobenthic nematodes the higher levels of physical disturbance appeared to ameliorate the effects of high levels of organic enrichment. Although meiobenthic nematodes appear to be less sensitive to physical disturbance alone, the combined effects of physical disturbance and high levels of organic enrichment appeared to be similar suggesting that meiobenthos may be more sensitive to interactions between physical disturbance and organic enrichment than macrobenthos.

Yet, the response of meiobenthic nematode and macrobenthos communities to different types of disturbance is not consistent. In the bioturbation disturbance experiments the response of the two faunal groups was not the same in the *Brissopsis* treatments. This may be a reflection that the disturbance to meiobenthos could have included predation by *Brissopsis* as well as physical disturbance of the sediment. In contrast, the positive correlation of the response of meiobenthic nematodes and macrobenthos to the bivalve disturbance treatments is rather peculiar. In multivariate analyses increasing transformation of the abundance data, which increases the importance of the less abundant and low dominance species in the analyses, often results in more equivocal statistical analyses as the data for these fauna are usually sparser and more variable. Yet the response of any component of the meiobenthic nematodes (regardless of transformation) was significantly correlated with the response of the macrobenthos provided the macrobenthos data was at least root transformed. There was no correlation between the response of high abundance, dominant species within the macrobenthic community (untransformed data analyses) to disturbance caused by the two bivalves and the response of any other component of the meiobenthos. The dynamics of these high abundance and dominant macrobenthic species appears to be completely out of equilibrium with the dynamics of any component of the meiobenthic nematode community. We can only speculate that due to the time-scale of the experiment this could be a reflection of the different recruitment strategies of the two fauna. Meiobenthic nematodes were probably able to respond quickly by recruiting rapidly in situ as well as emigration and immigration from surrounding control sediments in the biotic disturbance experiments. In comparison there was little or no juvenile recruitment in the macrobenthos. Within the mesocosm, macrobenthic response was a result of in situ survival and, within the biotic disturbance experiments, immigration–emmigration of smaller macrofauna from the surrounding control sediment. The short-comings of mesocosm experiments for longer-term studies, including lack of macrobenthic recruitment and scale issues, are discussed by Widdicombe and Austen (2001). The alternative is field studies and experiments, but comparisons of macro and meiobenthic communities in the field are surprisingly rare and field experiments simultaneously examining effects on both size components of the benthic community appear to be very rare. Netto et al. (1999a) and Schratzberger et al. (2004) observed that the distribution of different types of macrobenthic and meiobenthic communities across sites was very similar in both sand flats in an isolated South Atlantic atoll and subtidal sites around the UK, respectively. A detailed examination of the small-scale field distribution of subtidal meiobenthic nematode and macrobenthic assemblages in the presence of natural macrobenthic bioturbators indicated that distribution of macrobenthos and meiobenthic nematodes was correlated (Austen et al., 2003). The limited available evidence does suggest that, where hydrodynamic conditions or physical disturbance differs between sites, distribution of assemblages of macrobenthos and meiobenthos differs (Austen et al., 1989; Warwick et al., 1990; Netto et al., 1999b). The current comparative study further demonstrates the need for further large-scale field experimentation to comprehensively test for the relevance of unifying theories such as the Dynamic Equilibrium Model to marine benthic communities.

5. Conclusion

Meiofauna and macrofauna show similar and strongly related responses to the interactive effects of physical disturbance and productivity. Highest diversity is observed in treatment combinations of low levels of disturbance and enrichment and this supports the "Dynamic Equilibrium Model" of Huston (1979). The structure of faunal communities was more variable at treatment combinations of low levels of disturbance and high levels of organic enrichment. Physical disturbance subdued the effects of high levels of nutrient enrichment.

The response of meiobenthos to different types of physical disturbance, including bioturbation, is often, but not always, the same as that of macrobenthos. Reasons for inconsistencies can probably be explained by the constraints of the experimental design of the mesocosm, where macrobenthic recruitment is not possible, as well as the different ecology of these two faunal groups.

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