

Dense aggregations of *Pygospio elegans* (Claparède): effect on macrofaunal community structure and sediments

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Abstract

Epibenthic biogenic structures such as polychaete tubes are conspicuous features of many marine soft-bottom habitats. This paper compares the benthic macrofauna in patches with high and low densities of the tube-dweller *Pygospio elegans* on intertidal sandflats in eastern Scotland (UK). The main aim of this study was to determine potential differences in the macrofaunal community structure, the size distribution of individual species and sediment properties.

Multivariate data analyses revealed that the macrofaunal community composition (excluding *P. elegans*) within patches was always significantly different from outside patches, mainly due to variability in the abundances of *Cerastoderma edule* and *Corophium volutator*. In addition to *P. elegans*, 5 taxa were sufficiently abundant for univariate analyses, 4 of these (*Capitella capitata*, *C. edule*, *Macoma balthica* and *C. volutator*) being significantly more abundant within *P. elegans* patches than in surrounding, non-patch sediments. The size distribution of *P. elegans* was significantly different between patches (bimodal distribution) and non-patches (skewed distribution). Similarly, there was a greater proportion of larger *C. capitata* individuals within patches compared to non-patch sediments. Sediment organic content and silt/clay fraction were always significantly higher in patch sediments while redox profiles showed no differences except at the end of the study period when the top 2 cm within patches were more positive and more negative at 4 cm. These results imply that even relatively small (1–1.5 m²) *P. elegans* patches can have large effects on the spatial variability of macrofaunal community structure on intertidal sandflats.

Towards the end of the study there were marked visual changes in the *P. elegans* patches, such as wave-ripple marks on the surface, which signified their demise. This coincided with dramatic changes in the invertebrate community structure within patches. Along with the decline in *P. elegans* numbers, dramatic increases in the densities of the 2 bivalve species *C. edule* and *M. balthica* occurred, while remaining comparatively stable outside patches. This suggested that the conditions within *P. elegans* patches were particularly favourable to successful bivalve spat settlement. We postulate that *P. elegans* patches have limited longevity and propose that enhanced bivalve competition within them leads to rapid decreases in *P. elegans* numbers. © 2003 Elsevier Science B.V. All rights reserved.

Keywords: Macrobenthos; Habitat structure; *Pygospio elegans*; Biological competition; Intertidal sandflat

1. Introduction

Epibenthic biogenic structures are conspicuous features of many marine soft-bottom habitats. Of these, the most widespread include seagrasses (e.g., [Thistle et](#)

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al., 1984), mussels (e.g., Ragnarsson and Raffaelli, 1999), macroalgal mats (e.g., Hull, 1987; Everett, 1994; Raffaelli et al., 1999; Bolam et al., 1999; Bolam and Fernandes, 2002a) and high densities of tube-dwelling polychaetes, or 'tube-beds' (e.g., Fager, 1964; Daro and Polk, 1973; Noji, 1994; Morgan, 1997). The effect of high densities of tube-builders on infaunal community structure has been studied for a number of species. These include the terebellids *Lanice conchilega* (Jones and Jago, 1993), *Loimia* sp. and *Axionice* sp. (Trueblood, 1991), *Diopatra cuprea* (Woodin, 1981), the oweniid *Owenia fusiformis* (Fager, 1964), the maldanids *Clymenella torquata* (Sanders et al., 1962; Featherstone and Risk, 1977) and *Axiiothella rubrocincta* (Weinberg, 1979) and the spionids *Pygospio elegans* (Dupont, 1975; Morgan, 1997), *Polydora ciliata* (Daro and Polk, 1973; Noji, 1994), *Boccardia syrtis* (Cummings et al., 1996) and *Spiophanes* cf. *wigleyi* (Featherstone and Risk, 1977). The general inference arising from such studies is that tube-beds play a major role in determining soft-sediment community structure (Woodin, 1981; Gallagher

et al., 1983). Sediments with biogenic structures have been found to differ physically, and to support different meio- and macrofaunal communities, from those of adjacent areas lacking such structures (Sanders et al., 1962; Trueblood, 1991; Noji, 1994). There are many factors responsible for these differences and the effects of tube-beds on community composition and sediment structure ultimately result from the interaction of many complex and interrelated processes.

The main tube-building polychaete species forming dense tube-beds in northern European shallow waters tend to be either *Lanice conchilega*, *Polydora ciliata* or *Pygospio elegans*. Several studies such as those by Eagle (1975) and Zühlke (2001) have described the fauna within *L. conchilega* tube-beds and Daro and Polk (1973) and Noji (1994) have studied *P. ciliata* beds. However, relatively few studies have focused on the beds formed by *P. elegans* (e.g., Dupont, 1975).

Pygospio elegans is a small, sedentary, tube-building polychaete with a wide habitat tolerance, a variety of feeding mechanisms and a remarkable diversity of

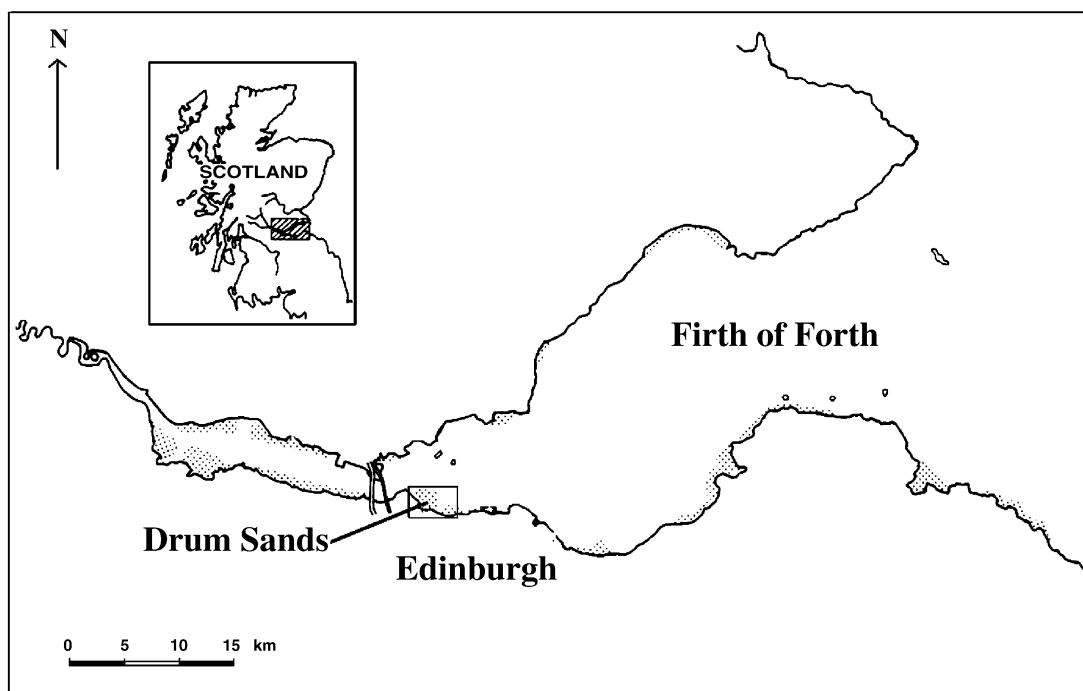


Fig. 1. Map of the Firth of Forth, Scotland, showing the location of Drum Sands.

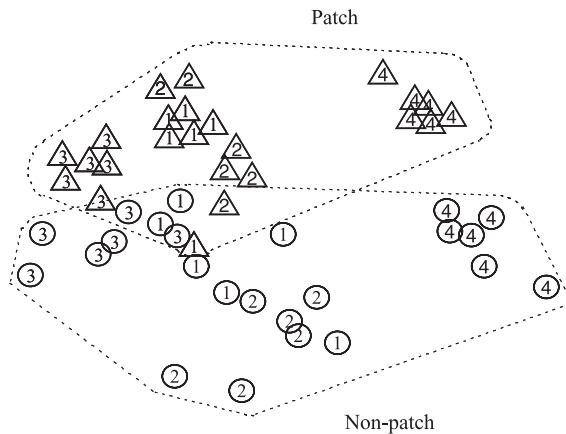


Fig. 2. Two-dimensional ordination plot of all patch (triangles) and non-patch (circles) replicates. The months April, August and December 1997 and August 1998 are labelled as 1,2,3 and 4 respectively. Stress=0.14.

reproductive strategies. The worm, which can reach 15 mm in length and has a lifespan of between one and two years (Anger et al., 1986), lives in a mucous secretion within a sandy tube (1 mm diameter) which has several openings at the sediment surface (Taghon et al., 1980). Although *P. elegans* has been found at various shallow depths (Hannerz, 1956; Rasmussen, 1973), it is generally regarded as a circum-boreal, intertidal species (Muus, 1967; Tufail et al., 1989) reaching its highest densities in sandy or mixed sediments (Muus, 1967). *P. elegans* is common in both marine and brackish waters, especially the latter where high abundances have been found at salinities as low as 2 ppt (Hempel, 1957). The species can filter-feed by building a mucus net within its tube, suspension-feed by trapping plankton with its palps or it can feed as a selective deposit-feeder (Hannerz, 1956; Hempel, 1957; Sanders et al., 1962; Fauchald and Jumars, 1979). *P. elegans* has been shown to be polytelic with a flexible reproductive

strategy (Gudmundsson, 1985; Anger et al., 1986). The species can reproduce sexually, producing either planktotrophic (Hannerz, 1956; Anger et al., 1986) or benthic larvae (Hannerz, 1956; Hempel, 1957; Rasmussen, 1973), or reproduce asexually by fragmentation (Gudmundsson, 1985; Wilson, 1985).

This study investigates the ecological significance of dense aggregations, or ‘patches’, of *P. elegans* on an intertidal sandflat, Drum Sands, Scotland. Specifically, we determine whether macrofaunal community structure, size distribution of individual species and sediment properties within *P. elegans* patches are different to those of surrounding, non-patch sediments. We also present the invertebrate and sediment changes occurring with the decline of patches and postulate a possible mechanism for their demise.

2. Methods

2.1. Study site

Drum Sands (55°59.50 N, 003°19.00 W) is located in the Firth of Forth on the east coast of Scotland (Fig. 1). A full account of the general ecology of the area can be found in Webb and Metcalfe (1987). Dominating macrofauna are the polychaete *P. elegans* and the bivalves *C. edule* and *M. balthica* (Bolam et al., 1999). Drum Sands is relatively flat and the majority lies below mid-tide level. An area of 250 × 400 m was marked out on the sandflat, within which the sediments were moderately sorted with a median particle size of 2.6 ϕ , loss on ignition 3–5%, and with no obvious environmental gradient. Within this area, a number of *P. elegans* patches (1–1.5 m²) were present, in which adult densities of this polychaete reached an order of magnitude higher than those in surrounding, non-patch sediments. For example, adult densities reached

Table 1

The 3 most discriminating taxa contributing to the dissimilarity between patch and non-patch communities from April 1997 to August 1998

April 1997		August 1997		December 1997		August 1998	
Taxa	%	Taxa	%	Taxa	%	Taxa	%
<i>C. edule</i>	22.9	<i>C. edule</i>	22.2	<i>C. volutator</i>	19.1	<i>C. edule</i>	39.0
<i>C. volutator</i>	14.5	<i>C. volutator</i>	19.5	<i>C. capitata</i>	16.8	<i>M. balthica</i>	20.4
<i>C. capitata</i>	8.9	<i>P. cornuta</i>	10.7	Oligochaete	11.8	<i>C. capitata</i>	10.5

Values (%) refer to the percentage each taxon contributes to the total dissimilarity between patch and non-patch communities.

Table 2

Taxa found within *P. elegans* patches and non-patches

Taxon	Patch	Non-patch
<i>Pygospio elegans</i>	P	P
<i>Capitella capitata</i>	P	P
<i>Polydora cornuta</i>	P	P
<i>Streblospio shrubsolii</i>	P	P
<i>Spio martinensis</i>	P	P
<i>Spiophanes bombyx</i>	P	P
<i>Eteone cf. flava</i>	P	P
<i>Anaitides mucosa</i>	P	P
<i>Glycera tridactyla</i>		P
<i>Aricidea catherinae</i>	P	
<i>Scoloplos armiger</i>	P	P
<i>Nephtys hombergii</i>	P	P
Oligochaeta	P	P
Polynoidae	P	P
<i>Cerastoderma edule</i>	P	P
<i>Macoma balthica</i>	P	P
<i>Angulus tenuis</i>	P	
<i>Mya arenaria</i>	P	
Nemertea	P	P
<i>Corophium volutator</i>	P	P
<i>Urothoe brevicornis</i>	P	P
<i>Gammarus</i> sp.	P	

P indicates presence in any plot type at any sampling period.

11,000 m⁻² in patches while up to 1000 m⁻² occurred outside patches (Bolam and Fernandes, 2002b). These patches are visible as areas of smooth, raised sediment on the wave-rippled sandflat.

2.2. Sampling design

Sampling was conducted on 18 April, 18 August and 18 December 1997 and 18 August 1998. On each occasion, 6 independent *P. elegans* patches (hereafter referred to as 'patch' plots) were randomly chosen. Similarly, 6 plots were chosen outside *P. elegans* patches (hereafter referred to as 'non-patch' plots) by random co-ordinates within the study area. Different patch and non-patch plots were sampled on each occasion. Faunal samples were randomly taken using a corer (8 cm internal diameter to a depth of 12 cm) from within each plot and each sample was then

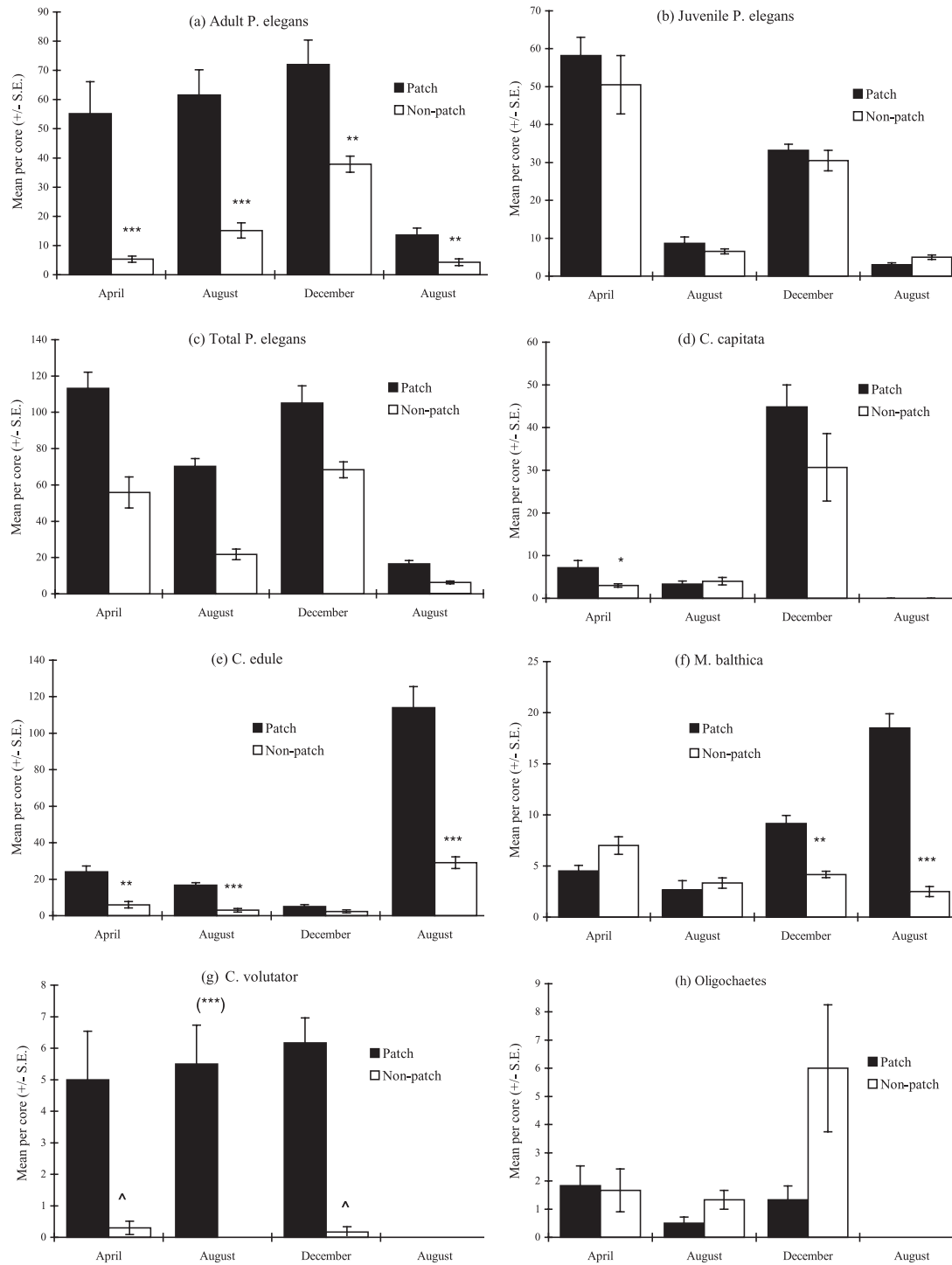
sectioned into 2 parts. The top 3 cm were removed and preserved in neutralised 10% saline formaldehyde solution with 0.01% Rose Bengal. These samples were later washed through a 500 µm and 212 µm mesh sieve stack in the laboratory. Juvenile *P. elegans* and *C. capitata* were sorted and identified under a dissecting microscope. These were the only 2 species sorted from the 212 µm mesh sieve since no other species in this sample fraction was present in sufficient numbers. Very few young stages of the other macroinvertebrate species were retained by this sieve. The 3–12 cm fraction of the samples was sieved on a 500 µm mesh sieve before preserving. Previous studies have shown that the use of an 8 cm corer sufficiently samples the more common species on Drum Sands, while most species are too rare for density approximation using corers (Bolam and Fernandes, 2002b).

Population size-frequency analysis was carried out on taxa with a mean abundance of >20 per core for either plot type. This criterion was chosen to include only populations in which a representative size distribution could be ascertained (Bolam and Fernandes, 2002b). *P. elegans* and *C. capitata* were measured across their 5th setiger and 3rd setiger, respectively (Yokoyama, 1990; Zajac, 1991; Ragnarsson and Raffaelli, 1999; Bolam and Fernandes, 2002b). Additionally, the maximum shell length of bivalves was determined. *P. elegans* individuals less than 0.27 mm 5th setiger widths were classified as 'juveniles' while those above this size were termed 'adults' (see Bolam and Fernandes, 2002b). All size measurements were conducted using a microscope (×20 magnification) fitted with an eyepiece graticule, except for larger bivalves which were measured to the nearest millimetre using a pair of calipers.

2.3. Sediment sampling

One core (2.4 cm internal diameter, 3 cm deep) was taken from each of the 12 plots on each sampling occasion. These samples were frozen and then later

Fig. 3. (a–h). Mean abundances (± S.E. Mean, n=6) of the most abundant taxa together with the results of statistical tests between patch and non-patch means. * Denotes a statistical difference between patch and non-patch means using a two-sample t-test (Mann–Whitney for *C. volutator*) at 0.05 level of significance; ** at 0.01; and *** at 0.001. (***) Denotes a significant difference from zero at 0.001 level of significance using a one-sample t-test.



analysed for water, organic carbon (loss on ignition at 480 °C for 4 h) and silt/clay (wet sieving on a 63 µm mesh sieve) contents. Redox potential values were measured in situ at 1, 2 and 4 cm depths within each plot using the method outlined by Pearson and Stanley (1979).

2.4. Data analysis

The invertebrate data were analysed using both univariate and multivariate techniques. For univariate analyses, only those species with a mean abundance of at least 2 for any plot type were regarded as sufficiently abundant for statistical analysis. The data were checked for normality using the Anderson–Darling test and homogeneity of variances were assessed by the Bartlett test. Any data not conforming to either of these two assumptions were transformed using an appropriate transformation (Zar, 1984). The transformed data were re-checked using the above tests, any data still not conforming to either test were analysed using an appropriate non-parametric test (Mann–Whitney U test). Differences in species means between patch and non-patch plots were otherwise assessed using two-sample t-tests. Statistical analysis was not carried out on total *P. elegans* numbers since they were the sums of the adult and juvenile means and these stages were analysed separately. Statistical analysis was not carried out for *C. capitata*, *C. volutator* and oligochaetes for August 1998 due to insufficient numbers in the samples. Since the aim of this study was primarily to compare population and community differences between patch and non-patch sediments, temporal differences were not investigated.

Size-frequency distributions were tested for differences between patch and non-patch plots using the χ^2 goodness of fit test. Size classes were grouped so that no expected values were below 5 for the χ^2 test, as recommended by Elliot (1977).

Multivariate data analyses were carried out on the faunal data to assess (dis)similarities between patch and non-patch community assemblages. Since sampling was stratified, *P. elegans* was omitted to avoid including this species as both a response variable and as a factor. All multivariate analyses were performed using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package, version 4.0 (see Warwick

and Clarke, 1994). Dendrograms were produced by hierarchical agglomerative clustering with group-average linking from the Bray–Curtis similarity matrices. The raw data were $\sqrt{\cdot}$ -transformed. This was chosen as a compromise between no transformation in which different community assemblages may result from the variability in the most common taxa, and a strong transformation, such as $\sqrt{\sqrt{\cdot}}$ or $\log(x+1)$, where rarer species have strong influences on community (dis)similarities. Non-metric Multi-Dimensional Scaling (or MDS) was carried out to produce 2-dimensional ordination plots, in which the relative distances apart of the samples reflect relative (dis)similarities in species composition. Since the MDS ordination represents a multi-dimensional ordination in 2 dimensions, each algorithm has an associated stress value, discussed by Warwick and Clarke (1994).

Testing for significance between patch and non-patch communities was performed using a priori, one-way ANOSIM (analysis of similarities) tests in which the null hypothesis (H_0) in each case was that there were no significant community differences between the 2 plot types. The ANOSIM test can be regarded as a non-parametric equivalent of the MANOVA test (e.g., Mardia et al., 1979) in which few, if any, assumptions about the data are made. The SIMPER (similarity of percentages) program was used to indicate which were the most discriminating taxa between samples.

3. Results

3.1. Multivariate analysis of community structure

Fig. 2 shows an MDS plot of all the replicates from each sampling time. This plot allows an assessment of the differences in patch and non-patch community structures. There is very little overlap between the patch and non-patch replicates which implies that there were large community differences between these 2 plot types. The community change which occurred during August 1998 is very apparent from the MDS with a clear separation from the others. Differences in the faunal communities between patches and non-patches on each sampling occasion were statistically analysed by one-way ANOSIM tests. In each of the ANOSIM tests carried out, only one permuted statistic out of 462 permutations was greater than the sample

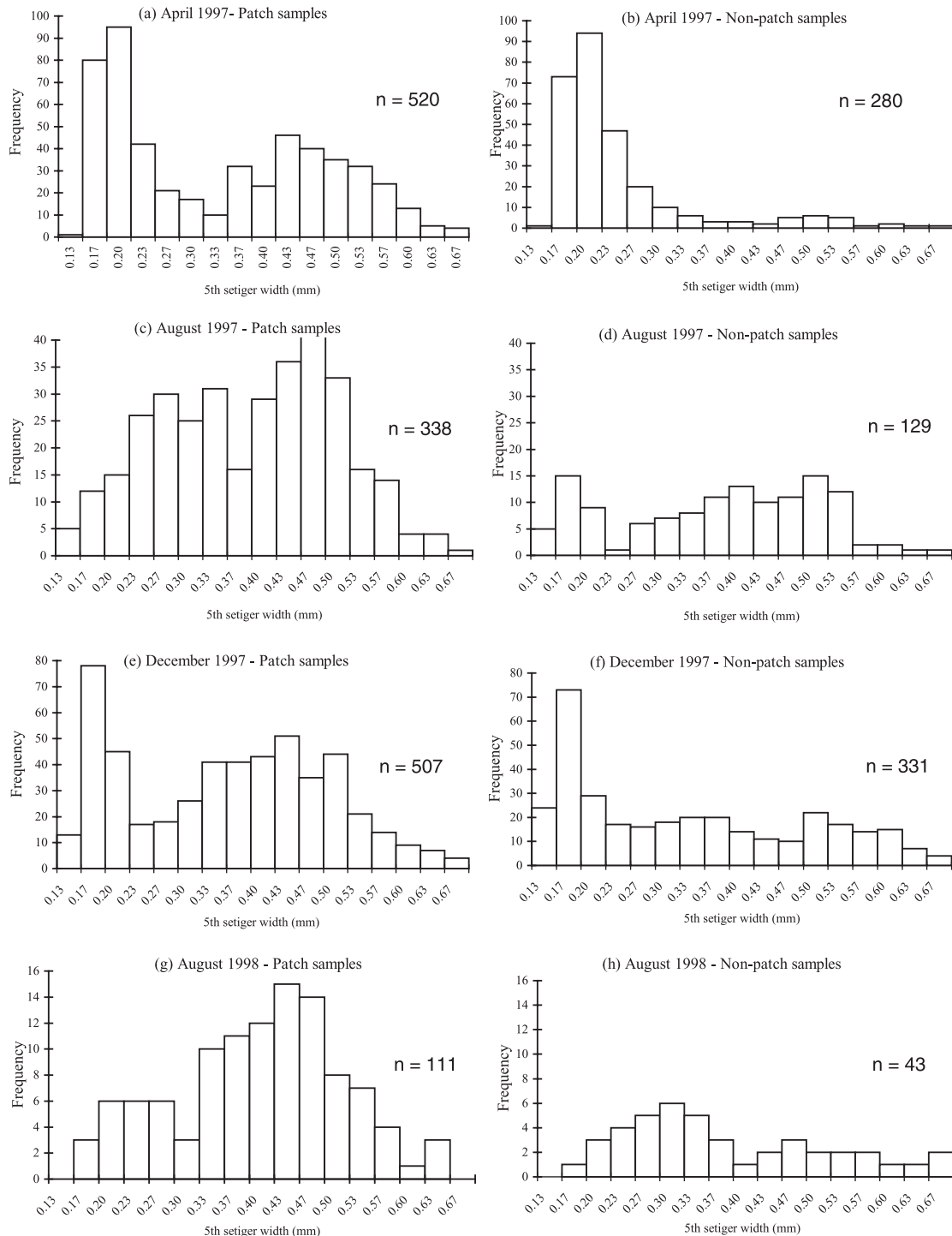


Fig. 4. (a–h). Size-frequency histograms of *P. elegans* in patch and non-patch samples for each sampling occasion, 'n' denotes the total number of individuals measured for each plot type.

Table 3

P. elegans size-frequency distribution χ^2 goodness of fit test results between patches and non-patches for April 1997 until August 1998

Size (mm)	0.13– ≤ 0.20	>0.20– ≤ 0.27	>0.30– ≤ 0.37	>0.37– ≤ 0.40	>0.40– ≤ 0.47	>0.47– ≤ 0.53	>0.53	p value
April 1997	23.8	12.9	0.1	14.2	25.9	12.6	10.6	<0.001
August 1997	41.9	29.7	5.2	6.1	6.5	8.2	2.4	<0.001
December 1997	20.6	5.5	1.2	13.8	42.9	0.5	15.6	<0.001
August 1998	5.0	11.6	20.2	14.6	32.8	1.8	14.0	0.06

The percentage of the total χ^2 values are given for each size class together with the p-values.

statistic R, giving significant levels of R equal to 0.2% in each case, and therefore H_0 was rejected at a significance level of $p < 0.2\%$ for each test. Although the significance levels were not adjusted for multiple testing, heeding caution with these significance levels, significant differences were supported by the global R values which were all above 0.5.

The relative contribution of individual species to the total dissimilarity between groups (patches and non-patches) was calculated, the 3 species with the highest percentage dissimilarity each month being shown in Table 1. The main species responsible for the statistical differences in faunal communities between patch and non-patch areas were *C. edule*, *C. volutator* and *C. capitata*, with *Polydora cornuta*, *M. balthica* and oligochaetes (mainly tubificids) being influential at certain times of the year. These taxa, except for *P. cornuta*, were the most abundant species overall (see Section 3.2). For each of these taxa, it was their increased numbers in patches relative to non-patches which led to their dominance in the SIMPER results.

3.2. Univariate analysis of species abundances

A total of 22 taxa were recorded from the 4 sampling occasions, 21 from the patch samples and 18 taxa from the non-patch samples (Table 2). Six of these were sufficiently abundant for univariate statistical analysis (i.e., mean abundances ≥ 2 per core for either plot type). These were the polychaetes *P. elegans* and *C. capitata*, the bivalves *C. edule* and *M. balthica*, the amphipod *C. volutator* and oligochaetes. Changes in the densities of these 6 taxa were responsible for the majority of the (dis)similarities between patches and non-patches (Section 3.1). Mean densities, together with standard errors and statistical differences between patch and non-patch densities, are presented in Fig. 3 (a–h).

The numbers of adult *P. elegans* were always significantly higher in patches than outside patches (Fig. 3a). Since the sampling was separated into patches and non-patches this result is not surprising; it confirms the density differences between the two plot types. The numbers of juveniles in patches and non-patches were never significantly different, suggesting there was no preferential juvenile recruitment to the ambient sediments of patches compared with non-patch areas.

The results suggest that for the majority of the most abundant taxa, significantly higher densities were attained in *P. elegans* patches than outside patches, at least at certain times of the year. For example, significantly higher densities of *C. capitata* (April,

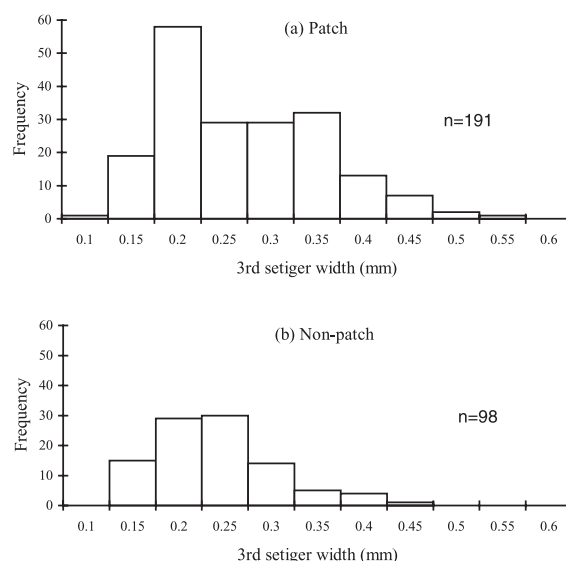


Fig. 5. (a–b). Size-frequency histograms of *C. capitata* from December 1997 patch and non-patch samples, 'n' denotes the total number of individuals measured for each plot type.

Table 4

C. capitata size-frequency distribution χ^2 goodness of fit test results between patches and non-patches for December 1997

Size (mm)	≤ 0.15	0.20	0.25	0.30	0.35	≥ 0.40	p value
% explained	6.60	0.07	39.88	0.18	36.27	17.00	0.002

The percentage of the total χ^2 values are given for each size class together with the p-values.

1997; Fig. 3d); *C. edule* (April and August, 1997 and August 1998; Fig. 3e); *M. balthica* (December 1997 and August 1998; Fig. 3f); and *C. volutator* (April to December 1997; Fig. 3g) were found in *P. elegans* patches compared to outside patches.

3.3. Size-frequency analysis

In addition to *P. elegans*, 2 species were sufficiently abundant to allow size-frequency measurements and the statistical assessment of differences between patches and non-patches. These were *C. capitata* (December 1997 only) and *C. edule* (April 1997 and August 1998).

The size-frequency histograms of *P. elegans* throughout the sampling period are given in Fig. 4 (a–h) and the results of the χ^2 goodness of fit test is shown in Table 3. In April 1997, the size distributions of *P. elegans* were significantly different ($p < 0.001$) between patch and non-patch individuals with the greatest χ^2 differences being due to both the smallest size class, 0.13–0.20 mm (23.8%) and the >0.40–0.47 mm size class (25.9%). This was due to the bimodal distribution in patches where large numbers of juveniles and adults were present and the skewed distribution in non-patches where there were very few adults.

The results for the *P. elegans* distributions in August 1997 were more equivocal: although the two distributions were statistically different ($p < 0.001$), the reasons why are less obvious than those for April. The χ^2 goodness of fit results suggest that the majority of the difference, 41.9% and 29.7%, lie in the two smallest size classes, $0.13 \leq 0.20$ mm and $>0.20 \leq 0.27$ mm, respectively. In other words, there were relatively fewer *P. elegans* individuals in the smallest size class and more individuals in the $>0.20 \leq 0.27$ mm size class in *P. elegans* patches compared to those of the

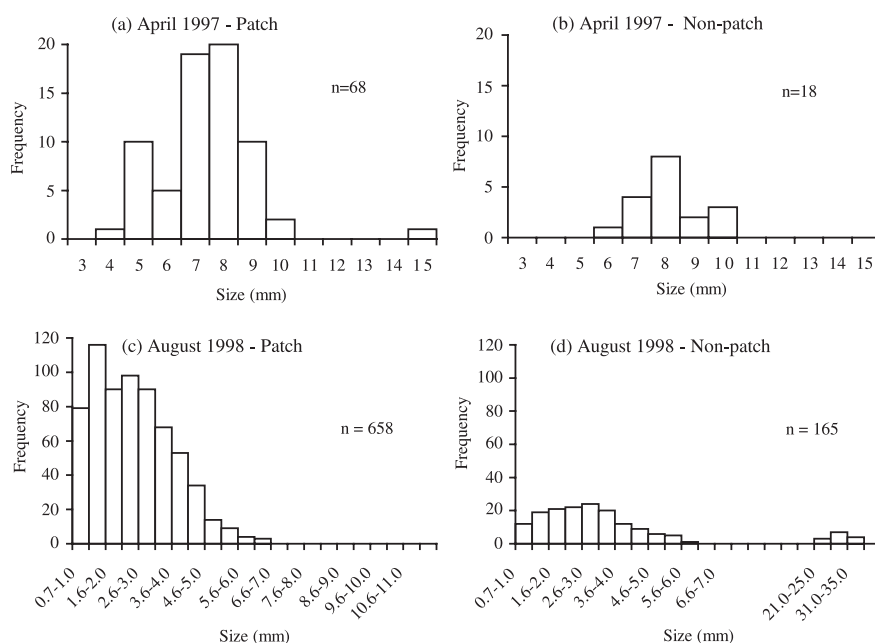


Fig. 6. (a–d). Size-frequency histograms of *C. edule* from April 1997 and August 1998 patch and non-patch samples, 'n' denotes the total number of individuals measured for each plot type.

non-patch distribution. This can be seen in Fig. 4 (c–d) in which the modal size in the peak of juveniles appears to be smaller in non-patch samples compared to the corresponding modal size in patches.

The *P. elegans* size-frequencies for December 1997 were similar to those in April. A second recruitment period of *P. elegans* occurred in December resulting in significant differences in size distributions ($p < 0.001$) due to a bimodal distribution in patch samples and a skewed distribution in non-patches. Consequently, the greatest χ^2 differences were in the same size classes as those in April: 20.6% for 0.13–0.20 mm and 42.9% for the $>0.40 \leq 0.47$ mm size classes.

In August 1998, there were no longer any significant differences between the size distribution of *P. elegans* in patches and non-patches ($p = 0.06$). The greatest χ^2 difference, 32.8%, was due to the size class $>0.40 \leq 0.47$ mm, i.e., there were fewer adults of this size in non-patch samples. However, this result could alternatively be viewed as fewer juveniles in patches compared with non-patches (see Fig. 3b).

The size-frequency distributions of *C. capitata* in patch and non-patch samples in December 1997 are presented in Fig. 5 (a–b). There were statistical differences between these two distributions ($p = 0.002$, Table 4). This was mainly because of the smaller numbers of individuals with a 3rd setiger width of 0.25 mm and higher numbers with 3rd setiger widths of 0.35 mm in patches, i.e., there was a greater proportion of larger individuals in patches compared to non-patches.

The size-frequency distributions of *C. edule* in patch and non-patch samples for April 1997 are shown in Fig. 6 (a–b). Sampling must have occurred before the annual settlement of spat and the mean shell lengths in both patches and non-patches were 7–8 mm with no significant differences between the 2 plot types ($p = 0.201$). The size distributions for August 1998 (Fig. 6c–d) show that the population was predominantly composed of young individuals. The size distribution of the individuals with shells less than 6.6 mm long is highly skewed. These individuals had no obvious growth rings on their shells and were much smaller than individuals which possessed growth rings. This suggests that all the individuals found in the patches were that year's cohorts. Although there was no difference in the size-frequency distributions ($p = 0.536$), large individuals at least 1 year old were only found outside *P. elegans* patches.

3.4. Sediment water, organic and silt/clay contents

There were no statistical differences found between patches and non-patches for water content (Fig. 7a), while % silt/clay and % organic contents were significantly higher in *P. elegans* patches throughout the sampling period (Fig. 7b–c).

3.5. Redox potentials

Whilst sedimentary variables such as the silt/clay and organic contents showed clear differences between

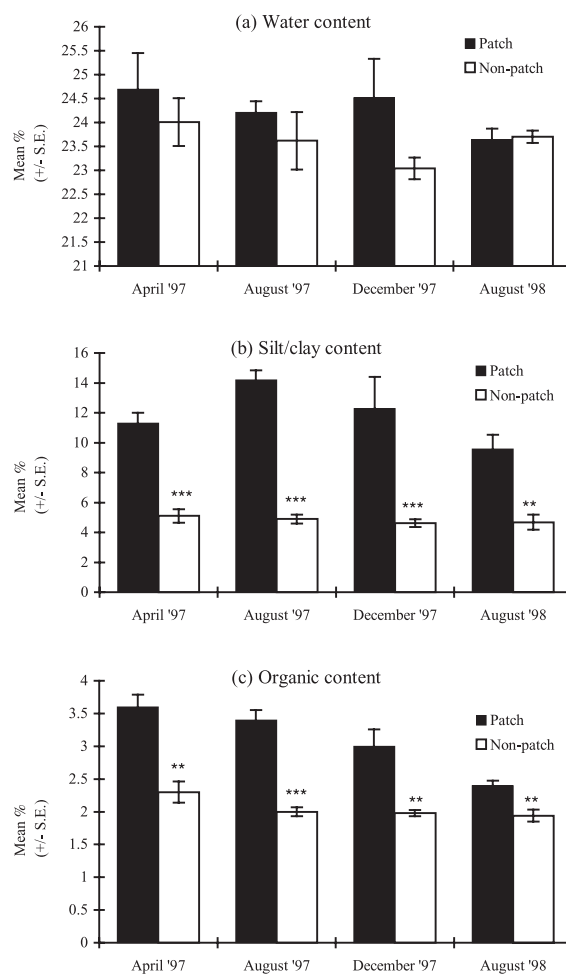


Fig. 7. (a–c). Mean sediment results (\pm S.E. Mean, $n = 6$) for each sampling occasion showing the results of statistical tests between patch and non-patch values. ** Denotes a statistical difference between patch and non-patch means using two-sample t-test at 0.01 level of significance and *** at 0.001.

patch and non-patch sediments, the results of the redox measurements were more equivocal. Fig. 8 (a–c) shows that the redox profiles of the 2 plot types were very similar between April and December 1997. However, during August 1998, the sediments at 1 and 2 cm depths in *P. elegans* patches were significantly more reducing than those in non-patch areas, while at the 4

cm depth, they were significantly less reducing than non-patch sediments (Fig. 8d).

4. Discussion

4.1. Faunal differences between *P. elegans* patches and non-patch areas

The significant differences between the fauna of *P. elegans* patches compared with those of non-patch areas in this study support the results of previous studies on polychaete tube patches. Fager (1964) noted that several species including the isopod *Munna ubiquita*, the pycnogonid *Oropallene heterodontata*, the hermit crab *Pagurus* sp. and the anemone *Zaolitus actius*, were only found in the stabilised sediments within the dense *Owenia fusiformis* tube-beds in his study. Woodin (1981) experimentally demonstrated that increases in the density of *Diopatra cuprea* tubes resulted in increases in macroinvertebrate species richness and abundances. Within the spionids, Noji (1994) noted that areas with moderate abundances of *P. ciliata* had more diverse meiofaunal and macrofaunal communities compared with areas of low abundances, while Reise (1983a) found that the presence of dense assemblages of *P. elegans* promoted the abundance of small benthic organisms by approximately 40%. Morgan (1997), using a correlation approach, indicated that the majority of the most common taxa in the Baie de Somme, France, e.g., *Eteone longa*, *Hediste diversicolor* and *C. edule*, were significantly positively correlated with *P. elegans* abundances. The results presented here indicate that such faunal differences occur even when the spatial scale of tube-builder patches are relatively small, 1–1.5 m².

Polychaete tubes are thought to exert important and complex effects on near-bed flow and at high densities lead to sediment stabilisation (Sanders et al., 1962; Fager, 1964; Daro and Polk, 1973; Nowell and Church, 1979; Nowell et al., 1981; Eckman, 1983) where larvae are passively deposited (Eckman, 1983). The organisms themselves significantly affect processes at the sediment-water interface by their behaviour, e.g., feeding, burrowing, defecation and tube irrigation (Rhoads and Young, 1970; Frithsen and Doering, 1986; Noji and Noji, 1991). Other theories

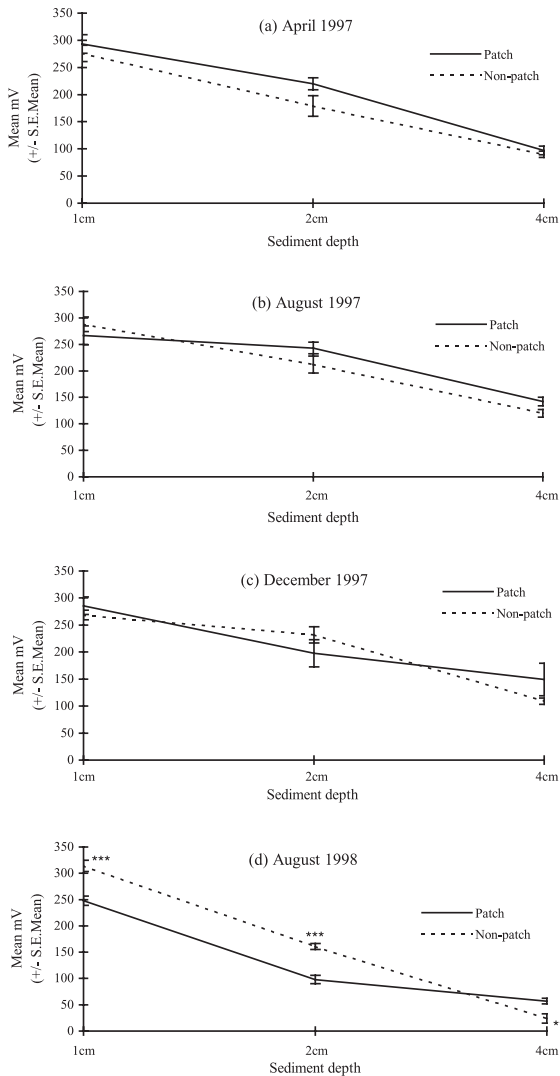


Fig. 8. (a–d). Mean redox potential results (\pm S.E. Mean, $n=6$) for each sampling occasion showing the results of two-sample t-tests between patch and non-patch values. ** Denotes a statistical difference between patch and non-patch means at 0.01 level of significance and *** at 0.001.

have been postulated for the observed community differences within tube-beds. Woodin (1978, 1981) suggested that the observed effects result from the ‘refuge’ provided by the high numbers of tubes: both predation and local disturbances have been shown to be important structuring forces for soft-bottom infauna (Reise, 1978; Zajac and Whitlatch, 1982; Ambrose, 1984; Thrush, 1988; Hall et al., 1993), refuges may be created by organisms whose structures buffer the impact of physiological stress or inhibit the access of predators (Woodin, 1978). Woodin (1976) viewed soft-bottom community structuring from the perspective of ‘functional group’ interactions in which ‘tube-dweller’, ‘bioturbator’ and ‘suspension-feeder’ functional groups should be unfavourable to each other. This ‘functional group’ interaction hypothesis implies that the maintenance of discrete dense assemblages in infaunal systems is due to interactions between established infaunal individuals and settling larvae.

The present study was observational and not intended to determine the mechanisms responsible for any differences in abundances between patch and non-patch communities. However, the increased silt/clay fraction and higher meiofaunal abundances in patches may have been due to increased passive deposition resulting from the reduction in velocity of near-bed flow. In the same way, passive larval entrainment may be responsible for some of the differences in this study. Once an individual of a species had colonised a *P. elegans* patch, the physico-chemical effects of the tubes possibly concurred to provide an increased food supply in the form of microbial and meiofaunal communities in this study. Furthermore, the resistance to shearing forces provided by the beds may have allowed a dense community by virtue of individuals not being ‘swept’ away (Morgan, 1997). Increased abundances of meiofauna (43%) were observed by Reise (1983a) in *P. elegans* patches compared to areas lacking the spionid, whilst a similar increase has been documented for beds of another spionid, *Polydora ciliata*, by Noji (1994), who suggested that the meiofauna were utilising the worms’ faecal pellets as a food source. Bolam and Fernandes (2002b) experimentally showed that for the community under study here some taxa do indeed recruit more successfully within *P. elegans* patches, although they were not able to unequivocally conclude which process(es) was responsible.

4.2. Sediment differences between *P. elegans* patches and non-patch areas

The lack of a significant difference between the water content of the patch and non-patch sediments during this study was contrary to that of other *P. elegans* tube-beds (e.g., Tufail et al., 1989; Morgan, 1997) where reduced sediment water contents have been observed. Dense arrays of tube-builders have been shown to enhance sediment permeability (Sanders et al., 1962; Morgan, 1997). It is possible that the increase in the silt/clay fraction of the sediments in *P. elegans* patches on Drum Sands retained water to such an extent that it counteracted the effect of the raised sediments to produce the non-significant differences in this study.

The increased levels of silt/clay and organic content within the *P. elegans* patches were consistent with the findings of other studies (e.g., Daro and Polk, 1973; Dupont, 1975; Eckman et al., 1981; Frithsen and Doering, 1986; Noji, 1994; Morgan, 1997). The stabilised conditions within patches probably resulted in increased deposition of silt/clay particles and lower erosion rates, while the increased organic contents were possibly due to both the feeding of *P. elegans* and increased microbial and meiofaunal communities.

The effect of a tube-building species on the below-sediment surface redox potential depends on a number of factors including worm feeding mechanism and density. While some tube-builders such as *Clymenella torquata* feed from sediments below their tubes, drawing water down from the surface (Sanders et al., 1962) and oxygenating the sediments, *P. elegans* has been shown to create reduced sediments below the surface (Morgan, 1997). It is uncertain how the lack of any measurable reduction in redox in patches between April and December 1997 should be explained. It is possible that *P. elegans* densities were not sufficient to produce any discernible effect on such a spatially mutable variable, or deposit-feeding spionids have varying effects on sediment redox potentials in different environments (cf. Featherstone and Risk, 1977; Noji, 1994; Morgan, 1997). In August 1998, however, the sediments of *P. elegans* patches were significantly more reducing compared to non-patch sediments at 1 and 2 cm depths, despite the high numbers of *C. edule* and *M. balthica* which tend to oxygenate surficial sediments (Reise, 1985; Flach, 1996). Consequently,

the reasons why patch sediments at 1 and 2 cm depths were more reducing during August 1998 remain unclear based on the information obtained from this study.

4.3. Demise of *P. elegans* patches on Drum Sands

In the few weeks preceding the August 1998 sampling, it was noticeable that the *P. elegans* patches at Drum Sands became less visually distinct, and it became more difficult to distinguish them from non-patch areas. The golden brown coloration due to diatoms was much less obvious and some of the patches had ripple-marks across them. The samples taken during August 1998 showed that although the numbers of *P. elegans* adults were still significantly higher in patch compared to non-patch areas, there was a large decline in their numbers from the previous December. Concurrently, the numbers of the two bivalve species *C. edule* and *M. balthica* had significantly increased, their densities being far higher than those of the same month the previous year. Furthermore, bivalve densities only increased within *P. elegans* patches: they remained relatively stable in the surrounding sediments.

Populations of opportunistic species such as *P. elegans* are unstable (Whitlatch and Zajac, 1985; Bolam and Fernandes, 2002b) and dense beds have been found to be replaced by subsequent colonisers (Grassle and Sanders, 1973; Noji and Noji, 1991). Many field observations (Smidt, 1944; Desprez et al., 1992; Noyer, 1993, cited by Morgan, 1997) and field experiments (Reise, 1985; Flach, 1996) have suggested a negative interaction between *P. elegans* and *C. edule*. Although most of the literature reports an interaction between *P. elegans* and *C. edule*, the functionally similar *M. balthica* is likely to evoke a similar interaction.

The bivalve spat-fall on Drum Sands during the spring of 1998 was particularly successful. The high spat settlement in patches observed in this study may have resulted from the slower net water flow. After settlement, it is possible that in *P. elegans* patches, post-settlement mortality and/or emigration of juvenile *C. edule* and *M. balthica* was low. Once established, the juvenile bivalves may have benefited from the indirect effects of the tubes slowing the water flow across the beds, promoting the *C. edule* feeding, and increased protection from erosion.

Competition, predation and sediment disturbance by *C. edule* and *M. balthica* have all been suggested to be responsible for their negative effect on spionids (Daro and Polk, 1973; Whitlatch and Zajac, 1985; Noji and Noji, 1991; Flach, 1996). Reise (1983b) observed *P. elegans* withdrawing into their tubes when touched by *M. balthica* siphons. *C. edule* has been shown to inhale settling *P. elegans* larvae (Noyer, 1993; cited by Morgan, 1997). Reise (1983b, 1985), Jensen (1985) and Flach (1996) have suggested that *C. edule* could affect other infaunal species by disturbing the upper sediment layer by its crawling (ploughing) and 'shaking' (Flach, 1996) behaviour. Consequently, we propose that direct competition and/or adult/juvenile interactions with *C. edule* and *M. balthica* were responsible for the dramatic reduction of *P. elegans* numbers in patches.

5. Conclusion

The results of this study indicate that even relatively small-scale patches of the tube-building polychaete *P. elegans* can have significant effects on infaunal species abundance and community composition on intertidal sandflats. These effects are likely to result from the interplay of a number of processes, but near-bed hydrodynamic processes resulting in local bed-stability are likely to be dominant. Such patches increase the number of species and small-scale spatial heterogeneity on intertidal sandflats. Dense aggregations of these opportunistic polychaetes are not long-lived: enhanced biological competition and/or negative adult/juvenile interactions within such patches may lead to the reduction of *P. elegans* densities and may ultimately result in the demise of such patches. The ephemeral nature of these patches results in a dynamic spatial heterogeneity compared to that created by more stable biogenic structures.

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