Comparison of tidepool phytal ostracod abundance and assemblage structure on three spatial scales

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ABSTRACT: Triplicate samples of *Corallina officinalis* L. were collected from either side of 5 large mid-shore pools on 3 shores in north-eastern England (Ravenscar, Filey Brigg and Flamborough) in order to examine the patterns of variation in abundance of different ostracod species and in assemblage structure over a range of spatial scales. Three-way nested ANOVA showed that there was no significant difference in total ostracod abundance at any of the spatial scales examined. However, the 9 most abundant ostracod species showed different patterns of abundance at the different spatial scales. Only 3 species showed significant variation in abundance between shores; however, most of the variation was recorded at the between-pool, within-shore level. Seven species showed a significant variation in abundance between pools nested within shores (100 to 200 m scale), but not from within pools (5 to 10 m scale). *Semicytherura nigrescens* showed a significant variation in abundance at the km scale and within-pool level but not between pools, whereas *Hirschmannia viridis* showed a significant difference in abundance at 5 to 10 m scales, but not at the other scales. There was significant variability in species richness (i.e. number of species per quadrat) at the km scale, but not at the other scales. However, there was a significant variability in assemblage diversity (H') at the km scale and the 100 to 200 m scale, but not at the 5 to 10 m scale. H' and the number of species per quadrat were significantly higher at Filey Brigg than on the other 2 shores. An MDS plot generated from a Bray-Curtis similarity matrix showed that the Flamborough samples formed a discrete cluster, whereas there was some overlap between the Filey and Ravenscar samples. Two-way nested ANOSIM showed that there was a significant difference in assemblage similarity both between shores using pools as samples and between pools using shores as samples. SIMPER indicated that the absence of *S. nigrescens* and relative abundance of 2 other species accounted for most of the dissimilarity between Flamborough and the other 2 shores. There was a significant negative correlation between the percent similarity and the spatial distance between quadrat pairs. The current study showed that there was considerable variation in individual ostracod species abundance and in the assemblage composition at the 3 spatial scales and that overall assemblage similarity decreased with spatial distance between samples.

KEY WORDS: Meiofauna · Marine ostracods · Assemblage structure · Spatial scale · Rocky shores · Tidepools · Diversity · Abundance · Similarity

INTRODUCTION

One of the primary concerns of marine ecologists has been to determine why different habitats support different numbers of species (Heck & Wetstone 1977). However, not only does the number and abundance of species vary between habitats, but also within a habitat at different spatial scales. This patchiness often complicates the patterns of species abundance and, as has been suggested, may not have been adequately

addressed in many marine studies (Morrisey et al. 1992). In emergent substrate intertidal assemblages, small-scale substrate heterogeneity appeared to account for most of the variance in species abundance, whereas much of the variance in species richness occurred at larger scales (km) (Archambault & Bourget 1996). In a study of the spatial patterns of distribution in intertidal invertebrates, Underwood & Chapman (1996) detected variation in abundance at all spatial scales examined. They suggested that the small-scale variability was the result of behavioural responses to small-scale differences in the micro-habitat, whereas variability at the scales of hundreds of metres along-

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shore was the result of differential recruitment and mortality of the species under study. They concluded that, by examining the abundance of organisms at a variety of spatial scales, both the processes acting upon the distribution of marine invertebrates and the scale at which they operate could be more clearly defined. Variation in the distribution of the rocky shore benthos has also been demonstrated at a micro-scale. Thompson et al. (1996) observed large differences in micro-algal species composition and diversity between bare rock, barnacle plates and the pits upon the surface of the barnacles. They also examined the diversity and abundance of the macrobiota and noted that barnacles supported a more diverse assemblage than did bare rock or clumps of *Fucus* spp. They stressed the importance of biological habitat provision in the maintenance of biodiversity and that, in order to describe biodiversity, assemblage structures should be examined at a variety of spatial scales.

Tidepools have not been as extensively studied as the emergent subtrata of rocky shores (Metaxas & Scheibling 1993). Recent studies have demonstrated that there is marked variability in tidepool faunal and algal assemblage composition with tidal elevation (for reviews see Hugget & Griffiths 1986, Metaxas & Scheibling 1994), within and between shores (e.g. harpacticoids: Hicks 1980; ostracods: Hull 1998; nematodes: Trotter & Webster 1983) and temporal variations in assemblage structure (for reviews see Hicks & Coull 1983, Hicks 1985, Metaxas & Scheibling 1994). Each tidepool is considered to be unique with respect to its physical structure, rate of flushing by the sea, etc., which may account for the observed high degree of variability in the structure of tidepool assemblages (Metaxas & Scheibling 1993). However, few studies have investigated the effect of spatial scale on the composition and abundance of tidepool meiofaunal assemblages.

Ostracods are important components of the phytal meiofaunal assemblage, along with nematodes, mites and harpacticoid copepods, which tend to be the dominant phytal taxa in terms of both species richness and abundance (Hicks 1985). Ostracod abundance and assemblage structure have been shown to vary on a temporal scale (Hull 1997), within shore related to tidal elevation (Horne 1982, Hull 1998), between different algal species with differing structural complexity (Whately & Wall 1975, Hull 1997), and between shores (Hull in press). As each tidepool can be considered a distinct habitat, there may be significant levels of variation between pools due to founder effects, physical processes or local population extinctions (Metaxas & Scheibling 1993). Although not as diverse or abundant as harpacticoids, phytal ostracod assemblages are a useful tool for examining the dynamics of tidepool assemblages as they form an important part of the

meiofaunal assemblage. The current study tests the hypothesis that variation is not significant in ostracod species abundance or in assemblage structure between 3 spatial scales: within pools on a 5 to 10 m scale, between pools within shores (100 to 200 m scale) and between shores (km scale).

METHODS

Sample collection and identification. Samples of intertidal algae were collected from 3 shores; the exposed shore on Peak Steel, Ravenscar (RS) (Grid Reference NZ/984021), the exposed shore of Filey Brigg (FBE) (Grid Reference TA/128816) and Selwicks Bay a moderately exposed bay on the north side of Flamborough Head (SB) (Grid Reference TA/257708). The location of the 3 shores is illustrated in Fig. 1.

Samples of *Corallina officinalis* L. (hereafter referred to by genus only) were collected from 5 large pools (minimum dimensions, 5 m length, 2 m width) in the mid-shore region of each of the 3 shores. As ostracod abundance and assemblage composition varies with both tidal height (Hull in press) and between different algal species (Hull 1997), only samples of *Corallina* were collected from mid-shore pools. Care was taken to ensure that there was little variation in *Corallina* morphology between pools and shores and that the percent cover of algae was similar in all pools sampled (approximately 60 to 70% coverage). Within each pool, 3 replicate samples of *Corallina* were collected from a depth of 10 to 15 cm using a 10 cm quadrat placed at random from within a 50 cm^2 area from both the left- and right-hand-side of each pool. An inverted plastic bag was placed over the quadrat, and the algae were scraped from the substrate into the bag in order to min-
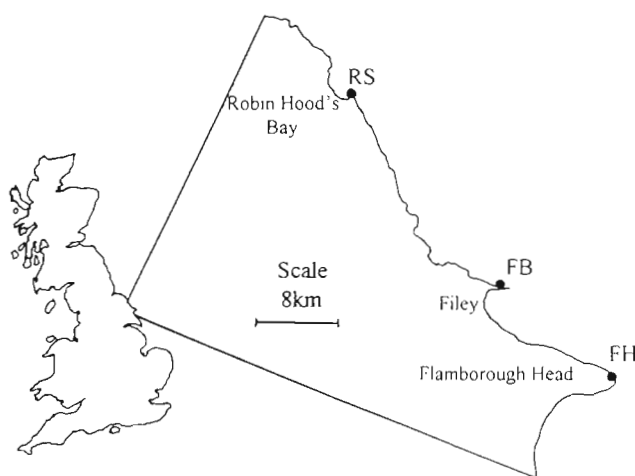

Fig. 1. Map of the north-east coast of England showing the location of the 3 shores sampled during the current study (RS: Ravenscar, FB: Filey Brigg; FH: Flamborough Head)

imise the loss of ostracods during sampling. By comparing the samples from either side of the pool, the variation in ostracod abundance and assemblage structure could be compared over a 5 to 10 m scale. The sampling regime allowed for the comparison of ostracod species abundance and assemblage structure at a km scale (between shores), 100 to 200 m scale (between pools within a shore) and a 5 to 10 m scale (opposing sides of each pool). All samples were collected during 3 d of sampling during 1 wk of spring tides in the last week of June 1997. The ostracods were removed from the algae and identified as described in Hull (1997). The taxonomy is based upon that of Athersuch et al. (1989), and all results are expressed as number of ostracods per 25 g dry weight of *Corallina*.

Data analysis. Cochran's test (Underwood 1997) was used to test for the homogeneity of variances, and to remove any heterogeneity all ostracod density data were $\log_{10} x + 1$ transformed prior to analysis of variance (ANOVA). Student-Newman-Keuls (SNK) tests were performed *a posteriori* to determine the source of the significance between means after 1-way ANOVA (Fowler et al. 1998). Three-factor nested ANOVA was used to determine if there was any significant variation in total ostracod abundance between shores (S), between pools (P) nested within shores, and between replicates collected from opposite sides of the pools (SP) nested within pool. The same procedure was also used to examine the patterns of abundance of the 9 most abundant ostracod species (total number of individuals sampled > 250). Shore, pool nested within shore and the side of pool nested within pool were random factors in the analysis.

Shannon-Wiener diversity (*H*') and number of species (*S*) were calculated for each replicate quadrat sample. As *H*' was normally distributed, ANOVA was used to test for significant differences in diversity as described above (Magurran 1989).

A Bray-Curtis similarity matrix was produced using group average clustering on square-root transformed ostracod abundance data (the default transformation) for each quadrat using the PRIMER (Plymouth Routines In Multivariate Ecological Research) analysis package. The resulting similarity matrix was then used to generate a multi-dimensional scaling (MDS) plot to produce a visual representation of the similarity of the quadrats. A 2-way nested analysis of similarities (ANOSIM) was applied to the similarity matrix in order to test the null hypothesis that there was no significant difference in similarity between the different shores or between pools nested within shores. ANOSIM calculates an overall global rho statistic (R-statistic), which is then compared to the R-statistic calculated for all the possible permutations of the replicates (Clark & Warwick 1994).

Using the quadrats as samples, the programme SIMPER from the PRIMER package was used to estimate the overall dissimilarity in assemblage structure between the shores (i.e. Filey versus Ravenscar, Filey versus Flamborough and Ravenscar versus Flamborough) and overall similarity of the samples within a shore. SIMPER was also used to determine the magnitude of the contribution of each species to the overall dissimilarity between the shores (Clark & Warwick 1994). The Bray-Curtis similarity matrix was also used to examine the relationship between distance between quadrat pairs and the ostracod assemblage similarity. The matrix was re-organised into a file which represented the percent similarity between paired quadrats on a variety of spatial scales, e.g. all within-pool, right- or left-hand-side sample comparisons (cm scale), between either side of the pool comparisons (5 to 10 m scale), between pools within shore (100 to 200 m scale), between Filey and Ravenscar (17 km), between Filey and Flamborough (25 km), and between Ravenscar and Flamborough (42 km). A Spearman rank correlation coefficient was used to determine if there was a relationship between distance between samples and percent similarity of the ostracod assemblage (Fowler et al. 1998).

RESULTS

Species abundance

A total of 19 ostracod species were recovered from the samples collected from the 3 shores. The mean abundance (expressed as number of individuals per 25 g dry weight of *Corallina*) of the total number of ostracods and the 9 most abundant species (>250 ind.) was examined at a variety of spatial scales using a 3-way nested ANOVA (Table 1). There was no significant difference in total ostracod abundance at any of the spatial scales examined. However, the pattern of variation in abundance at various spatial scales was not the same for the 9 most abundant species. Five species (*Paradoxostoma variabile* [Baird], *P. hibernicum* Brady, *P. ensiforme* Brady, *Heterocythereis albomaculata* [Baird] and *Xestoleberis aurantia* [Baird]) showed no significant variation between shores and either side of a pool nested within pool, but significant variation between pools nested within shores. *Cytherois fischeri* G. W. Müller and *Cythere lutea* O. F. Müller demonstrated significant levels of variation between shores and between pools nested within shores but not between samples from either side of the pool nested within pool. There was a significant difference in the abundance of *Semicytherura nigrescens* (Baird) between shores and between either side of a pool nested

Table 1 Summary table of the results of 3-way nested ANOVA for the total abundance of ostracods and the 9 most abundant ostracod species (total number of individuals sampled >250). S: shore, P: pool, PS: opposite sides of pool

Source	df	Mean square	F	p	Source	df	Mean square	F	p
Total ostracod abundance					**Paradoxostoma variabile**				
S	2	0.0317	0.95	0.415	S	2	0.6514	2.83	0.098
P (S)	12	0.0335	1.30	0.313	P (S)	12	0.2299	13.93	<0.0001
PS (P[S])	15	0.0258	1.81	0.054	PS (P[S])	15	0.0165	0.72	0.759
Residual	60	0.0142			Residual	60	0.0230		
Paradoxostoma hibernicum					**Paradoxostoma ensiforme**				
S	2	0.7732	1.53	0.257	S	2	0.5954	1.51	0.260
P (S)	12	0.5065	4.48	<0.0001	P (S)	12	0.3944	9.05	<0.0001
PS (P[S])	15	0.1131	1.36	0.200	PS (P[S])	15	0.0436	0.67	0.803
Residual	60	0.0834			Residual	60	0.0650		
Heterocythereis albomaculata					**Xestoleberis aurantia**				
S	2	0.2450	0.69	0.520	S	2	0.4706	1.34	0.300
P (S)	12	0.35641	8.69	0.001	P (S)	12	0.3527	6.03	0.001
PS (P[S])	15	0.0622	1.42	0.166	PS (P[S])	15	0.0584	0.99	0.481
Residual	60	0.0437			Residual	60	0.0593		
Cytherois fischeri					**Cythere lutea**				
S	2	1.7393	4.06	0.045	S	2	0.2450	10.61	0.002
P (S)	12	0.4288	6.49	<0.0001	P (S)	12	0.3541	3.24	0.017
PS (P[S])	15	0.0660	0.83	0.645	PS (P[S])	15	0.0622	1.26	0.255
Residual	60	0.0790			Residual	60	0.0437		
Semicytherura nigrescens					**Hirshmannia viridis**				
S	2	16.05	278.74	<0.0001	S	2	0.1635	0.84	0.455
P (S)	12	0.0576	0.44	0.921	P (S)	12	0.1943	1.26	0.331
PS (P[S])	15	0.1311	2.18	0.017	PS (P[S])	15	0.1540	4.69	<0.0001
Residual	60	0.0603			Residual	60	0.0348		

within pool but not between pools nested within shores. *Hirschmannia viridis* O. F. Müller showed significant differences in abundance only between samples from either side of the pool nested within pools.

Assemblage composition

There was a significant difference in the total number of species per quadrat at the shore level, but not at the other spatial scales examined (Table 2). At the shore level, samples from Filey Brigg contained significantly more species per quadrat (mean = 13.4 ± 1.1 standard deviation [SD]) than those from Ravenscar (mean = 12.3 ± 2.0 SD) and Flamborough (mean = 9.9 ± 0.9 SD), and the Ravenscar quadrats contained significantly more species than those from Flamborough (ANOVA, $F_{2,87}$ = 45.85, p < 0.001: SNK p = 0.05). There was also a significant difference in diversity (Shannon-Wiener H') between shores and between pools nested within shores (Table 2), but not between samples from opposing sides of the pools nested within pools. Overall, the diversity of the samples from Filey Brigg (mean = 2.20 ± 0.9 SD) was signifi-

cantly higher than that found at Flamborough (mean = 1.79 ± 0.15 SD) and Ravenscar (mean = 1.91 ± 0.27 SD) (ANOVA, $F_{2,87}$ = 36.4, p < 0.001: SNK p = 0.05), and there was considerable variation in diversity between the pools nested within each shore. In terms of individual species distribution, 14 species occurred on all 3 shores (*Paradoxostoma variabile*, *P. ensiforme*,

Table 2. Summary table of the results of 3-way nested ANOVA for the total number of ostracod species per quadrat and Shannon-Wiener diversity (*H'*). S: shore, P: pool, PS: opposite sides of pool

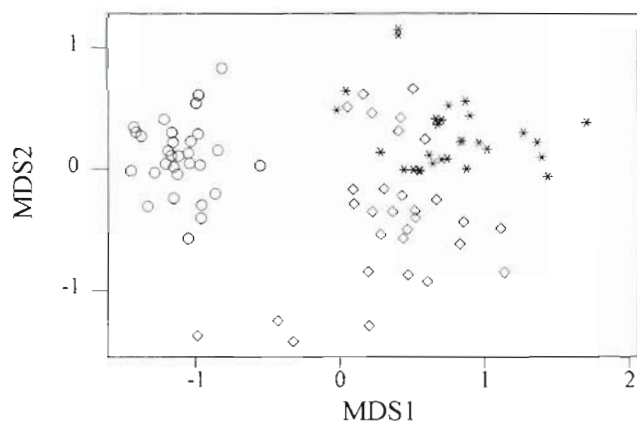| Source	df	Mean square	F	p
Number of species per quadrat				
S	2	95.67	26.58	<0.0001
P (S)	12	3.60	1.91	0.119
PS (P[S])	15	1.889	1.03	0.438
Residual	60	1.833		
Shannon Wiener (*H'*)				
S	2	1.2983	13.18	0.001
P (S)	12	0.0985	2.43	0.050
PS (P[S])	15	0.0397	1.81	0.054
Residual	60	0.0220		

Fig. 2. MDS plot generated from a Bray Curtis similarity matrix of the individual samples collected from each of the 3 shores. (O) Flamborough, (◊) Filey Brigg, (*) Ravenscar Stress = 0.078

in all cases (Filey average similarity between samples = 70.2%, Ravenscar = 75.9% and Flamborough = 78.9%). Tables 3 to 5 illustrate the species that contributed the most to the average dissimilarity between shores. Table 3 shows that 6 species accounted for 49.3% of the dissimilarity between Filey and Ravenscar; however, all 6 species were present on both shores. Five species accounted for 48.6% of the dissimilarity between Filey and Flamborough (Table 4). *Semicytherura nigrescens* accounted for 17.3% of this dissimilarity and was totally absent from Flamborough, yet it was a common species at Filey. A similar pattern was seen between Flamborough and Ravenscar where 5 species accounted for 45% of the dissimilarity between the shores (Table 5). *S. nigrescens* was common at Ravenscar but did not occur at Flamborough, and 1 further species, *Xestoleberis depressa*, was

P. hibernicum, P. nealei Horne & Whittaker, *P. normani* Brady, *P. robinhoodi* Horne & Whittaker, *Cythere lutea, Heterocythereis albomaculata, Hirschmannia viridis, Cytherois fischeri, C. pusilla* Sars, *Xestoleberis aurantia, Palmoconcha laevata* [Norman], and *Hemicytherura cellulosa* [Norman]). However, 2 species were found at Filey Brigg that did not occur at either Ravenscar or Flamborough (*Xestoleberis rubens* Whittaker and *Hemicythere villosa* [Sars]). A further 2 species were found at both Ravenscar and Filey Brigg but not at Flamborough (*Semicytherura nigrescens* and *Semicytherura sella* [Sars]) and *Loxoconcha rhomboidea* (Fischer) only occurred at Flamborough.

The MDS plot in Fig. 2 was generated from the calculated Bray-Curtis similarity matrix. The Flamborough quadrats formed a discrete separate cluster to the left of the diagram, and although most of the Filey Brigg samples clustered together there was an overlap in similarity between the Ravenscar and Filey Brigg samples. The nested ANOSIM indicated that there was a significant difference in assemblage similarity between shores using all pools as samples (R = 0.815, p < 0.001%) and between pools using shores as samples (R = 0.318, p <0.001%). Most of the observed difference in similarity appeared to be accounted for by the separation of the Flamborough samples from those of the 2 other shores. The within-shore average similarity between samples was high

Table 3. Species (ranked in order of importance) which contributed the most to the average dissimilarity in assemblage structure between the shores; comparison between Filey and Ravenscar (average dissimilarity = 30.6%)

Species	Average abundance at Filey	Average abundance at Ravenscar	% contribution to overall dissimilarity between shores
Paradoxostoma variabile	36.8	16.2	10.6
P. hibernicum	8.2	4.6	8.2
Hirschmannia viridis	20.6	14.1	8.0
Semicytherura nigrescens	21.0	20.7	7.5
P. ensiforme	14.6	11.6	7.5
Cytherois fischeri	3.3	5.1	7.5

Table 4. As for Table 3; comparison between Filey and Flamborough (average dissimilarity = 39.0%)

Species	Average abundance at Filey	Average abundance at Flamborough	% contribution to overall dissimilarity between shores
Semicytherura nigrescens	21.0	0.0	17.3
Cythere lutea	3.2	12.9	8.9
Paradoxostoma variabile	36.8	28.2	8.0
Cytherois pusilla	4.2	0.2	7.7
Hirschmannia viridis	20.6	18.6	6.6

Table 5. As for Table 3; comparison between Ravenscar and Flamborough (average dissimilarity = 42.3%)

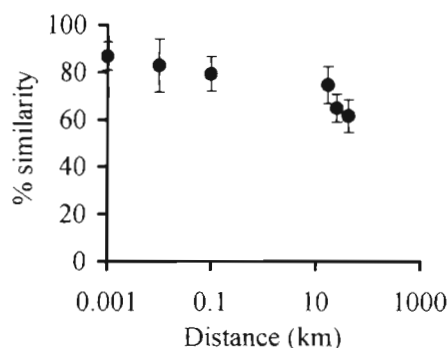| Species	Average abundance at Ravenscar	Average abundance at Flamborough	% contribution to overall dissimilarity between shores
Semicytherura nigrescens	20.8	0.0	17.8
Cytherois pusilla	5.6	0.2	8.0
Cythere lutea	4.1	12.9	7.2
Cytherois fischeri	5.1	0.4	6.1
Xestoleberis depressa	2.5	0.0	6.0

Fig. 3. Graph to illustrate the relationship between percent similarity (mean ± SD) and the distance on a log10 scale between quadrat pairs

found in low densities at Ravenscar but did not occur at Flamborough.

Fig. 3 illustrates the percent similarity in ostracod assemblages (mean ± SD) between 2 quadrats plotted against the distance between the quadrat pairs on a log scale. There was a significant negative correlation between the percent similarity between paired quadrats and the sampling distance between them (Spearman rank correlation coefficient, $r_s = -0.723$, p < 0.001). Therefore, the similarity of the ostracod assemblage decreased with increasing distance between the quadrat pairs. The relationship at first glance appears to be linear; however, further sampling is needed before the nature of the relationship can be fully described.

DISCUSSION

There were different patterns of variation in individual species abundance and in assemblage structure between the 3 spatial scales examined. Many different processes affect the distribution and observed differences in abundance of intertidal organisms, and hypotheses about these processes can be proposed once patterns have been identified at the appropriate spatial scales (Underwood & Chapman 1996). There was no significant variation in total ostracod abundance at any of the spatial scales examined; however, individual species showed variation in abundance at the different spatial scales. In 3 of the 9 species examined there was a significant variation in abundance between shores (km scale). Unlike many benthic invertebrates, ostracods have a limited dispersal capacity between shores as they deposit eggs upon the substratum, have no planktonic larval stage, nor are they active swimmers (Athersuch et al. 1989). However, all developmental stages of harpacticoids (once thought to have limited dispersal capacity) have been found suspended in the

water column and also attached to algal drift (Hicks & Coull 1983). The shores examined during the current study were inter-spaced by sandy beaches (an unsuitable habitat for phytal ostracods). However, ostracods may be able to disperse between shores by clinging to algal drift or transport in the water column (Hull in press). Such large-scale variation in species abundance could also be attributed to differences in reproductive activity, recruitment and mortality of the adults of the individual species between the shores (Underwood & Chapman 1996).

In a study of emergent substrate intertidal assemblages, Archambault & Bourget (1996) showed that much of the variation in species richness occurred at a large scale (km). In the current study, the number of species per quadrat also varied on a km scale but not at the smaller scales. Both diversity (H') and the number of species per quadrat were significantly higher at Filey Brigg than the other 2 shores. Average within-shore assemblage similarity was reasonably high (70 to 78.9%), but the figures also reflect within-shore variation between the separate quadrats. The MDS plot (Fig. 2) showed that much of the variation between shores was accounted for by the separation of the Flamborough samples from those of Filey Brigg and Ravenscar, and ANOSIM suggested that there was a significant difference in assemblage structure between shores and within shores. A closer examination of the pattern using the SIMPER procedure revealed that 3 relatively common species accounted for most of the dissimilarity between the Flamborough samples and those of the 2 other shores. One of these species, *Semicytherura nigrescens*, demonstrated a marked discontinuity in distribution between shores, being totally absent from Flamborough but present on the other 2 shores. This species is known to have a wide distribution throughout the British Isles (Athersuch et al. 1989), and the absence of this species from Flamborough cannot be explained at present. The overall pattern in assemblage structure was one of decreasing similarity with distance between quadrat pairs (Fig. 3), although total ostracod abundance did not vary between shores. This is a typical pattern, as samples collected from small spatial scales are generally more similar than those from further apart (Underwood & Chapman 1996). However, further sampling is required at intermediate distances between 0.1 and 17 km and at >42 km in order to further examine the nature of this relationship.

Seven out of 9 ostracod species showed variation in abundance on a scale of 100s of metres, i.e. between pools, reflecting local processes acting upon the tide-pool assemblages. Similarly, Metaxas & Scheibling (1994) found significant levels of variation in the abundance of most taxa sampled from between pools within

a tidal zone. Local differences in recruitment and extinction processes could be important factors that create variation in abundance between pools (Metaxas & Scheibling 1993). As already mentioned, most ostracods produce benthic egg masses and some species (e.g. the genus *Xestoleberis*) retain the eggs inside the carapace during the early stages of development (Hagerman 1978). Therefore, differences in abundance between pools could be the result of the differential patterns of reproduction between the separate pools.

It is possible that due to differential flushing rates, etc. (Metaxas & Scheibling 1994), small differences in temperature or differences in duration of higher temperatures between the pools could also affect patterns of abundance. Temperature affects the rate of growth and development of ostracod eggs and instars (Hagerman 1978), and Horne (1982) suggested that the development of instars proceeded at a faster rate at higher tidal levels. Therefore it is possible that minor variations in temperature regime could lead to differential hatching and development rates of the constituent species and therefore differences in abundance between pools. This may also account for the within-pool variability of *Hirschmannia viridis*, where samples taken from different sides of the pools showed significant variation in abundance.

Although not active swimmers, most ostracods are active crawlers and both *Cythere lutea* and *Heterocythereis albomaculata* are thought to undergo seasonal migration to the sublittoral zone during the winter months (Whately & Wall 1975). During periods of immersion, dispersal between pools is therefore highly likely in such species. However, other rarer species appear very patchy in their distribution, present in some pools but absent in neighbouring pools, and further investigations are required in order to estimate the ability of the different species to move between and colonise different pools.

The effects of grazing and predation are thought to be more intense in tidepools (Metaxas & Scheibling 1993). Coull & Wells (1983) investigated the effects of fish predation on meiofaunal assemblages. They found that *Corallina* acted as a refuge to the meiofauna preyed upon by the blenny *Helicogramma medium*. Sea anemones were thought to affect the abundance of the harpacticoid *Tigriopus californicus*, although fish were thought to be the major predators of this species (Dethier 1980). During the current study, the presence or absence of predators was not recorded, and the ostracods were sampled from *Corallina*, which is thought to provide a refuge against fish predators (Coull & Wells 1983). Some workers believe that fish predation is only important when the fish are trapped for long periods of time in a pool (Gibbons 1988); how-ever, it is not possible to rule out predation as a factor which may have affected ostracod abundance between pools.

Only 2 species, *Hirschmannia viridis* and *Semicytherura nigrescens*, demonstrated significant variation in abundance within pools (i.e. 5 to 10 m scale). Small-scale abundance patterns have been suggested to result from the behaviour of the organism in response to microhabitat changes (Underwood & Chapman 1996). Although the samples were collected from *Corallina*, variability in abundance may be the result of small-scale processes such as changes in food availability and water flow (Metaxas & Scheibling 1993).

Tidepools can be regarded as an intermediate habitat type between the subtidal and the emergent rocky shore benthos (Metaxas & Scheibling 1993), and care must be taken when comparing these habitats with the emergent benthos. Despite this note of caution, there are similarities between the dynamics of tidepool assemblages and those of the emergent substratum. Like the assemblages found upon the emergent substratum, tidepool assemblage structure has been shown to vary with tidal elevation and season (algae: Dethier 1982; ostracods: Hull 1997, 1998; hyperbenthic assemblages: Metaxas & Scheibling 1993; tidepool macrofaunal assemblages: Huggett & Griffiths 1986). Phytal meiofaunal assemblages have been shown to demonstrate variation in assemblage structure and diversity on a temporal scale (e.g. Johnson & Scheibling 1987, Preston & Moore 1989, Jarvis & Seed 1996) and between algal species with differing complexity (Gee & Warwick 1994, Jarvis & Seed 1996, Hull 1997). The current study also reflected the similarity between tidepool assemblages and those of the emergent substratum. In both assemblage types, species richness appeared to demonstrate significant variation on a large spatial scale (km) whereas variation in species abundance appeared to occur on a smaller scale (i.e. 100 m and 10 m scales). In order to describe the species richness and abundance of tidepool assemblages, samples should be collected from a range of spatial scales, both within and between shores.

LITERATURE CITED

Archambault P, Bourget E (1996) Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. Mar Ecol Prog Ser 136:111–121

Athersuch AJ, Horne DJ, Whittaker JE (1989) Marine and brackish water ostracods. Synopses of the British fauna (New Series) No. 43. EJ Brill, Bath

Clark KR, Warwick RM (1994) Changes in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, Plymouth

Coull BC, Wells JBJ (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64:1599–1609

Dethier MN (1980) Tidepools as refuges: predation and the limits of the harpacticoid copepod *Tigriopus californicus* (Baker). J Exp Mar Biol Ecol 42:99–111

Dethier MN (1982) Patterns and processes in tidepool algae: factors affecting seasonality and distribution. Bot Mar 25: 55–66

Fowler J, Cohen L, Jarvis P (1998) Practical statistics for field biology, 2nd edn. John Wiley & Sons, Chichester

Gee JM, Warwick RM (1994). Metazoan community structure in relation to the fractal dimensions of marine macroalgae. Mar Ecol Prog Ser 103:141–150

Gibbons MJ (1988) Impact of predation by juvenile *Clinus superciliosus* on phytal meiofauna: are fish important as predators? Mar Ecol Prog Ser 45:13–22

Hagerman L (1978) The life-cycle of three species of algal-living ostracods from brackish water. Ophelia 17: 231–237

Heck KL Jr, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J Biogeogr 4:135–142.

Hicks GFR (1980) Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. J Exp Mar Biol Ecol 44:157–192

Hicks GFR (1985) Meiofauna associated with rocky shore algae. In: Moore PG, Seed R (eds) The ecology of rocky coasts. Hodder and Stoughton, London, p 36–56

Hicks GFR, Coull BC (1983) The ecology of marine meiobenthic harpacticoid copepods. Oceanogr Mar Biol Annu Rev 21:67–175

Horne DJ (1982) The vertical distribution of phytal ostracods in the intertidal zone at Gore Point, Bristol Channel. J Micropalaeontol 1:71–84

Hugget J, Griffiths CL (1986) Some relationships between elevation, physico-chemical variables and biota of intertidal rockpools. Mar Ecol Prog Ser 29:189–197

Hull SL (1997) Seasonal changes in ostracod abundance and diversity on four species of algae with differing complexity. Mar Ecol Prog Ser 161:71–82

Hull SL (1998) The distribution and assemblage structure of ostracods (Crustacea: Ostracoda) on Filey Brigg, North Yorkshire. J Nat Hist 32:501–520

Hull SL (in press) Comparison of intertidal phytal ostracod (Crustacea: Ostracoda) species abundance and assemblage structure within and between four shores in northeast England. J Mar Biol Assoc UK

Jarvis SC, Seed R (1996) The meiofauna of *Ascophyllum nodosum* (L.) Le Jolis: characterisation of the assemblages associated with two common epiphytes. J Exp Mar Biol Ecol 199:249–267

Johnson SC, Scheibling RE (1987) Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. Mar Ecol Prog Ser 37:209–227

Magurran AE (1989) Ecological diversity and its measurement. Chapman & Hall/Princeton University Press, New York

Metaxas A, Scheibling RE (1993) Community structure and organisation of tidepools. Mar Ecol Prog Ser 98:187–198

Metaxas A, Scheibling RE (1994) Spatial and temporal variability of tidepool hyperbenthos on a rocky shore in Nova Scotia. Mar Ecol Prog Ser 108:175–184

Morrisey DJ, Howitt L, Underwood AJ, Stark JS (1992) Spatial variation in soft sediment benthos. Mar Ecol Prog Ser 81: 197–204

Preston A, Moore PG (1989) Seasonal cycles of abundance of the flora and fauna associated with *Cladophora albida* (Huds.) Kátz in rockpools. J Nat Hist 23:983–1002

Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. J Exp Mar Biol Ecol 202:73–84

Trotter D, Webster JM (1983) Distribution and abundance of marine nematodes on the kelp *Macrocystis intergrifolia*. Mar Biol 78:39–43

Underwood AJ (1997) Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, New York

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107:212–224

Whatley RC, Wall DR (1975) The relationship between Ostracoda and algae in littoral and sublittoral marine environments. In: Swain FM (ed) Biology and palaeobiology of Ostracoda. Bull Am Palaeontol Soc 65:173–203