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Intra-annual variability and patchiness in living assemblages of salt-marsh foraminifera from Mill Rythe Creek, Chichester Harbour, England

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ABSTRACT - The areas of coastal marsh studied in Mill Rythe Creek, Chichester Harbour, southern England, support a fluctuating foraminiferal assemblage which, although similar to those recorded in other parts of the UK and the Atlantic seaboard of North America, has its own distinctive assemblage of species. This is due to the constantly high salinity of the water here. Unusually, these marshes do not receive freshwater input from a nearby river and thus are not subject to tidal fluctuations in salinity.

The mid-marsh Site 1 has a fauna consisting of typical marsh species, e.g., *Jadammina macrescens*, *Trochammina inflata* and *Miliammina fusca*. In addition, normal marine salinity allows *Quinqueloculina oblonga* to flourish and even dominate the fauna in most samples. The lower marsh Site 2 contains a typical marsh fauna dominated by hyaline forms. The dominance of *Ammonia beccarii* [*aberdoveyensis*] is most characteristic of the lower marsh, together with *Haynesina germanica*. The normal marine salinity of the marsh can again be confirmed by the high abundance of *Quinqueloculina oblonga*.

The results of a replicate sampling regime employed in this study clearly demonstrate the patchy nature of the living foraminiferal distribution in marsh environments over small lateral distances as well as the high seasonal variability of foraminiferal abundances. *J. Micropalaentol.* **19**(1): 9–22, May 2000.

INTRODUCTION

Foraminiferal faunas living in marsh environments have been described from coastal areas around the British Isles, e.g., Dovey Estuary (Adams & Haynes, 1965; Haynes & Dobson, 1969); Christchurch Harbour (Murray, 1968); Norfolk (Phleger, 1970); Severn (Murray & Hawkins, 1976); Humber (Brasier, 1981); Southampton Water (Sharifi *et al.*, 1991); Tees Estuary (Horton, 1999); east, south and west coasts (Horton *et al.*, 1999a, b) and, closest to the present study area, the Hamble (Alve & Murray, 1994). Alve & Murray (1994) remark that the estuaries of southern England each have their own distinctive foraminiferal characteristics even though there are broad similarities. However, in Britain, as well as on the Atlantic coast of North America (e.g., Phleger, 1970; Steineck & Bergstein, 1979; Scott & Medioli, 1980; Scott *et al.*, 1981; Scott & Martini, 1982 and Goldstein & Frey, 1986) the marshes studied usually have freshwater input from a nearby river. Exceptions include De Rijk (1995), Saffert & Thomas (1998) and Gehrels & van de Plassche (1999). Also, many previous studies (with the exception of Horton's work) have sampled foraminifera from a single transect at one time during the year. Such studies therefore ignore intra-annual (and spatial) variations. The aim of the present study is to investigate an area of normal marine to hypersaline marsh, specifically to elucidate the temporal variation and small-scale spatial variation in the distribution of the foraminiferal faunas living there.

Mill Rythe Creek is located on the western side of Chichester Harbour. This harbour opens out into the sea just beyond the eastern end of the Solent estuarine system, Hampshire (Fig. 1a). The modern conformation of the Solent is derived from the post-glacial transgression of the sea into the Tertiary and Quaternary 'Solent River' system. The extensive intertidal basin of Chichester Harbour, and neighbouring Langstone and Portsmouth harbours, formed where the transgression flooded broad, unconfined valleys (Tubbs, 1980).

LOCATION

The area of Mill Rythe Creek is significantly different to many areas previously chosen for foraminiferal studies due to its constantly higher salinity (normal marine to hypersaline). Direct rain and run-off from surrounding land may temporarily depress the local salinity of the creek water, but this area is not subject to the regular large fluctuations in salinity that characterizes a tidal river estuary. With no fresh water input from a nearby river, Mill Rythe Creek has normal marine salinity, modified by evaporation and precipitation. Interstitial pore water salinity ranges from 32 to 41‰ (Table 1).

Table 1. Air temperature and intersitial pore water salinity measurements taken at time of sample collection (April 1996 to March 1997)

Date	Air temperature (°C)	Salinity of intersitial pore water (‰)	
		Site 1	Site 2
17/4/96	12.5	33	32
14/5/96	16.5	35	32
14/6/96	18.0	41	41
18/7/96	25.5	40	38
13/8/96	22.0	37	36
23/9/96	16.5	37	37.5
22/10/96	15.0	35	35
22/11/96	7.0	10 (heavy rain)	10 (heavy rain)
21/12/96	4.0	32.5	32
20/1/97	5.0	36	35
21/2/97	11.0	34	33
21/3/97	11.5	38	35

Chichester Harbour experiences a relatively large and regular diurnal variation in water temperature. Temperature variations in the harbour over a tidal cycle are more pronounced than in Southampton Water, for example, due to insolation of intertidal mud flats in summer or evaporative cooling in winter (Carr *et al.*, 1980). Air temperature was recorded in the present study, at the marsh surface at low tide (Table 1). Air temperature is probably several degrees lower than the surface water tempera-

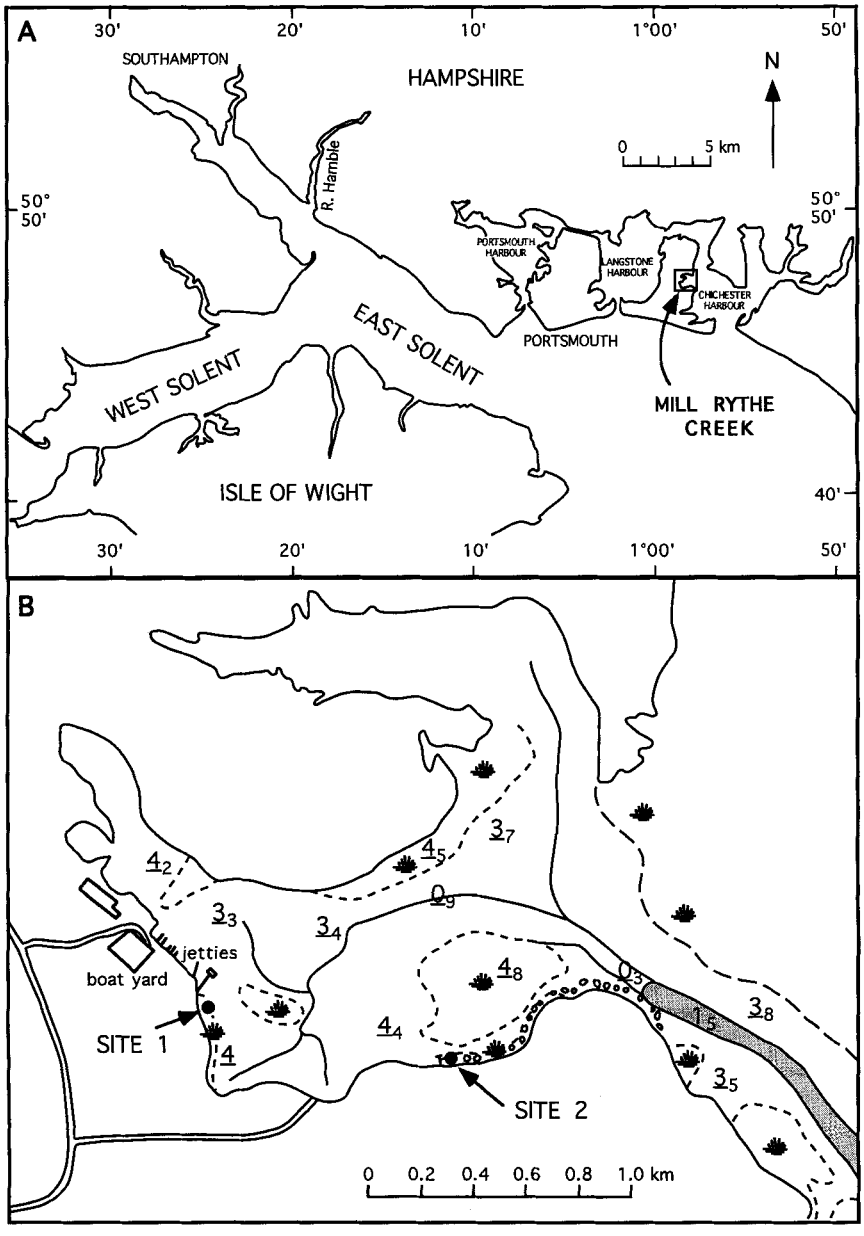

Fig. 1. A, B, Location maps for study area; B based on Admiralty Chart 3418, Langstone and Chichester Harbours, 1987. Drying heights, in metres (whole numbers underlined, fractions in subscript), are above chart datum. Shaded area shows channel which never dries out (always $\geq$1.5 m below chart datum); grass symbols indicate areas of salt-marsh; small circles following coastline near Site 2 indicate presence of gravel.

ture at high tide in winter and several degrees higher than the surface water temperature at high tide in summer. However, it provides a temperature measurement close to where the foraminifera are living at a known time in the tidal cycle, and so gives an indication of the temperature regime the foraminifera were experiencing.

Two readily accessible marsh sites were studied (Fig. 1b). Site 1 was located near to the head of the creek, on a mud bank colonized by *Spartina anglica*. The site chosen was close to the seaward extent of the marsh, which extended back at the same height about 20 m to a sea wall. The sediment consisted of soft, pale yellow mud and was in excess of 1 m thick. Grain size analysis showed that the sediment was 93% silt and clay ($<63\,\mu$m) and 7% sand (63–500 μm). This location is 4.4 m above chart datum, as calculated by measuring the height of water above the sediment surface at high tide on a specific day. This means that the site is usually covered at high water, but remains uncovered at lowest high water neaps, which is about 25% of the tides in a year. At mean high water springs the site is covered for 3 hours, 50 minutes in 12 hours (i.e., in each tidal cycle). (Chart datum is 2.74 m below Ordnance Datum (Newlyn); tidal data from Great Britain Admiralty Hydrographic Department, 1998.)

Site 2 was located about half-way to the main body of

Chichester Harbour. This site was again about 20 m from the sea wall, but the ground this time sloped gently upwards and there was a narrow strip of gravel between the marsh and the sea wall. The sediment here consisted of black mud, with fine sand and occasional gravel (85% $< 63\,\mu m$, 15% 63–500 μm). In addition, there was a higher concentration of minute plant fragments (of the cord grass (*Spartina anglica*) that makes up the marsh) in the sediment of Site 2, compared to Site 1. This mud was 45 cm deep, with a hard ground beneath. Site 2 is 3.9 m above chart datum, and so is covered at every high tide. The height of the mean high water neap tide is 4.0 m, (Great Britain Admiralty Hydrographic Department, 1998).

MATERIALS AND METHODS

Samples were taken at monthly intervals for 12 months from April 1996 to March 1997 at or slightly before low tide, when the marsh was fully exposed. Air temperature and salinity were recorded at the same time (salinity was measured using a refractometer; interstitial pore water was obtained by creating a small depression in the mud and waiting until sufficient water had filled it).

10 mm thick discs of mud were collected by gently pressing a section of plastic tubing into the mud to a depth of 10 mm (as marked on the tubing). A metal plate was then slid underneath to remove the disc. This was placed in a sample bottle and formalin added to cover the sample. Two discs (diameter 65 mm) were collected from immediately adjacent patches of mud for each sample, making the total volume of each sample 66 cm^3. Three replicate samples (each consisting of two discs) were taken from each sampling site. The replicate samples were collected (from a randomly chosen spot) within a 2 m^2 area, between cord grass (*Spartina anglica*) plants.

In the laboratory, processing was undertaken within two months of collection. Each sample was washed through a 63 μm mesh sieve, the residue placed in a bowl and stained with rose Bengal for 2–3 hours, washed again, during which the $> 500\,\mu m$ fraction (plant material and gastropods) was separated and discarded. The 63–500 μm fraction was then placed in an air-tight bottle together with enough water to prevent it drying out.

The sample was split so that all stained foraminifera from a known fraction of the original sample could be picked. The fraction was chosen in order to obtain at least 100 specimens, except where the fauna was too sparse. The water was carefully filtered off the sample using a hardened paper filter and the resulting cone of wet sediment was carefully divided with a knife into as many fractions as was feasible by this method. These fractions were stored in sample bottles, again under water. Rose Bengal stained foraminifera were then picked, under water, from the whole of the smallest fraction (dead specimens were not picked). If this did not provide enough specimens, further fractions were picked.

RESULTS

1. The relationship between the number of specimens and the number of species in a sample

The samples collected proved to contain a very variable concentration of living (stained) foraminiferal specimens, both between different months of collection and different sites, and also between replicate samples. From some samples over 300 specimens were picked, whilst from others it was impractical, due to time restraints, to pick through a large enough fraction to obtain 100 specimens (Appendix 2).

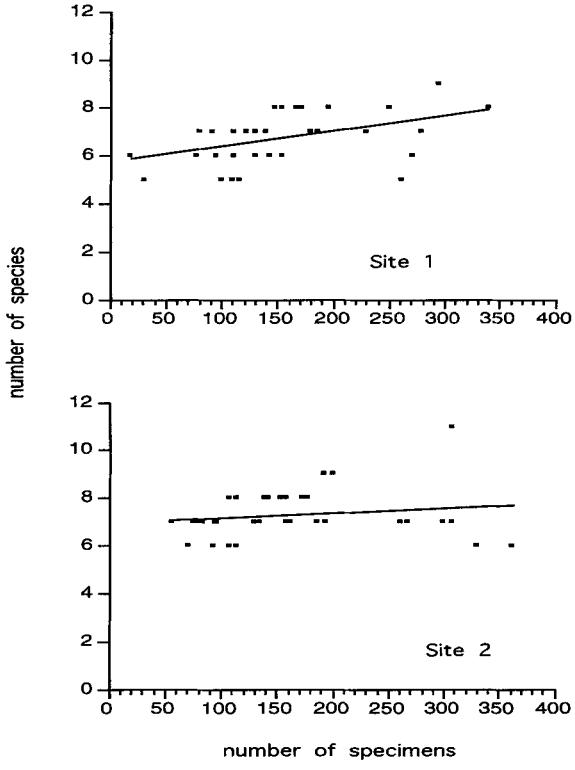

Fig. 2. Plots of number of species versus number of specimens for samples from Sites 1 and 2, with regression lines. (Very small samples excluded, see text.)

To assess the influence of these different sample sizes on the perceived composition of foraminiferal assemblage, the number of specimens was plotted against the number of species for all samples, data for Sites 1 and 2 being analysed separately. The regression coefficients for these plots are 0.64 for Site 1 and 0.34 for Site 2. Six samples have less than 60 specimens and have a notably lower number of species present than the rest. These are, for Site 1, one replicate of the samples collected in July and all replicates collected in August; and, for Site 2, one replicate collected in May and July. If these samples are excluded from the species vs. specimens plots the regression coefficients drop to 0.46 for Site 1 and 0.16 for Site 2 (Fig. 2a, b).

Only eight species consistently occur in the majority of the samples collected in this study. There are an additional eight rare species which only occur as isolated specimens. If the rare species are excluded from the regression analysis the coefficients drop further to 0.44 for Site 1 and 0.09 for Site 2. Thus, the data can be used to document real changes in faunal abundance of the of the dominant foraminiferal species; these variations are not merely artefacts of changing sample size. Data from Site 2 can be considered totally free of distortion. Potential distortion of the Site 1 data has to be considered.

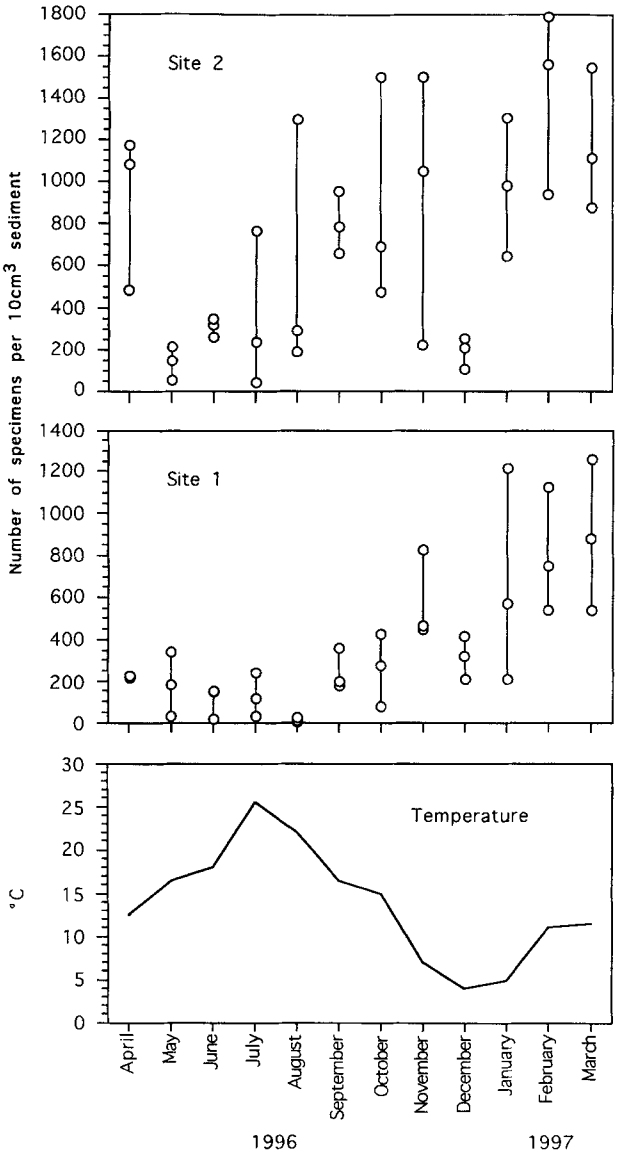

Fig. 3. Number of stained foraminifera per 10 cm^3 sediment in each of three replicate samples recovered per month for Sites 1 and 2 (lines connecting replicate samples included for visual clarity). Air temperature recorded at the same time.

2. Variation in numbers of foraminiferal specimens per 10 cm^3 through 12 months

Figure 3 shows numbers of stained foraminifera per 10 cm^3 for each month; data for sites 1 and 2 are plotted separately (Appendix 2). Replicate samples are shown: mean values are not given because of the high variability between the three replicates. The air temperature recorded at the time of sample collection is included for comparison (Table 1).

Site 1 first shows a general inverse relationship between numbers of foraminifera and temperature. The record begins with a relatively low abundance of foraminifera (≈220 per 10 cm^3) in April and then there is a general decrease to a minimum in August, mirroring a concurrent increase in temperature. From September, through October and November, there is a general increase in foraminiferal density as the temperature decreases. However, there is a notable reduction in December, coincident with the lowest recorded temperature of the year. Following this, foraminiferal numbers generally increase dramatically to their highest values in March, now following an increase in temperature into spring. The high abundance in the spring of 1997 indicates the presence of the benthic microfloral bloom, to which the benthic foraminifera respond opportunistically (Alve & Murray, 1994). An autumn algal bloom may have been present in 1996, as occurs along the Atlantic seaboard of North America (Murray, 1991).

Foraminiferal abundance is even more variable at Site 2, both from month to month and between replicates. There is a discernible minimum in May 1996 and numbers are consistently quite low in June. Replicate samples for July and August show very variable foraminiferal abundance. Samples collected in September show intermediate numbers, then data for October and November are again very variable. Foraminiferal density drops notably in December, after which there is a significant increase in spring 1997.

Comparing the two sites, the figures show that summer minima in foraminiferal numbers per 10 cm^3 occur earlier at Site 2 (May or June) than at Site 1 (August), but that there is a comparable decrease at both sites in December. Site 2 also supports generally higher numbers of foraminifera in each month, except December. It is also notable that, for Site 2, the figures for March 1997 are close to those of April 1996, suggesting that the cycle might repeat itself, but this is certainly not true of Site 1. Here, foraminifera were far more abundant in March 1997 than they were in April 1996. This hints at variability on a longer time scale, beyond the scope of this project.

3. Diversity indices

The Shannon species diversity index, $H(S)$ (Shannon, 1948), and the measure of equitability, E (Buzas & Gibson, 1969), were calculated for each replicate sample. These are plotted, together with number of species (S) in Figure 4a–f. Apart from low diversity values calculated for samples having a very low number of specimens, foraminiferal diversity appears to change little over the sampling period of one year. This reflects the consistently low number of species found in the marsh environment. Table 2 shows the ranges of S, $H(S)$ and E values calculated for all samples analysed except the very small samples (as highlighted in Figure 4). The variability of the diversity indices between replicate samples is illustrated by the range of the numerical difference between the highest and lowest value of the three replicates for ten replicate sets. (Two month's data sets are excluded from each site because they contain the very small samples: those with < 60 specimens and an anomalously low number of species.) The mean of this range is also given.

S and $H(S)$ values suggest that the foraminiferal fauna at Site 2 is slightly more diverse than that at Site 1. There also appears to be less variation between replicates at Site 2. Site 2 (with a more distal location) may represent a more homogenous environment with foraminifera living within a 2 metre area all experiencing more similar conditions than are present at Site 1. This is logical as Site 2 (low marsh) is covered at every high tide,

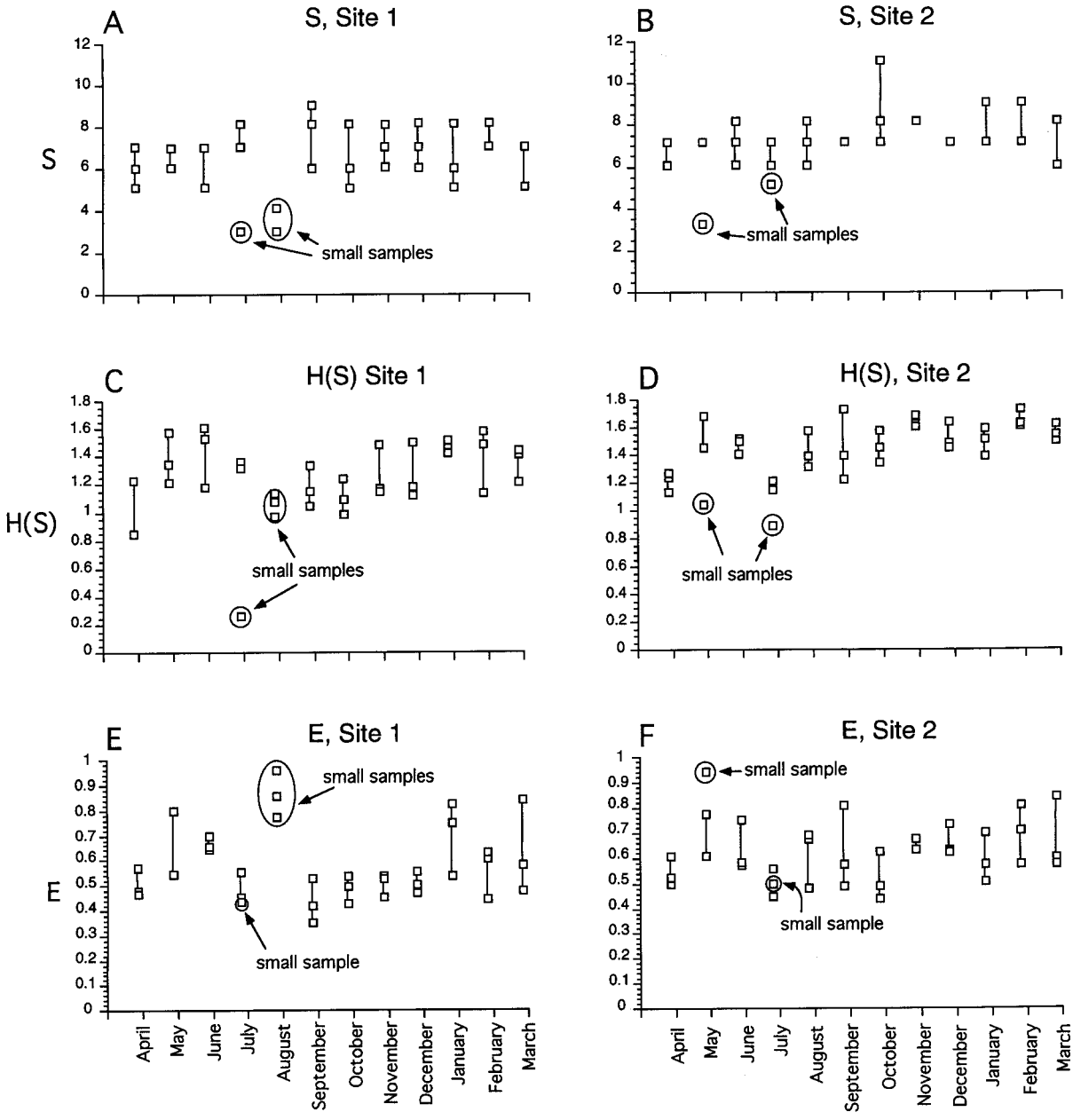

Fig. 4. Diversity indices for Sites 1 and 2; A, B: number of species, *S*; C, D: *H*(*S*) (Shannon, 1948); E, F: *E* (Buzas & Gibson, 1969). Lines connect replicate samples except small samples, which are those with < 60 specimens and anomalously low number of species.

whilst Site 1 (mid- to high marsh) is covered at only 75% of high tides and thus is a more variable environment. However, increased variability at Site 1 may also be at least partially attributed to the higher variability in the size of samples recovered from here. Values for *E* are not significantly different between the two sites.

The Fisher α index (Fisher *et al.*, 1943) is often used as a measure of species richness for foraminiferal faunas living in tidal environments (Murray, 1973). α values calculated for the present samples range from 0.9 to 1.95 (2.2 in one sample only). The range and variability of α are noted in Table 2, and α values and *S*, *H*(*S*) and *E* values are shown in Appendix 2.

4. Triangular plots of shell types

The relative proportion of agglutinated, porcelaneous and hyaline foraminifera in a sample can be described using triangular plots. Murray (1973) showed that foraminiferal faunas from tidal marshes of different salinity plotted in different areas of the triangle. Hyposaline marsh faunas generally do not contain any porcelaneous foraminifera, normal marine marsh faunas have generally ≥52% porcelaneous foraminifera and hypersaline marsh faunas can plot anywhere on the triangle. Figures 5(a) and 5(b), show plots for all samples from Site 1 and Site 2, respectively. The six anomalous samples (with < 60 specimens and a notably lower number of species)

Table 2. Diversity indices, S, $H(S)$, E and α; summary data for Sites 1 and 2, (data obtained from very small samples are excluded)

		Site 1	Site 2
S	Overall range of values	5–8 (9)*	6–9 (11)*
	Range of numerical difference between replicates	1–3	0–3
	Mean difference between replicates	2.1	1.4
$H(S)$	Overall range of values	0.8–1.6	1.1–1.7
	Range of numerical difference between replicates	0.23–0.44	0.11–0.25 (0.52)†
	Mean difference between replicates	0.32	0.19
E	Overall range of values	0.3–0.8	0.4–0.8
	Range of numerical difference between replicates	0.05–0.36	0.04–0.32
	Mean difference between replicates	0.16	0.19
α	Overall range of values	0.90–1.76	1.00–1.95 (2.2)*
	Range of numerical difference between replicates where α calculated for three replicates‡	0.40–0.50	0.19–0.48
	Mean difference between replicates where α calculated for three replicates‡	0.44	0.33

* one replicate only
† one set of 3 replicates only
‡ α only calculated for samples with over 100 specimens

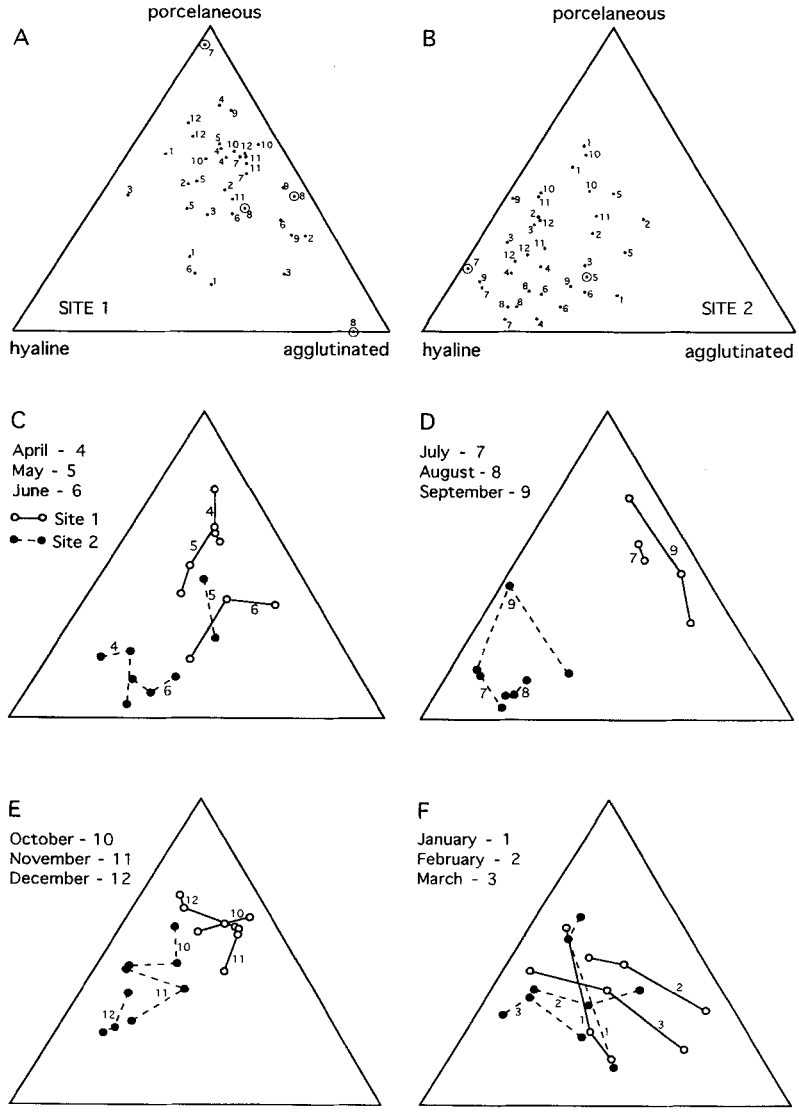

Fig. 5. Triangular diagrams of the ratio of the three foraminiferal shell types. Numbers refer to the month the sample was taken. Encircled points: anomalously small samples, not included in C–F. A–B: All samples plotted for Site 1 and Site 2 respectively. C–F: The same data divided into three-month periods. Lines join replicate samples. Site 1 data: open circles and solid lines, Site 2 data: filled circles and dashed lines.

shown as encircled points, are ignored in the analysis. Site 1 samples generally plot towards the top of the triangle, with 26 out of the 32 samples falling into the ≥33% porcelaneous area. Thirteen samples have ≥33% agglutinated foraminifera and only five samples have ≥33% hyaline foraminifera. By contrast, Site 2 samples generally plot towards the bottom left, hyaline, corner. Twenty-eight out of 34 samples have ≥33% hyaline forms. Thirteen samples have ≥33% porcelaneous and only five samples have ≥33% agglutinated foraminifera. Hence, there is a considerable difference between the foraminiferal fauna of Site 1 and Site 2, with hyaline forms being the least important component of the fauna at Site 1, but the most important at Site 2. Porcelaneous foraminifera are dominant to agglutinated foraminifera at both sites. According to Murray (1973) these results would be most characteristic of a hypersaline marsh, especially Site 1. This is expected as there is very little fresh water input (no streams) into the creek. Salinity recorded for the interstitial pore waters at Sites 1 and 2 in fact ranged from 32–41‰, depending on evaporation/precipitation (Table 1). The salinity at Site 2 was usually 1–3‰ less than at Site 1, due to the higher elevation of Site 1 and therefore the longer period of exposure and evaporation at low tide (or continuous exposure at lowest low water neap tides).

Figures 5(c)–(f) show the same data divided into three-month periods and show both Site 1 and Site 2 data on the same plots. Data collected for Site 1 in April to June 1996 plots within the ≥33% porcelaneous, ≥33% hyaline area of the triangle (except for one June replicate). During the months of July and September hyaline forms fall to a minimum. During October, November and December the fauna is consistently high in porcelaneous forms. In January, February and March 1997, Site 1 samples have a much wider range of composition between replicates, and generally have fewer porcelaneous foraminifera and more agglutinated foraminifera.

Site 2 samples taken between April and September 1996 comprise >50% hyaline forms, except for those for May (27–33%). October's samples plot nearer to the porcelaneous corner of the triangle, but November and December's samples plot progressively closer to the hyaline corner once more. In January, February and March 1997 Site 2 samples have a much wider range of composition and plot more towards the centre of the triangle. During these months the foraminiferal fauna from Sites 1 and 2 is most similar; the plots overlap in the central area of the triangle.

5. Distribution of major species: relative abundance

The dominance of porcelaneous foraminifera at Site 1 is due to the high relative abundance of *Quinqueloculina oblonga* (Montagu). This species dominates the fauna in 25 of the 32 samples (the six anomalous samples are excluded from analysis) (Appendix 2). All replicate samples show *Q. oblonga* as dominant, except some of those taken in June, September, January, February and March. At these times *Jadammina macrescens* (Brady) dominates one or two of the replicates. This species makes a significant contribution (10–30%) to most samples throughout the year, except April and May, when *Miliammina fusca* (Brady) is a more common agglutinated species. *Trochammina inflata* (Montagu) makes up <1–7% of the foraminiferal fauna in most samples from Site 1. The subordinate hyaline forms are represented by the *Ammonia beccarii* (Linné) group [form: *A. aberdoveyensis* Haynes, 1973], which comprises over 10% of the fauna in some samples taken in April to June 1996 and December 1996 to March 1997. Also, *Elphidium williamsoni* Haynes comprises over 10% of the fauna in one sample replicate taken in October and November, and two or three replicates taken in January to March. *Haynesina germanica* (Ehrenberg) comprises over 10% of the fauna in only one sample, taken in May, but as this is one of the very small samples containing an anomalously low number of specimens, this is not significant.

The *Ammonia beccarii* group [form: *A. aberdoveyensis*] dominates the fauna at Site 2 in all samples taken between April and September 1996 (except one replicate taken in May) (Appendix 2). (This species is referred to as *Ammonia beccarii* in the continuing text and figures to facilitate comparison with previous studies in which this broader taxonomic category is used.) From October 1996 to March 1997, *Quinqueloculina oblonga* is usually the dominant single species, although *A. beccarii* dominates again in one replicate taken in November, in December, and in two replicates taken in March. However, hyaline forms are also represented by *Haynesina germanica*, which forms over 10% of the fauna in September 1996 and from November 1996 to March 1997. This is despite the fact that this species is more usually associated with lower salinity marsh environments (Murray, 1991). *Haynesina germanica* also forms over 10% of the fauna in one or two replicates taken from June to August and in October 1996. The agglutinated foraminifera *Jadammina macrescens* and *Miliammina fusca* make up a significant portion of the faunas from Site 2, and each dominates in one sample (in January 1997 and May 1996, respectively). *Elphidium williamsoni* is a minor component of all Site 2 samples, taken throughout the year.

6. Distribution of major species: absolute abundance

The absolute abundance (number of specimens per $10\,cm^3$ sediment) measured each month can be used to detect when each species is reproducing in the area of marsh represented by each replicate sample. Although the abundance (per $10\,cm^3$) of every foraminiferal species varies considerably between replicate samples taken at the same time, the replicate with the highest abundance recorded for each month gives an indication of the potential level of reproduction of the species. At Site 1, *Ammonia beccarii*, *Quinqueloculina oblonga* and *Jadammina macrescens* all have peaks of abundance (in one replicate at least) in May and November 1996 and January and March 1997, the 1997 peaks being considerably larger, (Fig. 6). *Elphidium williamsoni* also has peaks of abundance at these times, with the exception of May 1996. *Miliammina fusca* peaks in April 1996 and January 1997, and *Trochammina inflata* peaks in November 1996 and February 1997.

At Site 2, the foraminiferal species differ more in their precise times of peak abundance. However, *A. beccarii* and *Q. oblonga* peak first in April 1996. Then there are peaks between August and November in *A. beccarii*, *Q. oblonga*, *J. macrescens* and *Haynesina germanica*. A large peak in abundance is seen in all these species in January, February or March 1997. All species exhibit a large drop in numbers in December 1996 (Fig. 6).

The foraminifera therefore appear to be reproducing fastest in

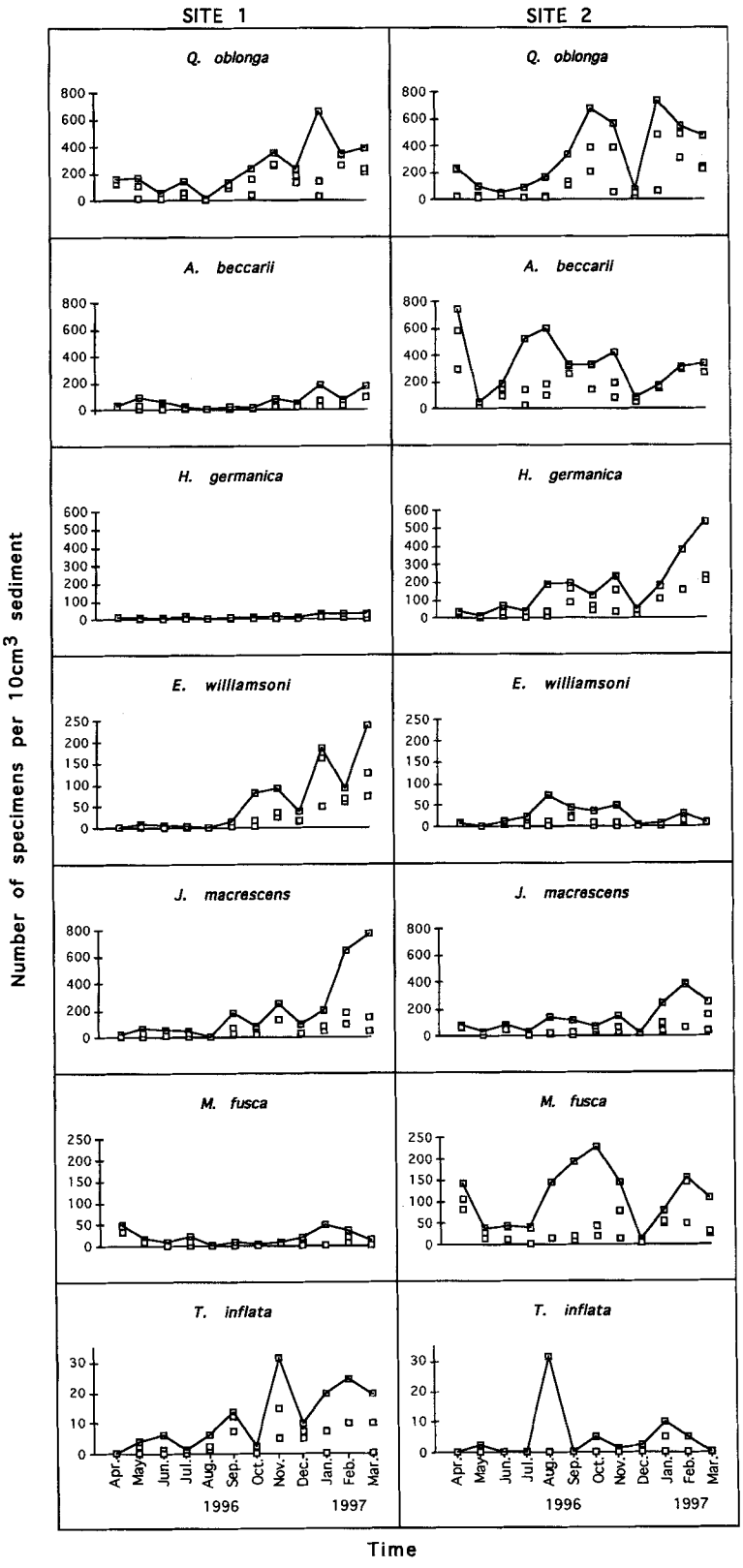

Fig. 6. Abundance plots (specimens per 10 cm^3 sediment) for the seven most common species in Sites 1 and 2, between April 1996 and March 1997. (Lines connect replicates with maximum species abundance.)

Spring 1996, Autumn 1997 and Spring 1997. These times coincide with the Spring and Autumn algal blooms, as deduced by the variations in specimens per $10\,cm^3$ of the whole foraminiferal assemblage.

DISCUSSION

Patchiness and seasonal variability

Perhaps the most striking feature of the foraminiferal fauna investigated in this study is the high variability between replicate samples collected at the same time within an area of about $2\,m^2$. Concerning the number of foraminifera per $10\,cm^3$, the average variability is 459% for Site 1 and 353% for Site 2. These findings equate with Murray's theoretical Model 1 of low diversity, patchy distribution, which he notes is characteristic of marshes and other variable environments (Murray, 1973, 1991). Murray considers that this clumped distribution pattern is caused by microenvironments and the need for reproduction (sexual reproduction needs an aggregation of the same species). Schafer (1971) also describes how such schizogamy may favour clumping and Shifflett (1961) suggests that patchiness is caused by certain species living in colonies. Schafer (1971) suggests that patchiness may be eliminated by simply using mean or modal values of replicate samples. However, seven to ten replicates per sample are needed to ensure an accurate mean value (Brooks, 1967). This was beyond the resources of the present study and so mean values are not discussed here.

Reproduction is to a large extent controlled by food supply. The increase in foraminiferal numbers per $10\,cm^3$ in Spring 1997 is probably the result of a phytoplankton bloom. Murray (1991) suggests that because blooms are patchy in their distribution, it is possible that this in turn causes patchiness in the abundance of foraminifera. In May 1996 there is almost a 1500% difference between the highest and lowest number of foraminifera per $10\,cm^3$ recorded in the replicate samples taken at Site 1. This variability is greater than at any other time. High variability in foraminiferal abundance at Site 2 in Spring 1996 is evident by the particularly low numbers of specimens recovered from samples in May.

Patchy distributions of marsh foraminifera have also been described by Hohenegger *et al.* (1989), on a decimetre scale, in an intertidal pool in the North Adriatic Sea. They consider that the microdistribution patterns of foraminifera were related to those of algae, but that, as well as food resources, competition between foraminiferal species could control foraminiferal distribution.

The patchy nature of species distribution is illustrated by the large difference in specimens per $10\,cm^3$ between replicate samples (Fig. 6). This is shown, for example, by the differing number of *Quinqueloculina oblonga* specimens recovered in each replicate taken in January 1997 at Sites 1 and 2; by the *Ammonia beccarii* data (August 1996, Site 2) and by the *Jadammina macrescens* data (February 1997, Site 1). The replicate samples that contain very high numbers of a species may have been located at sites of clumped reproduction, whereas those collected only $\geq 2\,m$ away have missed these sites.

Size distribution in *Ammonia beccarii* was investigated to see if clumped reproduction sites could be identified this way. This would be suggested by a higher number of small (juvenile) individuals. All *A. beccarii* specimens from all replicate samples from Site 2 were measured (longest dimension). The most striking record of juveniles occurring in one replicate and not another taken at the same time is found in the data from June 1996. Juveniles (specimens $< 0.2\,mm$) make up 43% of *A. beccarii* individuals in one replicate (2C), whereas no specimens of this size range were found in replicate 2B and only 3% juveniles occurred in 2A. Three other replicate sets show juveniles to be present in significantly greater proportions in one replicate versus the other two. These are samples taken in October 1996 (% specimens $\geq 0.1\,mm$ diameter: 2A = 0, 2B = 18, 2C = 2), February 1997 (% specimens $\geq 0.1\,mm$ long: 2A = 14, 2B = 0, 2C = 0) and March 1997 (% specimens $\geq 0.13\,mm$ long: 2A = 0, 2B = 3, 2C = 0). The large number of *A. beccarii* juveniles in one replicate out of the three, collected in June (particularly) and October, February and March, suggest the presence of clumped reproduction sites. However, Figure 6 shows that the absolute abundance of *A. beccarii* in each replicate sample does not vary as much in these months as it does in others. The abundance of *A. beccarii* in all replicates collected in June 1996 is relatively low. Alve & Murray (1994) reported that the standing crop of living assemblages of *A. beccarii* was low in the River Hamble (Hampshire coast) in June (1992) and inferred the cessation of the Spring benthic microfloral bloom. A high abundance of juveniles may not therefore be indicative of high reproduction rates in the population as a whole, but can locate a reproduction site.

Comparison between the two sites

Despite the patchiness of the foraminiferal populations in Mill Rythe Creek, a distinct difference in the composition of the fauna at Site 1 and Site 2 can be recognized. Porcelaneous forms (*Q. oblonga*) and agglutinated forms (*J. macrescens, M. fusca* and *T. inflata*) dominate Site 1, with subordinate hyaline forms (*A. beccarii* and significant *E. williamsoni*). Conversely, hyaline forms dominate Site 2 (*A. beccarii* and *H. germanica*, but fewer *E. williamsoni*); porcelaneous forms (*Q. oblonga*) are secondary and agglutinating forms (*J. macrescens* and *M. fusca*) are least important. Differences in other aspects of the foraminiferal fauna are more subtle. There is generally a greater abundance of foraminifera at Site 2, compared to Site 1, but numbers are also more variable in Site 2. The Spring peak of foraminiferal abundance occurs at both sites, but the Summer minimum occurs earlier at Site 2: May to June, as opposed to August for Site 1. Site 2 faunas are slightly more diverse than those of Site 1.

The prime reason for the differences in the foraminiferal faunas at the two sites must be the difference in elevation. Site 1 is an area of mid- to high marsh, as it does not get covered at every high tide (only 75% of them). Site 2 is an area of low marsh that is covered at every high tide. Site 1 is about 1 km farther inland than Site 2; Site 2 is nearer to the main body of Chichester Harbour and thence to the open sea. Hayward *et al.* (1996) found that proximity to the open sea was a factor in determining faunal distribution by canonical correspondence analysis, but was less important than tidal exposure, salinity and percentage of mud. De Rijk (1995) found that the distribution of salt marsh foraminifera in the Great Marshes, Massachusetts was related to salinity variation rather than elevation. The major influences on the salinity of the pore water were seepage of fresh groundwater and infiltration of sea water and rain-water.

However, in the present study only minor differences in salinity were apparent between Sites 1 and 2. The slightly higher salinity of Site 1 is probably due to the longer time of exposure between tides.

Site 1 is located on a mud bank; the sediment consists of pale (more aerated) mud with plant fragments and a relatively low concentration of sand or silt grains. At Site 2, there is a thin surficial grey (aerated) layer, from which the samples were collected (0–1 cm depth) overlaying black (anaerobic) mud. Both include more silt or fine sand than at Site 1 and some gravel. There is also a more dense growth of *Spartina anglica* at Site 2. Hayward *et al.* (1996) consider substrate type to be third in importance in determining faunal distribution. In the present study, infaunal foraminiferal morphotypes (*Ammonia beccarii*, *Haynesina germanica* and *Miliammina fusca*) are more abundant at Site 2 (Fig. 6). Conversely, some epifaunal morphotypes are more common at Site 1: e.g., *Jadammina macrescens*; *Trochammina inflata* (which can be epifaunal or infaunal, Murray, 1991). However, *Quinqueloculina oblonga*, which is epifaunal, free or clinging to plants (Murray, 1991), is more abundant at Site 2. The high abundance of this species at Site 2 may be due to the denser growth of *Spartina* grass there.

Comparison with other areas

Murray (1991) describes five species associations that occur in the marshes of northern Europe. The *Jadammina macrescens* and *Trochammina inflata* associations are characteristic of high marshes, which are not covered with water every day, only at Spring tides. Porcelaneous tests are present only in normal marine examples (e.g., the *T. inflata* association of the Netherlands, Phleger, 1970). The Netherlands example compares with that found at Site 1 except that Site 1 has *J. macrescens* as the dominant agglutinated species, and that, whereas miliolids (*Q. oblonga*) are usually dominant here, in the Netherlands miliolids are always significantly less important than agglutinated species. Phleger (1970) also notes that miliolids are usually more common in low marsh environments. Horton (1999) also found *Quinqueloculina* spp. in his samples from the Tees Estuary, although, again, only at relatively low abundance. The foraminiferal fauna at Site 1 compares with Horton's middle marsh Zone JM and low marsh Zone MF, except for his high abundance of *Miliammina fusca* in the latter. Other features of high marsh faunas are a low diversity ($\alpha < 2$, compared with Site 1: $\alpha = 0.9$–1.8) and a preference for a fine-grained substrate.

Murray (1991) also describes *Trochammina inflata* associations from the Atlantic seaboard of North America, which he categorizes as 'mid marsh'. This height is comparable to Site 1 of this study, which is covered by the high tide 75% of the time. The *Trochammina inflata* association was found by Scott *et al.* (1981) on Prince Edward Island and Scott & Medioli (1980) in Nova Scotia. These authors defined vertical zonations with respect to elevation. The zonations vary slightly between marshes but appear to remain broadly similar throughout the world (Scott & Medioli, 1980). The highest zone, IA, consisting almost exclusively of *Jadammina macrescens* (their *Trochammina macrescens*), occurs just below higher high water. *Trochammina inflata* is found below this in Zone IB (high to mid-marsh), which is usually dominated by *J. macrescens* (again, their *Trochammina macrescens*). Scott & Medioli (1980) remark that *Trochammina inflata* is present in higher abundance at this level in more saline marshes. They also observe that in marshes of normal to higher salinity (Holland, California), Zone I is dominated by *T. inflata* and *Jadammina polystoma* (a name they assign to *Jadammina macrescens* possessing supplementary apertures). Site 1 of the present study may be assigned to Zone IB of Scott & Medioli (1980) and Scott *et al.* (1981) as *Jadammina macrescens* (with supplementary apertures) and *Trochammina inflata* occur here. However, there are some differences between the faunas. *Miliammina fusca*, which sometimes occurs quite abundantly at Site 1, is a key species of the mainly low marsh Zone II (Scott & Medioli, 1980). The fauna studied by Scott *et al.* (1981) has a complete absence of calcareous species, which they attribute to reduced dissolved oxygen and depressed pH levels. In Mill Rythe Creek, these are not limiting factors, calcareous foraminifera thrive. The dominant calcareous form at Site 1, *Quinqueloculina oblonga*, was also found abundantly near Sapelo Island, Georgia, by Goldstein & Frey (1986, their *Triloculina oblonga*).

The other three northern European marsh foraminiferal associations described by Murray (1991) occur in low marshes, which are covered at every high tide. The *Ammonia beccarii* association is the fauna characteristic of marshes of normal marine salinity. This association typically has an α diversity value of < 3, occurs in muddy silt and sand substrates, and contains *Haynesina germanica* and miliolids as well as a minor *Jadammina macrescens* component. The foraminiferal fauna found at Site 2 in Mill Rythe fits well into this association. The main components of this association are found widely in Britain, e.g., Dovey Estuary (Haynes & Dobson, 1969); Norfolk (Phleger, 1970); Hamble Estuary (Alve & Murray, 1994); Tees Estuary (Horton, 1999); Europe, e.g., the Netherlands (Phleger, 1970) and Jade Bay, Germany (Langer *et al.*, 1989); and the Atlantic seaboard of North America, e.g., Long Island (Steineck & Bergstein, 1979); Nova Scotia (Scott & Medioli, 1980) and Sapelo Island, Georgia (Goldstein & Frey, 1986). However the precise composition of the fauna is very variable. For example, in the Hamble (Alve & Murray, 1994) *Elphidium excavatum* (Terquem), *Ammobaculites balkwilli* Haynes, *Nonion depressulus* (Walker & Jacob) and *Bolivinellina pseudopunctata* (Höglund) were common, but these species do not occur in the present study area. Scott & Medioli (1980) describe their low marsh faunal Zone II as 'much more complex' than the high and mid-marsh Zone I, 'being controlled more by locally dominant estuarine-lagoon forms than by marsh forms'. Alve & Murray (1999) studied the living (stained) foraminifera from low salinity marginal marine areas of the Skagerrak and Kattegat coast, eastern North Sea. They categorized *Trochammina inflata* and *Jadammina macrescens* as being 'basically, but not entirely associated with marsh plants' and *Miliammina fusca*, *Elphidium williamsoni*, *Haynesina germanica* and *Ammonia beccarii* (*A. tepida*) as being 'characteristic of non-marsh areas but sometimes present at the seaward edge of marshes'. This accords with the findings of the present study, where *T. inflata* and *J. macrescens* are more typical of the mid- or high marsh and the calcareous species are more typical of the low marsh.

Implications for palaeo-environmental interpretation

Various taphonomic processes may alter the composition of the

foraminiferal fauna found living in the marshes of Mill Rythe Creek. Firstly, the empty tests of exotic species may be transported into the area, as discussed by Alve & Murray (1994). This would probably result in minor differences between the living and dead assemblage: few dead specimens were observed in this study except for those belonging to species also found alive.

Agglutinated forms may be lost by post-depositional processes (as postulated for a deep water assemblage by Swallow & Culver (1999)). The average proportion (percentages) of agglutinated to hyaline to porcelaneous foraminifera in the living assemblages studied is 33 : 19 : 48 for Site 1 and 20 : 51 : 29 for Site 2. If agglutinated foraminifera were lost, Site 1 would average 28% hyaline and 72% porcelaneous and Site 2 would average 64% hyaline and 36% porcelaneous. The coexistence of the porcelaneous species *Quinqueloculina oblonga* and the hyaline species *Haynesina germanica*, *Elphidium williamsoni* and *Ammonia beccarii* would still suggest a normal marine salinity marsh environment, but the agglutinated species characteristic of the high marsh would be lost. The results of the present study suggest that the lower ratio of hyaline to porcelaneous foraminifera may be useful in distinguishing a mid–upper marsh environment but only if it had normal marine salinity.

Dissolution may also be a major taphonomic process in marsh settings. Alve & Murray (1994) observed that the effects of dissolution on a foraminiferal fauna from a marsh sample left the abundance of *Trochammina inflata* and *Jadammina macrescens* enhanced. Also, Murray & Alve (1999) and Horton (1999) found that dissolution of calcareous species greatly increased the proportion of agglutinated species in dead (versus living) assemblages. With only agglutinated species present, differentiation of high and low marsh palaeo-environments would be more difficult, although a high abundance of *Miliammina fusca* is characteristic of a low marsh environment. If, in the present locality, only the hyaline species were lost, porcelaneous tests being more robust, the average ratio of agglutinated to porcelaneous foraminifera would be identical for Site 1 and Site 2 (41 : 59 percent).

CONCLUSIONS

The areas of marsh found in Mill Rythe Creek support a fluctuating foraminiferal assemblage which, although similar to those recorded in other parts of the UK and the Atlantic seaboard of North America, has its own distinctive assemblage of species. The mid-marsh Site 1 has a fauna consisting of typical marsh species, e.g., *Jadammina macrescens*, *Trochammina inflata* and *Miliammina fusca*. In addition, normal marine salinity allows *Quinqueloculina oblonga* to flourish and even dominate the fauna in most samples. *Elphidium williamsoni* also occurs, together with *Ammonia beccarii* and *Haynesina germanica*, but it is the low relative abundance of hyaline forms that characterizes the mid-marsh assemblage.

The lower marsh Site 2 contains a typical marsh fauna dominated by hyaline forms. The dominance of the *Ammonia beccarii* group [form: *A. aberydoveyensis*] is most characteristic of the lower marsh, together with a higher abundance of *Haynesina germanica*. The normal marine salinity of the marsh can again be confirmed by the high abundance of *Quinqueloculina oblonga*. Agglutinated foraminifera as a whole are least abundant in Site 2, but *Miliammina fusca* is more abundant here than at Site 1.

The results of the replicate sampling regime employed in this study clearly demonstrate the patchy nature of the living foraminiferal distribution in marsh environments over small lateral distances as well as the seasonal variability of live foraminiferal abundances. This is in contrast to foraminiferal death assemblages, which Horton (1999) found to be relatively stable over a twelve-month period and which were similar to subsurface samples collected at a depth of 70 mm.

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APPENDIX 1. FAUNAL REFERENCE LIST AND NOTES

Quinqueloculina oblonga (Montagu)
Vermiculum oblongum Montagu, 1803, p. 522, pl. 14, fig. 9.
There is some difficulty with regard to the identity of the Montagu species as the type specimens (Walker and Boys) are lost. Until the species concept has been clarified and the neotype designated the present specimens are placed into *Q. oblonga*. They have a distinct bifid tooth.

Ammonia beccarii (Linné) (group)
Nautilus beccarii Linné, 1758, p. 710.
Forms described as *A. aberdoveyensis* (Haynes, 1973).

Jadammina macrescens (Brady)
Trochammina inflata (Montagu) var. *macrescens* Brady 1870, pp. 290–291, pl. 11, fig. 5a–c.
Typical trochospiral forms.

Haynesina germanica (Ehrenberg)
Nonion germanicum Ehrenberg, 1840, p. 23.

Elphidium williamsoni Haynes 1973
Elphidium williamsoni Haynes 1973, pp. 207–209; pl. 24, fig. 7; pl. 25, figs 6–9; pl. 27, figs 1–3.

Miliammina fusca (Brady)
Quinqueloculina fusca Brady, 1870, p. 286, pl. 11, figs 2–3.

Trochammina inflata (Montagu)
Nautilus inflatus Montagu, 1808, p. 81, pl. 18, fig. 3.

Cornuspira involvens (Reuss)
Operculina involvens Reuss, 1850, p. 370, pl. 46, fig. 20a, b.

Minor species:

Bulimina elongata d'Orbigny
Bulimina elongata d'Orbigny, 1846, p. 187, pl. 11, figs 19, 20.

Elphidium macellum (Fichtel and Moll)
Nautilus macellus Fichtel and Moll, 1798, p. 68, pl. 10, figs e-i, k.

Reophax moniliformis Siddall
Reophax moniliforme Siddall, 1886, p. 54, pl. 1, fig. 2.

Pateoris hauerinoides (Rhumbler)
Quinqueloculina subrotunda (Montagu) forma *hauerinoides* Rhumbler, 1936, pp. 206, 217, 226, text-figs 167 (p. 205), 208–212 (p. 225).

All specimens used in this study are held (as faunal slides) in the Micropalaeontology Section, Palaeontology Department, The Natural History Museum, London.

Appendix 2. Foraminiferal data for Sties 1 and 2

SITE 1	*Quinqueloculina oblonga*			*Ammonia beccarii*			*Jadamminia macrescens*			*Haynesina germanica*			*Miliammina fusca*			*Elphidium williamsoni*			*Trochammina inflata*			*Comuspira involvens*			Total no./ sample	No. forams. /10cm3	No. of Species, S	H(S)	E	α**
Date / Sample	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3						
17/4/96 1A	165	58.7	133	32	11.4	26	9	3.2	7	13	4.6	10	59	21.0	48	1	0.4	1	0	0.0	0	2	0.7	2	281	227	7	1.195	0.472	1.30
1B	155	56.8	125	38	13.9	31	18	6.6	15	6	2.2	5	55	20.1	44	1	0.4	1	0	0.0	0	0	0.0	0	273	220	6	1.202	0.555	1.14
1C	194	73.8	156	20	7.6	16	1	0.4	1	7	2.7	6	41	15.6	33	0	0.0	0	0	0.0	0	0	0.0	0	263	212	5	0.828	0.458	0.90
14/5/96 1A	69	48.9	167	35	24.8	85	24	17.0	58	2	1.4	5	7	5.0	17	3	2.1	7	1	0.7	2	0	0.0	0	141	341	7	1.323	0.537	1.60
1B	8	40.0	10	3	15.0	4	1	5.0	1	3	15.0	4	4	20.0	5	1	5.0	1	0	0.0	0	0	0.0	0	20	24	6	1.557	0.791	
1C	89	61.4	108	19	13.1	23	23	15.9	28	0	0.0	0	8	5.5	10	3	2.1	4	3	2.1	4	0	0.0	0	145	176	6	1.178	0.541	1.30
14/6/96 1A	23	18.7	28	41	33.3	50	41	33.3	50	7	5.7	8	5	4.1	6	5	4.1	6	1	0.8	1	0	0.0	0	123	149	7	1.509	0.646	1.60
1B	43	38.1	52	17	15.0	21	32	28.3	39	5	4.4	6	6	5.3	7	5	4.4	6	5	4.4	6	0	0.0	0	113	137	7	1.580	0.693	1.63
1C	12	36.4	7	0	0.0	0	16	48.5	10	2	6.1	1	1	3.0	1	2	6.1	1	0	0.0	0	0	0.0	0	33	20	5	1.165	0.641	
18/7/96 1A	51	94.4	31	2	3.7	1	1	1.9	1	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	54	33	3	0.250	0.428	
1B	115	58.1	139	13	6.6	16	35	17.7	42	13	6.6	16	19	9.6	23	1	0.5	1	1	0.5	1	1	0.5	1	198	240	8	1.285	0.452	1.68
1C	47	50.5	57	8	8.6	10	25	26.9	30	3	3.2	4	7	7.5	8	2	2.2	2	1	1.1	1	0	0.0	0	93	113	7	1.346	0.549	
13/8/96 1A	11	44.0	7	0	0.0	0	3	12.0	2	1	4.0	1	0	0.0	0	0	0.0	0	10	40.0	6	0	0.0	0	25	15	4	1.111	0.759	
1B	2	40.0	1	0	0.0	0	0	0.0	0	0	0.0	0	0	0.0	0	1	20.0	1	2	40.0	1	0	0.0	0	5	3	3	1.055	0.957	
1C	0	0.0	0	0	0.0	0	5	50.0	3	0	0.0	0	0	0.0	0	1	10.0	1	4	40.0	2	0	0.0	0	10	6	3	0.943	0.856	
23/9/96 1A	107	71.8	130	3	2.0	4	22	14.8	27	4	2.7	5	2	1.3	2	4	2.7	5	6	4.0	7	0	0.0	0	149	181	8	1.015	0.345	1.80
1B	74	47.4	90	7	4.5	8	61	39.1	74	0	0.0	0	1	0.6	1	2	1.3	2	11	7.1	13	0	0.0	0	156	189	6	1.135	0.519	1.30
1C	92	31.1	112	15	5.1	18	152	51.4	184	7	2.4	8	7	2.4	8	11	3.7	13	10	3.4	12	1	0.3	1	296	359	9	1.309	0.411	1.71
22/10/96 1A	61	60.4	37	0	0.0	0	31	30.7	19	2	2.0	1	0	0.0	0	5	5.0	3	2	2.0	1	0	0.0	0	101	61	5	0.971	0.528	1.67
1B	96	55.5	232	4	2.3	10	34	19.7	82	3	1.7	7	1	0.6	2	33	19.1	80	1	0.6	2	1	0.6	2	173	419	8	1.209	0.419	1.76
1C	64	57.1	155	5	4.5	12	34	30.4	82	0	0.0	0	0	0.0	0	7	6.3	17	0	0.0	0	0	0.0	0	112	271	6	1.079	0.490	1.35
22/11/96 1A	106	56.7	257	10	5.3	24	54	28.9	131	1	0.5	2	4	2.1	10	10	5.3	24	2	1.1	5	0	0.0	0	187	453	7	1.152	0.452	1.48
1B	145	42.5	351	31	9.1	75	104	30.5	252	5	1.5	12	4	1.2	10	38	11.1	92	13	3.8	31	1	0.3	2	341	826	8	1.444	0.530	1.50
1C	55	57.3	266	3	3.1	14	27	28.1	130	0	0.0	0	1	1.0	5	7	7.3	34	3	3.1	14	0	0.0	0	96	464	6	1.131	0.516	
21/12/96 1A	54	65.9	131	11	13.4	27	6	7.3	15	0	0.0	0	1	1.2	2	6	7.3	15	2	2.4	5	2	2.4	5	82	199	7	1.162	0.457	
1B	94	56.0	228	18	10.7	44	12	7.1	29	2	1.2	5	8	4.8	19	16	9.5	39	4	2.4	10	14	8.3	34	168	407	8	1.470	0.544	1.76
1C	76	58.0	184	6	4.6	15	38	29.0	92	1	0.8	2	0	0.0	0	7	5.3	17	3	2.3	7	0	0.0	0	131	317	6	1.096	0.499	1.35
20/1/97 1A	136	54.2	657	38	15.1	184	10	4.0	48	5	2.0	24	10	4.0	48	38	15.1	184	4	1.6	19	10	4.0	48	251	1213	8	1.433	0.524	1.61
1B	28	23.7	135	13	11.0	63	41	34.7	198	3	2.5	14	0	0.0	0	33	28.0	159	0	0.0	0	0	0.0	0	118	570	5	1.401	0.812	1.11
1C	12	15.2	29	9	11.4	22	32	40.5	77	3	3.8	7	0	0.0	0	20	25.3	48	3	3.8	7	0	0.0	0	79	191	6	1.496	0.744	
21/2/97 1A	69	44.5	333	9	5.8	43	38	24.5	184	6	3.9	29	7	4.5	34	19	12.3	92	5	3.2	24	2	1.3	10	155	749	8	1.560	0.595	1.80
1B	71	30.7	343	5	2.2	24	132	57.1	638	2	0.9	10	4	1.7	19	12	5.2	58	5	2.2	24	0	0.0	0	231	1116	7	1.113	0.435	1.36
1C	54	48.2	261	15	13.4	72	20	17.9	97	6	5.4	29	1	0.9	5	14	12.5	68	2	1.8	10	0	0.0	0	112	541	7	1.459	0.615	1.65
21/3/97 1A	42	37.8	203	20	18.0	97	30	27.0	145	0	0.0	0	0	0.0	0	15	13.5	72	4	3.6	19	0	0.0	0	111	536	5	1.420	0.828	1.17
1B	24	18.3	231	9	6.9	87	80	61.1	769	3	2.3	29	0	0.0	0	13	9.9	125	1	0.8	10	1	0.8	10	131	1260	7	1.186	0.468	1.60
1C	79	43.4	382	36	19.8	174	10	5.5	48	4	2.2	19	3	1.6	14	49	26.9	237	0	0.0	0	1	0.5	5	182	879	7	1.376	0.565	1.48

Other species recorded		No.	%
23/9/96 1A	*Elphidium macellum*	1	0.7
1C	unidentified	1	0.3
23/10/96 1C	*Bolivina* sp.	1	0.9
22/11/96 1A	unidentified	1.0	0.9

**Fisher α index for samples with 100 or more specimens only

For each species:
"No." = number of specimens in sample
"%" = percent abundance in sample
"/10cm3" = number of specimens per 10cm3 sediment

SITE 2	*Quinquiloculina oblonga*			*Ammonia beccarii*			*Jadamminia macrescens*			*Haynesina germanica*			*Miliammina fusca*			*Elphidium williamsoni*			*Trochammina inflata*			*Comuspira involvens*			Total no./ sample	No. forams. /10cm3	No. of Species, S	H(S)	E	α**
Date / Sample	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3	No.	%	/10cm3						
17/4/96 2A	11	3.7	18	182	60.5	294	37	12.3	60	16	5.3	26	49	16.3	79	5	1.7	8	0	0.0	0	1	0.3	2	301	485	7	1.221	0.485	1.29
2B	71	21.4	229	179	53.9	577	25	7.5	81	11	3.3	35	44	13.3	142	2	0.6	6	0	0.0	0	0	0.0	0	332	1071	6	1.269	0.593	1.04
2C	69	19.0	223	230	63.2	742	20	5.5	65	11	3.0	35	32	8.8	103	2	0.5	6	0	0.0	0	0	0.0	0	364	1174	6	1.113	0.507	1.00
14/5/96 2A	12	20.7	29	16	27.6	39	7	12.1	17	3	5.2	7	16	27.6	39	0	0.0	0	1	1.7	2	3	5.2	7	58	140	7	1.668	0.757	
2B	3	17.6	7	8	47.1	19	0	0.0	0	0	0.0	0	6	35.3	15	0	0.0	0	0	0.0	0	0	0.0	0	17	41	3	1.028	0.932	
2C	38	44.7	92	20	23.5	48	12	14.1	29	2	2.4	5	11	12.9	27	0	0.0	0	1	1.2	2	0	0.0	0	85	206	7	1.434	0.599	
14/6/96 2A	31	11.8	38	123	46.8	149	65	24.7	79	7	2.7	8	33	12.5	40	2	0.8	2	0	0.0	0	2	0.8	2	263	319	7	1.384	0.570	1.36
2B	9	8.2	22	37	33.6	90	31	28.2	75	26	23.6	63	5	4.5	12	2	1.8	5	0	0.0	0	0	0.0	0	110	266	6	1.483	0.734	1.39
2C	17	11.7	41	74	51.0	179	19	13.1	46	10	6.9	24	18	12.4	44	5	3.4	12	0	0.0	0	1	0.7	2	145	351	8	1.489	0.554	1.84
18/7/96 2A	4	4.2	10	57	60.0	138	2	2.1	5	13	13.7	31	17	17.9	41	2	2.1	5	0	0.0	0	0	0.0	0	95	230	6	1.183	0.544	
2B	35	11.3	85	215	69.4	521	11	3.5	27	10	3.2	24	16	5.2	39	9	2.9	22	0	0.0	0	14	4.5	34	310	751	7	1.125	0.440	1.29
2C	10	19.6	6	36	70.6	22	0	0.0	0	3	5.9	2	1	2.0	1	0	0.0	0	0	0.0	0	0	0.0	0	51	31	5	0.887	0.486	
13/8/96 2A	8	7.0	19	73	63.5	177	5	4.3	12	4	3.5	10	6	5.2	15	5	4.3	12	13	11.3	31	1	0.9	2	115	278	8	1.305	0.461	1.90
2B	4	5.5	10	38	52.1	92	8	11.0	19	15	20.5	36	6	8.2	15	0	0.0	0	0	0.0	0	2	2.7	5	73	177	6	1.370	0.656	
2C	33	12.3	159	123	45.7	594	28	10.4	135	39	14.5	188	30	11.2	145	15	5.6	72	0	0.0	0	1	0.4	5	269	1300	7	1.557	0.678	1.32
23/9/96 2A	69	42.9	333	65	40.4	314	1	0.6	5	18	11.2	87	2	1.2	10	5	3.1	24	0	0.0	0	1	0.6	5	161	778	7	1.200	0.474	1.55
2B	27	13.8	130	54	27.7	261	23	11.8	111	40	20.5	193	40	20.5	193	9	4.6	43	0	0.0	0	2	1.0	10	195	942	7	1.720	0.798	1.43
2C	21	15.4	101	67	49.3	324	6	4.4	29	33	24.3	159	4	2.9	19	4	2.9	19	0	0.0	0	1	0.7	5	136	657	7	1.362	0.558	1.60
22/10/96 2A	42	42.9	203	29	29.6	140	5	5.1	24	14	14.3	68	4	4.1	19	0	0.0	0	0	0.0	0	2	2.0	10	98	473	7	1.441	0.604	
2B	80	56.7	386	29	20.6	140	10	7.1	48	8	5.7	39	9	6.4	43	2	1.4	10	1	0.7	5	2	1.4	10	141	681	8	1.329	0.472	1.85
2C	139	45.0	671	67	21.7	324	15	4.9	72	26	8.4	126	47	15.2	227	7	2.3	34	0	0.0	0	3	1.0	14	309	1493	11	1.546	0.427	2.20
22/11/96 2A	42	24.0	51	65	37.1	79	22	12.6	27	28	16.0	34	11	6.3	13	1	0.6	1	1	0.6	1	5	2.9	6	175	212	8	1.599	0.618	1.76
2B	40	36.4	385	20	18.2	192	15	13.6	144	16	14.5	154	15	13.6	144	1	0.9	10	0	0.0	0	2	1.8	19	110	1058	8	1.660	0.657	1.95
2C	59	37.8	567	44	28.2	423	6	3.8	58	24	15.4	231	8	5.1	77	5	3.2	48	0	0.0	0	9	5.8	87	156	1500	8	1.596	0.617	1.79
21/12/96 2A	29	29.9	70	29	29.9	70	8	8.2	19	19	19.6	46	5	5.2	12	1	1.0	2	0	0.0	0	6	6.2	15	97	235	7	1.619	0.721	
2B	17	21.3	21	39	48.8	47	8	10.0	10	9	11.3	11	2	2.5	2	0	0.0	0	2	2.5	2	3	3.8	4	80	97	7	1.463	0.617	
2C	17	21.8	41	32	41.0	77	9	11.5	22	17	21.8	41	1	1.3	2	0	0.0	0	0	0.0	0	1	1.3	2	78	189	7	1.447	0.607	
20/1/97 2A	99	49.0	478	30	14.9	145	7	3.5	34	37	18.3	179	16	7.9	77	0	0.0	0	1	0.5	5	10	5.0	48	202	976	9	1.489	0.493	1.91
2B	76	56.3	731	18	13.3	173	10	7.4	96	18	13.3	173	5	3.7	48	0	0.0	0	1	0.7	10	7	5.2	67	135	1298	7	1.365	0.560	1.60
2C	13	9.8	63	33	25.0	159	50	37.9	242	21	15.9	101	11	8.3	53	1	0.8	5	0	0.0	0	3	2.3	14	132	638	7	1.565	0.683	1.60
21/2/97 2A	57	35.0	548	30	18.4	288	40	24.5	385	16	9.8	154	16	9.8	154	1	0.6	10	0	0.0	0	3	1.8	29	163	1567	7	1.584	0.696	1.50
2B	51	27.3	490	32	17.1	308	39	20.9	375	39	20.9	375	15	8.0	144	3	1.6	29	0	0.0	0	8	4.3	77	187	1798	7	1.714	0.793	1.45
2C	64	33.0	309	63	32.5	304	12	6.2	58	32	16.5	155	10	5.2	48	3	1.5	14	1	0.5	5	8	4.1	39	194	937	9	1.603	0.552	1.91
21/3/97 2A	25	21.7	240	28	24.3	269	26	22.6	250	24	20.9	231	11	9.6	106	1	0.9	10	0	0.0	0	0	0.0	0	115	1106	6	1.605	0.829	1.37
2B	47	26.1	227	69	38.3	333	7	3.9	34	43	23.9	208	5	2.8	24	2	1.1	10	0	0.0	0	5	2.8	24	180	870	8	1.485	0.552	1.71
2C	49	30.6	471	28	17.5	269	16	10.0	154	55	34.4	529	3	1.9	29	1	0.6	10	0	0.0	0	7	4.4	67	160	1538	8	1.539	0.582	1.81

Other species recorded		No.	%
14/5/96 2C	*Bulimina elongata*	1	1.2
14/6/96 2C	unidentified	1	0.7
18/7/96 2C	*Elphidium macellum*	1	2
22/10/96 2A	*Fissurina* sp.	2	2
22/10/96 2C	*Elphidium macellum*	1	0.3
	Fissurina sp.	2	0.6
	Reophax moniliformis	1	0.3
	unidentified	1	0.3
22/11/96 2B	*Fissurina* sp.	1	0.9
2C	*Fissurina* sp.	1	0.6
21/12/96 2C	*Pateoris hauerinoides*	1	1.3
20/1/97 2A	*Fissurina* sp.	1	0.5
	Reophax moniliformis	1	0.5
21/2/97 2C	*Elphidium macellum*	1	0.5
21/3/97 2B	*Reophax moniliformis*	2	1.1
2C	*Fissurina* sp.	1	0.6

** Fisher a index for samples with 100 or more specimens only

for each species:
"No." = number of specimens in sample
"%" = percent abundance in sample
"/10cm3" = number of specimens per 10cm3 sediment

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