TEMPORAL VARIABILITY IN VERTICAL DISTRIBUTIONS OF LIVE (STAINED) INTERTIDAL FORAMINIFERA, SOUTHERN ENGLAND

ELISABETH ALVE\(^1\) AND JOHN W. MURRAY\(^2\)

**ABSTRACT**

The temporal variability (over 27 months) in abundance, depth of life in the sediment, and species diversity of hard-shelled, live (stained) foraminifera in an intertidal area has been determined. Throughout the investigation period, the same three species (*Haynesina germanica*, *Ammonia beccarii* (trepid), *Elphidium excavatum*) were dominant at the two investigated stations, the maximum abundance of all species (dominant and subsidiary) was in the surface 0.25 cm, and there was a general lack of seasonal change in the vertical distribution of the foraminifera. Seasonality does not seem to be a controlling factor for the vertical distribution of individuals in this area and none of the foraminifera showed high subsurface abundances. Because of the difference in depth position of the redox boundary within the sediment (often 1 cm) and the maximum abundance of individuals (surface 0.25 cm) the former cannot be the main factor limiting their vertical distribution of abundance. The generally high dominance of individuals in the surface few millimeters is probably related to the presence there of microalgal food and limited burrowing activity of the sparse macrofauna. Subsidiary species colonized the area ephemerally, thus the number of species recorded varied from one season to another. The minimum and maximum number of species found at any single sampling event were 5 and 22, whereas the cumulative number of stained species found throughout the investigation period was 35 (plus at least three soft-shelled forms). Species diversity is one of the principal univariate methods used to assess both natural variability and possible human impacts. The large natural seasonal variability demonstrated here suggests that caution should be taken in assessing the significance of diversity changes when based on occasional sampling only.

**INTRODUCTION**

Traditionally most ecological studies of benthic foraminifera have been based on a single sampling of the surface sediments (0–1 cm). In recent years there has developed a greater awareness that some taxa live infaunally to a considerable depth in the sediment. Some authors have recognized distinctive morphotypes related to depth and others have invoked a variety of controls (e.g., oxygen availability, food supply) acting with varying intensity. Experimental work has shown that infaunal depth habitats are not fixed but vary according to changing environmental conditions. All these aspects contribute to a fuller understanding of the benthic ecosystem. Also, time series and population dynamics studies are needed to understand the development of preserved benthic assemblages and to monitor short-term environmental variability.

Although several investigations have studied temporal variations based on frequent sampling (weeks) over a period of more than a year (see Table 1 in Murray and Alve, 2000) very few of these have considered temporal down-core distributions of such duration (Kitazato and Ohga, 1995; Ohga and Kitazato, 1997; Gustafsson and Nordberg, 1999). The only previous seasonal study of down-core foraminiferal distributions in a non-marsh intertidal area is that of Castignetti (1996) on the Plym Estuary, England, carried out over a period of 11 months.

The study area is the intertidal zone of the Hamble Estuary at Warsash, Hampshire, England (Alve and Murray, 1994, Fig. 1, W5-W8; see also Murray and Alve, 2000 and references therein). The extreme tidal range is around 4.9 m but mean spring tides are 4 m and neap tides 2 m. The river Hamble is very small so its discharge has very little effect on the salinity at Warsash which is commonly >30 psu. The climate is temperate with an annual water temperature range of around 6 to 18 °C although a wider range was measured during the survey. During the late spring to autumn there is a cover of macroalgae (especially *Ulva* and *Enteromorpha*) resting on the sediment surface in the mid- to upper intertidal zone when the tide is out. There are no published data on the annual contribution of organic carbon to the sediment. The area is moderately well sheltered from severe wave activity, the sediment is muddy sand, and there is no evidence of contemporary erosion in the area sampled.

The present study (the first part of which is presented in Murray and Alve, 2000) was designed to investigate the three-dimensional distributions of taxa (area, depth, patchiness) through time. The foraminifera of the study area were initially investigated in 1992 (Alve and Murray, 1994), and two stations from that study (W5 and W8) were selected for more detailed investigation because they had shown contrasting ecological features due to relative elevation in the intertidal zone.

The first part of the study discussed major faunal attributes, such as temporal variability of standing crop, dominant species, species diversity of the bulk assemblages in the top 1 cm of sediment, the size distribution and biomass of the three dominant species, and seasonal cyclicity. That paper focused on the top 1 cm of sediment studied over a 27 month period.

The second part of the study (present paper) examines in detail the hard-shelled foraminiferal depth distribution patterns in the surface 1 cm over 27 months (monthly sampling) and down to 4 cm for the first 14 months. Analyses of deeper sediment sections ceased because, over a one-year period the majority of the living fauna was found in the 0–1 cm interval at the two investigated stations. The aims include a detailed analysis of 1) seasonal microhabitat par-
tioning with respect to depth in the sediment, 2) the ephemeral colonization of the area by species not permanently living in the area, 3) temporal down-core variation in species diversity, and 4) compilation of a complete list of taxa found living in the area during the survey period.

METHODS

SAMPLING PROCEDURE

Samples were collected every month over a 27 month period from one low intertidal station (sta. 1) and one intermediate intertidal station (sta. 2), the latter being affected by a cover of macroalgae during the summer months. Full details of the methodologies are given in Murray and Alve (2000). In both January and February 1994 a single core was collected from each of the two stations, but thereafter two replicate cores were collected every month from each station until March 1996. The area studied for each sample at each station was 66.4 cm² for the first three months and subsequently 45.4 cm². Except for the first two months, when the surface sediment was sectioned in two 0.5 cm slices, each core was sampled in slices as follows: four slices 0.25 cm thick from the 0–1 cm interval, then 3 slices 1 cm thick from 1 to 4 cm. This yielded seven samples per core and therefore a total of 28 samples each month. Examination of samples deeper than 1 cm ceased after March 1995. Two 12 cm long cores (one from each station) were taken in December 1994 and the interval from 4 to 12 cm was divided into 2 cm slices.

SAMPLE PROCESSING AND PICKING

In the laboratory the foraminiferal samples were washed on a 63 μm sieve, stained with rose Bengal for 1 hour, washed again to remove the surplus stain, and dried in air. Rose Bengal is considered to be the most practical method to determine the occurrence of live specimens in this kind of study (Murray and Bowser, 2000). The samples were then gently brushed through a 1 mm sieve to break up organic aggregates and a flotation was carried out using trichloroethylene. Altogether, a total of 562 samples have been picked and analyzed for live (stained) benthic foraminifera. Of the 420 samples representing the upper 0–1 cm, 338 were picked completely, and for 82, where the number of living forms was very large (>500), only a portion (generally >300 individuals) was picked and the standing crop numbers calculated for the whole. All abundance data have been calculated to a standard unit of 10 cm³ to eliminate the effects of differing sample size between the sediment slices. The H(S) and Fisher alpha diversity index values are low in all surface (0–1 cm) samples (Murray and Alve, 2000), and the number of specimens in individual slices below 0.5 cm was often too low for reliable determinations of diversity indices. Therefore, for comparing the down-core sediment slices, the number of species in each sample is given instead. An additional single sample from sta. 2 (March 1995) was sieved on a 38 μm sieve and partly wet-picked to look for juveniles and soft-shelled taxa.

RESULTS

Although down-core data were collected for January and February 1994, these cores were divided into 0.5 cm slices in the top 1 cm as opposed to 0.25 cm slices for all other months. Therefore, the year over which the most detailed down-core data have been gathered runs from March 1994 to February 1995.

DOWN-CORE DEPTH DISTRIBUTIONS (0–4 CM)

Standing crop

Without exception, the highest abundances of all species were found in the top 0.25 cm of sediment not only in the first year, when samples were analyzed down to 4 cm (Fig. 1), but also in the second year, when only the surface 1 cm was analyzed. In the first year, both stations showed a similar overall pattern in standing crop per 10 cm³ with medium values in the surface 0–1 cm interval in March to May, lowest values in June and July followed by a rapid increase in August. The values were low at depths greater than 0.25 cm from March to July. In August the standing crop increased at all depths and remained higher until November. Overall the values were higher at sta. 2 than sta. 1.

Taking the cumulative relative abundance of the standing crop in the surface 4 cm sampled interval as 100%, throughout the study period the range of the surface 0.25 cm value was 46–79% (mean 60%) at sta. 1 and 40–82% (mean 59%) at sta. 2. Furthermore, for the surface 1 cm (pale bars in
Fig. 2) the values were 58–95% (mean 77%) for sta. 1 and 62–92% (mean 79%) for sta. 2. The four sediment slice data down to 1 cm are available for all 27 months. Here the standing crop of the surface 0.25 cm interval made up 44–93% (mean 78%) and 34–92% (mean 72%) of the 0–1 cm for stations 1 and 2 respectively (Fig. 3). Although there is a positive correlation between the percent values for years one and two at sta. 2 ($r = 0.78, p < 0.01$), there is no such correlation for sta. 1 ($r = 0.27$).

**Dominant species**

These were *Ammonia beccarii* (tepida), *Elphidium excavatum* and *Haynesina germanica*. For each species, the data are presented as standing crop and percent (each slice as a percent of the total 0–4 cm) (Fig. 4, sta. 1; Fig. 5, sta. 2). *Haynesina germanica* at sta. 1 showed minimum standing crop in summer (June–July) whereas the relative abundance showed an overall decline throughout the study period (March 1994–February 1995). *Ammonia beccarii* and *Elphidium excavatum* at sta. 1 showed a similar pattern with highest standing crop at the surface during autumn and winter but there was no obvious similar trend in the relative abundance. *Haynesina germanica* at sta. 2 showed maximum standing crop values in the surface 0.25 cm in late winter to spring whereas *A. beccarii* and *E. excavatum* had maximum values in autumn and winter (Fig. 5). *Ammonia beccarii* also showed higher subsurface values from August to November 1994. A general feature for all species is that the relative abundances at depth were inevitably greater when the standing crop values at the surface were at a minimum.

**Subsidiary species**

Because all species were generally more abundant in the surface 0.25 cm, comments are first made on their occurrence throughout the whole investigation period (i.e., 27 months). Additional comments are then made on the downcore data (0–4 cm) for the first year.

The pattern of abundance of subsidiary species in the surface 0.25 cm layer for the full study period did not show repetition from one year to another (Fig. 6). Two subsidiary species, *Elphidium williamsoni* and *Aubignyna hamblensis*, were common at both stations and the former occurred every month together with the three dominant species (Table 1). Additionally, *Hopkinsina pacifica* and *Stainforthia sp.* were abundant at sta. 1, whereas *Quinqueloculina dimidia-
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Figure 5. Time/depth distributions of standing crop and cumulative relative abundance for *Haynesina germanica*, *Ammonia beccarii* and *Elphidium just excavatum* for sta. 2 where the cumulative relative abundance from 0 to 4 cm sums to 100% for each species.

Table 1. Rank order of species by frequency of occurrence in the surface 1 cm.

<table>
<thead>
<tr>
<th>Number of months</th>
<th>Station 1</th>
<th>Number of months</th>
<th>Station 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>27</td>
<td><em>Ammonia beccarii</em></td>
<td>27</td>
<td><em>Ammonia beccarii</em></td>
</tr>
<tr>
<td>27</td>
<td><em>Elphidium excavatum</em></td>
<td>27</td>
<td><em>Elphidium excavatum</em></td>
</tr>
<tr>
<td>27</td>
<td><em>Haynesina germanica</em></td>
<td>27</td>
<td><em>Haynesina germanica</em></td>
</tr>
<tr>
<td>27</td>
<td><em>Elphidium williamsoni</em></td>
<td>27</td>
<td><em>Elphidium williamsoni</em></td>
</tr>
<tr>
<td>26</td>
<td><em>Hopkinsina pacifica</em></td>
<td>26</td>
<td><em>Elphidium oceanensis</em></td>
</tr>
<tr>
<td>26</td>
<td><em>Nonion depressulas</em></td>
<td>25</td>
<td><em>Fixsurrina lucida</em></td>
</tr>
<tr>
<td>25</td>
<td><em>Stainforthia sp.</em></td>
<td>24</td>
<td><em>Nonion depressulas</em></td>
</tr>
<tr>
<td>25</td>
<td><em>Aubignyna hamblessis</em></td>
<td>23</td>
<td><em>Aubignyna hamblessis</em></td>
</tr>
<tr>
<td>24</td>
<td><em>Elphidium oceanensis</em></td>
<td>23</td>
<td><em>Quinqueloculina dimidiata</em></td>
</tr>
<tr>
<td>24</td>
<td><em>Fixsurrina lucida</em></td>
<td>22</td>
<td><em>Bolimnella elegansissima</em></td>
</tr>
<tr>
<td>24</td>
<td><em>Quinqueloculina dimidiata</em></td>
<td>22</td>
<td><em>Stainforthia sp.</em></td>
</tr>
<tr>
<td>23</td>
<td><em>Bolivinellina pseudopunctata</em></td>
<td>20</td>
<td><em>Brizalina sp.</em></td>
</tr>
<tr>
<td>23</td>
<td><em>Balimnella elegansissima</em></td>
<td>18</td>
<td><em>Textularia tenuissima</em></td>
</tr>
<tr>
<td>22</td>
<td><em>Brizalina sp.</em></td>
<td>18</td>
<td><em>Bolivinellina pseudopunctata</em></td>
</tr>
<tr>
<td>14</td>
<td><em>Textularia tenuissima</em></td>
<td>17</td>
<td><em>Hopkinsina pacifica</em></td>
</tr>
<tr>
<td>12</td>
<td><em>Elphidium margaritaceum</em></td>
<td>6</td>
<td><em>Elphidium margaritaceum</em></td>
</tr>
<tr>
<td>10</td>
<td><em>Paratrochammina (L.) haynesi</em></td>
<td>6</td>
<td><em>Elphidium sp.</em></td>
</tr>
<tr>
<td>10</td>
<td><em>Elphidium sp.</em></td>
<td>5</td>
<td><em>Bolivina variabilis</em></td>
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<tr>
<td>10</td>
<td><em>Stainforthia fusiformis</em></td>
<td>5</td>
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<tr>
<td>9</td>
<td><em>Bolivina variabilis</em></td>
<td>4</td>
<td><em>Eggerelloides scaber</em></td>
</tr>
<tr>
<td>9</td>
<td><em>Nonion sp.</em></td>
<td>4</td>
<td><em>Paratrochammina (L.) haynesi</em></td>
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<tr>
<td>8</td>
<td><em>Balimina gibbaeolongata</em></td>
<td>4</td>
<td><em>Balimina gibbaeolongata</em></td>
</tr>
<tr>
<td>5</td>
<td><em>Eggerelloides scaber</em></td>
<td>4</td>
<td><em>Ammobaculites balkwilli</em></td>
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<tr>
<td>5</td>
<td><em>Ammobaculites balkwilli</em></td>
<td>4</td>
<td>calcareous unidentifed</td>
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<tr>
<td>4</td>
<td><em>Nonionella sp.</em></td>
<td>3</td>
<td><em>Miliammina fusca</em></td>
</tr>
<tr>
<td>3</td>
<td><em>Bolivina pseudopunctata</em></td>
<td>3</td>
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</tr>
<tr>
<td>3</td>
<td><em>Rolsalina sp.</em></td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td><em>Bolivina</em></td>
<td>2</td>
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</table>

ta, *Fissurina lucida*, and *Elphidium oceanensis* were abundant at sta. 2. There the latter three species and agglutinated taxa were hardly present from January to June, 1994, after which time their numbers increased dramatically. The abundance of only one of the subsidiary species, *A. hamblensis*, showed a significant positive correlation ($r = 0.648$, $p < 0.01$) over time between the two stations. The bolivinids (*Bolivina pseudopunctata*, *Bolivinellina pseudopunctata*, *Brizalina variabilis*, *Brizalina sp.*) were common (max. 29 individuals/10 cm$^3$ in 0–0.25 cm, Oct., 1994, sta. 2) only in the autumn/early winter of both years.

The agglutinated forms, mainly comprising *Ammoscalarium rutilans*, *Eggerelloides scaber* (small individuals only), *Paratrochammina (L.) haynesi*, and *Textularia tenuissima*, were either rare or absent at both stations but had a maximum of 51 individuals/10 cm$^3$ in the surface 0.25 cm at sta. 2 in September, 1994. A general trend for all the subsidiary species is that although they occasionally were present down to 4 cm, their abundance below 1 cm was extremely low (Fig. 7).

Number of species

The total number of live (stained) species throughout the study period (27 months) was 35 of which 26 were identified to species level (see faunal reference list). The single wet-picked sample revealed at least three additional species of soft-shelled taxa (one saccamminid and two allogomids) which collapsed when dried and are therefore not found in the studied assemblages. The cumulative number of recorded hard-shelled species at sta. 1 reached 28 in November 1994 and increased to 35 from August 1995 to March 1996 (Fig. 8). At sta. 2, the numbers reached a maximum value...
of 29 in May 1995 with no new occurrences after that. The maximum number of species recorded in any one core at a single sampling event was 22.

There is no obvious pattern in the number of species over time in the single sediment layers (Fig. 9). However, when considering all the species present in each core (0–4 cm) through time, there is a comparable pattern at both stations with a progressive increase from April through to November. The mean number of species over each year was highest in the surface 0.25 cm and showed a slight decrease down-core (Table 2). However, within each sediment interval the figures were essentially the same at both stations.

**DISCUSSION**

In a previous paper relating to the present study (Murray and Alve, 2000) the results from the bulk surface 0–1 cm showed that the assemblages were dominated by three species: *Haynesina germanica*, *Ammonia beccarii*, and *Elphidium excavatum*. Patchiness occurred on a scale of a few centimeters and had a major impact on tracking temporal changes in the standing crop. The seasonal cyclicity was not always well shown by the foraminiferal numerical abundance but was better shown by species diversity and biomass. In this paper, we focus on depth distributions within the sediment (microhabitat partitioning: within the surface 0–1 cm from all 27 months and down to 4 cm during the first 14 months) and biodiversity.

**VOLUME VERSUS AREA FOR REPORTING NUMERICAL ABUNDANCE?**

As pointed out by Alve and Olsgard (1999), numerical abundance can be presented in two fundamentally different ways: as number of individuals per unit area summed for the whole down-core section, and as number of individuals per volume of one particular core slice. In the former, the true numerical abundance for the unit area will be attained only if the core length is at least equal to the down-core distribution of living individuals. In the latter method, the numbers will to a much stronger extent depend on the thickness of the slice analyzed. Several studies have shown that the majority of foraminifera live in the surface one to two cm of sediment. In such cases, if the numerical abundance values are presented per unit area, the figures will not change dramatically if individuals from sections deeper than the zone of high abundance are included. However, if the numerical abundances are given per unit volume, the figures will strongly depend on the thickness of the sediment slice. For instance, in this study the majority of forms live in the surface 0.25 cm. If the results are averaged for a 1 cm thick slice of unit volume, then the numerical abundance is much lower than that of the thin surface layer. Of course, if the sediment slice is standardized at 1 cm thickness then for the surface 1 cm, the results per unit area and unit volume are identical. Consideration of the method of presenting the results is important when comparing data from different studies.

**MICROHABITAT PARTITIONING**

In order to obtain a high resolution record of infaunal depth distribution, the surface 0–1 cm was sampled in four 0.25 cm slices. The most striking features of this extensive dataset are that three species dominated at all depth levels throughout the investigation period, that the maximum standing crop of all species (dominant and subsidiary) was in the surface 0.25 cm throughout most of the 27 months, and that there was a general lack of seasonal change in the vertical distribution of the foraminifera. However, at times of low standing crop in the surface layer, the relative abundance increases down-core (Figs. 4 and 5). The lack of a consistent seasonal pattern for both stations (Fig. 3) indicates that seasonality is not a controlling factor for the vertical distribution of individuals in this area.

Although in this study vertical depth distribution is not really developed, in other environments there is a clearer habitat partitioning. The first reliable record of infaunal foraminifera is that of Richter (1961) based on cores from the intertidal zone in the southern North Sea. He recognized a relationship between maximum depth of life and the thickness of the surface oxidized zone. Since then, a large number of studies of vertical distributions have been made on environments ranging from high marsh to hadal ocean. The results sometimes appear contradictory and certainly there is no global pattern of specific taxa occupying one particular subsurface depth zone. The reasons for this are partly ex-
PLATE 1

SEM micrographs. Scale bar 100 μm. 1 *Ammonia beccarii* (Linne) forma tepida Cushman, juvenile. 2 *Haynesina germanica* (Ehrenberg), juvenile. 3 *Elphidium excavatum* (Terquem), juvenile. 4, 5 *Nonion depressulus* (Walker and Jacob). 6, 7 *Fissurina lucida* (Williamson). 8, 9 *Elphidium oceanensis* (d’Orbigny). 10, 11 *Elphidium margaritaceum* Cushman. 12, 13 *Stainforthia fusiformis* (Williamson). 14, 15 *Stainforthia* sp.
SEM micrographs. Scale bar 100 μm. 1 Buliminella elegantissima (d’Orbigny). 2 Bolivina pseudoplicata Heron-Allen and Earland. 3 Bulimina gibbulelongata Fornasini. 4 Caneata arctica (Brady). 5, 6 Brizalina variabilis (Williamson). 7–9 Bolivinellina pseudopunctata (Hoglund). 10, 11 Hopkinsina pacifica Cushman. 12, 13 Quinqueloculina dimidiata Terquem. 14, 15, 16 Aubignyna hamblensis Murray, Whittaker and Alve. 17 Ammonia beccarii (Linné) forma tepida Cushman.
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Figure 7. Time/depth distributions of standing crop for selected subsidiary species.

Figure 8. Cumulative number of species versus cumulative number of counted individuals (each entry on the x-axis represents one sampling event, i.e., one month, starting from January 1994).

Figure 9. Number of stained species in the surface 0.25 cm and 0.75–1.00 cm sediment slices and in the 0–4 cm interval combined.

Table 2. Mean number of species in each sediment slice.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>0.00–0.25</th>
<th>0.25–0.50</th>
<th>0.50–0.75</th>
<th>0.75–1.00</th>
<th>1.00–2.00</th>
<th>2.00–3.00</th>
<th>3.00–4.00</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sta. 1 (yr 1)</td>
<td>15</td>
<td>12</td>
<td>9</td>
<td>9</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Sta. 1 (yr 2)</td>
<td>15</td>
<td>11</td>
<td>8</td>
<td>8</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Sta. 2 (yr 1)</td>
<td>13</td>
<td>11</td>
<td>10</td>
<td>9</td>
<td>10</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Sta. 2 (yr 2)</td>
<td>12</td>
<td>11</td>
<td>9</td>
<td>9</td>
<td>—</td>
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</table>

Explained by Buzas and others (1993): ‘Because each core captures a variety of individuals found together in one instant of time, we are simply observing a transient phenomenon of a group of animals with a three dimensional aggregated spatial distribution’, by De Stigter and others (1998): ‘microhabitats of benthic foraminiferal species are not static, but may be highly variable from place to place, as determined by local environmental conditions’ and finally, as stated by Jorissen and others (1998): ‘The vertical zonation of foraminiferal species in the sediment shows a close correspondence with the depth distribution of oxic respiration, nitrate and sulphate reduction’.

From the mass of data collected over four decades, the main conclusions to emerge are:

- that benthic foraminifera have been recorded living infaunally from <1 cm down to at least 40 cm (the latter in marsh environments Akers, 1971, perhaps in part due to open burrows, Goldstein and others, 1995)
- typically the highest numbers are found in the surface 0–1 cm layer (e.g., Gooday, 1986; Mackensen and Douglas,
The essence of the TROX model is that in oligotrophic environments the infauna is shallow due to the limiting control of food (adequate oxygen); while in mesotrophic environments the infauna may penetrate deeply into the sediment according to the availability of food with oxygen not usually being a limiting factor. 

- the TROX-2 model was introduced to take into account other geochemical changes (apart from oxygen depletion) and the role of competition for labile organic matter (Van der Zwaan and others, 1999)

- combining the TROX models with the experimental evidence that forms change their depth in the sediment in response to oxygen gradients, then the concept of different morphotypes for different depths in the sediment (Corliss and Fois, 1990; Corliss, 1991) is loose (Van der Zwaan and others, 1999) and meaningless on a global scale although it might apply locally if the environment remains constant.

In this study, the sediments at both stations had a brown layer which rarely exceeded 1 cm and the minimum was about 0.2 cm. At station 2, below the brown layer it turned directly to dark gray/black, whereas at sta. 1 there was a transition from brown into medium gray. It is established that the base of such a brown layer does not necessarily coincide with the redox-boundary, meaning that the lower part of the brown layer may be anoxic (Revsbech and others, 1980). Microelectrode measurements performed once at each station (March, 1994) indicated that the redox boundary had a shallower position at sta. 2 (~0.3 cm) as compared to a more transitional boundary at sta. 1 (~1.2 cm).

At sta. 2 at the time of measurement there was a clear transition from brown to dark gray/black at 1.1 cm, whereas no clear color change was obvious at sta. 1. Despite this difference between the two stations in depth of the redox boundary, the average relative abundance of the standing crop over 14 months was nearly the same in the surface 0.25 cm layer (sta. 2 = 59%; sta. 1 = 60% as a proportion of the total number of stained individuals down to 4 cm). Comparable results were found by Castignetti (1996) in an 11 month survey of the Plym estuary, UK, where 93% of the foraminifera (in 8 cm long cores) occurred in the top 0.3 cm and 97% in top 1 cm. There the brown layer was 0.2–0.6 cm thick but the depth of the redox boundary was not given.

The fact that the redox boundary at sta. 1 seemed to be situated at about 1 cm or deeper, yet the large majority of individuals lived in the surface 0.25 cm, indicates that the redox boundary is not the main factor limiting their downcore abundance. Indeed, several of the common species are known to survive dysoxia or anoxia (e.g., *Ammonia beccarii* and *Elphidium excavatum*; Moodley and Hess, 1992) and many of them have been recorded living in reasonable numbers (as compared to their surface abundance) down to 25 cm sediment depth (Moodley, 1990). All the dominant and some of the subsidiary species have been shown to sequester chloroplasts (see Bernhard and Bowser, 1999, and references therein) or feed on benthic microalgae (e.g., Knight and Mantoura, 1985; Hohenegger and others, 1989). As these algae are obviously dependent on light, it seems reasonable that the maximum abundance of foraminifera in the surface few millimeters is primarily due to this irrespective of the position of the redox boundary. When the
tidal was out during daylight, a golden-brown layer of epipelagic diatoms developed on exposed sediment. They emerged from the sediment within a few minutes in response to light (see Paterson, 1986, for discussion) and we have observed this under the microscope in the laboratory on freshly collected surface sediment. The foraminifera were not observed to do this but their pseudopodia probably penetrated to the surface of the sediment. Similarly, on tidal flats in the southern North Sea, the upper surface of mud and muddy sand is covered with a dense mucilaginous layer of diatoms. Langer and others (1989) considered that the living foraminifera were embedded within this layer in order to protect themselves against disturbance by tidal currents. The mucilaginous material is a biofilm and recent studies show it to consist of carbohydrate-rich exopolymers (EPS) produced by the epipelagic diatoms during locomotion. This is utilized as a food source by bacteria which in turn also produce EPS (Underwood and Smith, 1998). The bacteria are a potential source of food for the foraminifera and the EPS helps to bind the sediment and reduce erosion. Both of these attributes are potentially beneficial to shallow infaunal foraminifera.

Despite the fact that the most optimal conditions for the present intertidal species are within the surface few millimeters of sediment, Moodley (1990) recorded 8 of them to be living in reasonable numbers (as compared to their surface abundance) down to 25 cm in subtidal southern North Sea sediments. He concluded that their vertical distribution was governed primarily by the burrowing activities of macrofauna. As opposed to other intertidal areas, where higher abundances of the present species have been recorded at greater sediment depths (e.g., Langer and others, 1989), only a few small worms and crustaceans (e.g., Corophium) and no typical estuarine infaunal bivalves (e.g., Scrobicularia) were recorded in the present study area. Consequently, the low abundance of foraminifera below the surface few millimeters throughout the investigation period probably reflects low bioturbation activity (e.g., as compared with the intertidal area of outer Jade Bay studied by Langer and others, 1989) causing sparcity both of oxygenated burrows and labile food at depth. However, the few stained individuals in the deeper sediment layers (recorded down to 12 cm, the limit of sampling) still indicate some bioturbation activity.

When infaunal foraminifera live to a considerable depth in the sediment, then estimates of the standing crop based on the surface 1 cm will be too low. For instance, Buzas (1974) pointed out that in the Rhode River, USA, estimates of standing crop based on the 0–2 cm interval represent barely one fifth of the true number. In the present study, this is not the case since such a high proportion live in the surface 1 cm. The implications of this are that in designing an ecological survey, it is essential to carry out a pilot study to determine the depth to which sampling needs to take place.

**Biodiversity and Colonization by Subsidiary Species**

In surveys based on a single period of sampling the number of stained (living) species recorded will be those present at that time only. The Hamble estuary is a region of low diversity with 5–22 species per sample according to season. In this study, the total number of hard shelled stained species found over the 27 month sampling period was 35 (plus at least three soft shelled taxa). It is evident from the time series data that certain species colonized the area ephemerally (Figs. 6 and 7) and therefore the number of species recorded varied from one month to another (Fig. 9) and never exceeded 22 (sta. 1, Sept. 1994). The cumulative increase in species from the start of the study reached a plateau at sta. 2 than at sta. 1 (Fig. 8) which is probably related to their positions relative to the main (seaward) source. No doubt over a longer period of time other species might be ephemerally introduced into the area. The pattern of cumulative increase obviously depends on the starting point of the survey. Had the study commenced in the autumn, the initial number of species would have been much higher at both stations although the cumulative total would have remained the same. On the other hand, temporal cumulative diversity increase should be much higher in the overall more stable and diverse offshore environments.

Forms such as Elphidium williamsoni and Quinqueloculina dimidiata were probably sourced from nearby tidal marshes where we have observed Q. dimidiata living attached to filamentous algae. Other forms, such as the bollinids, Buliminella elegantissima, Bulimina gibbaelongata, Nonion depressulus, and Fissurina lucida, were most probably sourced from the nearby marine shelf as these are more stenohaline taxa (Alve and Murray, 1994). Indeed, the same holds true for Stainforthia fusiformis which is a well-known opportunistic species in European waters (Alve, 1994). In the earlier study, Quinqueloculina spp. and Fissurina sp. were recorded only as unstained (dead) individuals and were considered to have been transported into the area in suspension. It is now clear that the reason why we did not record them living at that time is because they are ephemeral colonizers which reproduced there especially during the summer and autumn. This is probably linked to the greater penetration of the salt wedge during the drier summer months. A similar pattern was recorded for Quinqueloculina dimidiata in Christchurch Harbour (Murray, 1968). At least three species show blooms following summer colonization: E. williamsoni, F. lucida and Q. dimidiata and when they were present they occurred in both replicates showing that their occurrence was not patchy.

The great difference in number of species present during different times of the year is evident in Fig. 9. Similar records are available for a few other areas in which time series studies have been carried out for at least one year: Bottsand lagoon, Germany 2–8 species (Lutze, 1968), Samish Bay, USA, a maximum of 10 species but only 2–5 present at any one sampling event (Jones and Ross, 1979), 28 species found living in 1961 samples but by 1970 the number had increased to approximately 65 (Boltovskoy and Lena, 1970), an increase in H(S) from 0.1 to 1.6 in the intertidal zone, Bahrain (Basson and Murray, 1995). Unfortunately, in most studies temporal variation in diversity is not discussed, yet it is clear from these few results that the variability is very large. For studies where sampling is so infrequent that the temporal variabilities in species diversity are not recorded, only a partial record will be obtained and the season of sampling will have a significant influence on the number of
species found. This partly explains why, in most environments, the species diversity of the (time-averaged) dead assemblage invariably exceeds that of the living assemblage recorded at any one time.

The mechanisms of colonization of azoic environments have been shown to be passive dispersion (either physical or biological disturbance of the source area) and transport (in suspension at various growth stages) with the transit time dependent on the current energy of the environment (Alve, 1999). The same processes must operate even when the environment is already inhabited by a range of taxa. In this area, tidal currents are vigorous as the area is meso-macrotidal. It might be assumed that the transit time would be short (days) and colonization fairly rapid once conditions were favorable.

Species diversity is one of the principal univariate methods used to assess both natural variability and possible human impacts on marine soft bottom ecosystems (e.g., Coull and Chandler, 1992). In any particular environment, human impacts tend to reduce the species diversity. For example, the ranges of the Shannon-Wiener index and Hurlbert’s index for soft bottom macrofauna are included in the assessment of Norwegian environmental quality on a scale from very good to very poor (Molvær and others, 1997). Similar ranges have not yet been established for benthic foraminifera but in setting them up account would have to be taken of the large seasonal variability such as that recorded in the present study.

**Comparisons with Other Areas**

What attributes of the Hamble Estuary make it suitable for the three species, *H. germanica, A. beccarii* and *E. excavatum* to become dominant? In adjacent estuaries the combinations of dominant species differ and may include one or more of *E. williamsoni, Nonion depressulus, Miliammina fusca* and *Reophax moniliformis* (Murray, 1968). *Elphidium williamsoni* may not be dominant here because of a combination of the generally high salinity (mainly >30 psu) and the high mud content of the sediment (63–74%) as elsewhere it has been found not to tolerate mud values >60% (Langer and others, 1989; Alve and Murray, 1999). *Miliammina fusca* is very euryhaline (Murray, 1991) but occurs on a wide range of substrates (Alve and Murray, 1999). *Nonion depressulus* is an inner shelf species common only on sandy substrates and is not tolerant of very reduced salinities (Murray, 1983). Off southern Norway it occurs on sandy sediment with <12% mud and <1% TOC (Alve and Murray, 1999). Other studies have shown that there is no direct correlation between individual environmental variables and species distributions (e.g., Buzas and Severin, 1993). Thus, the combination of dominant taxa in each area depends on the local, often subtly different, environmental characteristics.

**Conclusions**

The distribution of live (stained) foraminifera has been determined with respect to abundance, depth of life in the sediment (down to 4 cm), and species diversity in replicate samples from two intertidal stations sampled 0–1 cm monthly over 27 months and 0–4 cm over the first 14 of these months. The following conclusions can be drawn based on the combined results from the pairs of replicates:

- The same three species (*Haynesina germanica, Ammonia beccarii* (tepid), *Elphidium excavatum*) were dominant at both stations, the maximum abundance of all species (dominant and subsidiary) was in the surface 0.25 cm, and there was a general lack of seasonal change in the vertical distribution of the foraminifera. The absence of a consistent seasonal pattern for both stations indicates that seasonality is not a controlling factor for the vertical distribution of individuals in this area.

- In contrast to many subtidal areas none of the foraminifera in this intertidal environment showed high subsurface abundances.

- When measured, the redox boundary was at 0.3 and 1 cm at sta. 2 and sta. 1 respectively below the sediment surface yet the large majority of individuals lived in the surface 0.25 cm thus indicating that this boundary was not the main factor limiting their down-core abundance. The generally high dominance of individuals in the surface few millimeters was probably related to the presence there of microalgal food.

- The total number of stained hard shelled species found over the 27 month sampling period was 35 (plus at least 3 soft shelled forms) although the number recorded during one sampling event ranged from a minimum of 5 to a maximum of 22. Subsidiary species colonized the area ephemerally, thus the number of species recorded varied from one season to another. Over a longer period of time other ephemeral species might be introduced into the area thus increasing the total number of species recorded.

- The mechanisms of colonization include passive dispersion and transport from the source area, with the transit time dependent on the current energy of the environment. In this case, transit time is likely to be short (days), due to the tidal currents, and colonization fairly rapid once conditions were favorable.

- Species diversity is one of the principal univariate methods used to assess both natural variability and possible human impacts on marine soft bottom ecosystems. Human impacts tend to reduce the species diversity but, in assessing the significance of diversity changes, caution should be exercised to take into account the large natural seasonal variability such as that recorded in the present study.

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**References**


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FAUNAL REFERENCE LIST

Generic names are in accordance with Loeblich and Tappan (1987).

The named species plus Stainforthia sp. are illustrated in Plates 1 and 2 (in Alve and Murray, 1994; Murray and others, 2000).

Ammonitida balticæi Haynes, 1973
Ammonitida balticæi (Linné) forma tepida Cushman = Rotalia beccarii (Linné) var. tepida Cushman, 1927
Ammonitida ranianæ (Hero-Allen and Earland) = Hoplophragmium ranianum Hero-Allen and Earland, 1916
Aubignyna hamblensis Murray, Whittaker and Alve, 2000
Brizalina pseudoplicata Hero-Allen and Earland, 1930
Bolivina pseudopunctata Högland = Bolivina pseudopunctata Högland, 1947
Brizalina variabilis (Williamson) = Textularia variabilis Williamson, 1858
Bulimina gibbulelongulata Fornasini, 1902'd’Orbigny, 1846
Bulimina elegansissima (d’Orbigny) = Bulimina elegantissima d’Orbigny, 1839 Cadirola obtusa Williamson, 1858
Conea arctica (Brady) = Reophax arctica, Brady 1881
Cornaspia involvens (Reuss) = Operculina involvens Reuss, 1850
Eggerelloides scaber (Williamson) = Bulimina scabra Williamson, 1858
Elphidium excavatum (Terquem) = Polystomella excavata Terquem, 1875
Elphidium margariaczum Cushman, 1930
Elphidium oceanensis (d’Orbigny) = Polystomella oceanensis d’Orbigny, 1826
Elphidium williamsoni Haynes, 1973
Fissurina lucida (Williamson) = Entosolenia marginata (Montagu) var. lucida Williamson, 1848
Haynesina germanica (Ehrenberg) = Nonionina germanica Ehrenberg, 1840
Hopkinsina pacifica Cushman, 1933
Miliammina fusca (Brady) = Quinqueloculina fusca Brady, 1870
Nonion depressus (Walker and Jacob) = Nautilus depressus Walk-er and Jacob, 1798
Paratrophammina (Lepidoparatrochammina) haynæi (Atkinson) = Trochammina haynæi Atkinson, 1969
Quinqueloculina dimidiatæ Terquem, 1876
Stainforthia fusiformis (Williamson) = Bulimina papoides d’Orbigny var. fusiformis, Williamson, 1858
Textularia tenuissima Earland, 1933

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