Journal of Foraminiferal Research, v. 33, no. 1, p. 32–61, January 2003

THE DISTRIBUTION OF BENTHIC FORAMINIFERA IN THE CELTIC SEA: THE SIGNIFICANCE OF SEASONAL STRATIFICATION

GILLIAN A. SCOTT, JAMES D. SCOURSE[2], AND WILLIAM E. N. AUSTIN[1]

School of Ocean Sciences, University of Wales (Bangor), Menai Bridge, Anglesey, LL59 5EY, UK

ABSTRACT

Seasonal stratification is an important phenomenon in tidally-stirred shelf seas, influencing biological productivity, sedimentation rates, the organic content of shelf sediments, and the climate of surrounding landmasses. Previous micropaleontological and stable isotopic investigation investigation of a Holocene sequence from the Celtic Sea suggests that benthic foraminiferal distributions are linked to the physical and biological oceanographic characteristics associated with stratification. We have tested this hypothesis by analyzing the living and dead foraminiferal faunas from surface samples collected during across-frontal cruises during the summers of 1995 and 1996. Foraminiferal and environmental data for 56 samples are presented. Live and dead foraminiferal data were analyzed by factor analysis and, along with the environmental data, canonical correspondence analysis (CCA). Four distinct assemblages were identified from factor analysis of the live data: (1) a frontal assemblage characterized by *Stainforthia fusiformis*, (2) a mixed water assemblage characterized by *Cibicides lobatulus, Textularia bockii, Spiroplectammina wrightii, Ammonia batavus* and *Quinqueloculina seminulum*, (3) a stratified assemblage characterized by *Bulimina marginata, Hyalinea balthica, Adercotryma wrighti* and *Nonionella turgida*, and (4) an eastern assemblage dominated by *Bulimina gibba, Elphidium excavatum* and *Eggerelloides scaber*. Factor analysis of the dead data reproduces all groupings except the frontal assemblage. These data therefore support interpretations based on earlier stratigraphic data, and highlight the significance of benthic foraminifera as faunal indicators of paleostratification in shelf seas. The distributions also support predicted cross-frontal transfer of nutrients and the existence of surface converging circulation cells. Statistical analyses indicate the significance of unmeasured ecological variables which we speculate might be food supply, and oxygen concentration of bottom and sediment pore waters.

INTRODUCTION

Although continental shelves account for just 10% of the ocean floor area, shelf seas contribute 20% or more of marine primary production (Walsh, 1988) and are therefore a significant component of the global carbon cycle. Much of this primary production is associated with seasonal stratification and shelf sea fronts (Berger and others, 1989). Seasonal thermal stratification is the dominant hydrodynamic phenomenon of tide-dominated shelf seas in the middle and high latitudes. Stratification occurs when summer heating of the sea surface exceeds tidal stirring. The resultant fronts, separating mixed from stratified water, are zones of enhanced primary production and support a coupled pelagic-benthic ecosystem which influences organic sedimentation and the production and preservation of microfossils (Fig. 1).

Austin and Scourse (1997) published an AMS ^{14}C dated Holocene benthic foraminiferal stable oxygen and carbon isotopic record from the central Celtic Sea (BGS vibrocore 57/-07/199), which they interpreted as a record of the onset of seasonal stratification during the early Holocene. The isotopic record was associated with changes in benthic foraminiferal assemblages in which an early mixed phase (thermocline state I), characterized by an epifaunal assemblage dominated by *Cibicides lobatulus* and *Quinqueloculina seminulum,* was progressively replaced (thermocline state II) by an infaunal assemblage dominated by *Bulimina marginata* in the later stratified phase (thermocline state III). These changes suggested that the foraminiferal assemblages themselves are linked to the plexus of factors defining, or associated with, stratification.

This paper tests the hypothesis that benthic foraminiferal distributions in the Celtic Sea are intimately linked to the physical and biogeochemical processes associated with seasonal stratification. Surface samples collected during two cruises during 1995 and 1996 have been analyzed for living and dead foraminiferal faunas and compared with associated environmental data. Dead assemblages integrate seasonal changes in the foraminiferal populations, and time-averaging is therefore a better analogue for interpretation of fossil assemblages than the live assemblages. Furthermore, sediment transport patterns and test preservation are linked to peak bed stress vectors, which are themselves a function of the hydrodynamic regime associated with seasonal stratification (Austin, 1991).

OCEANOGRAPHIC SETTING

The Celtic Sea extends from the 200m isobath in the south and west of the continental shelf bordering the North Atlantic, to southern Ireland and the entrances to the Irish, Bristol, and English channels (Pugh and Thompson, 1986). The study area is restricted to part of the northern Celtic Sea between 51° and 52°25′N between 4° and 7°W (Fig. 2). The St. George's Channel Trough in the southern Irish Sea trends in a NW–SE direction into the extensive and broad Celtic Deep basin, which is included within the study area.

As in all tide-dominated shelf seas, heating of the surface waters in the Celtic Sea induces buoyancy and stability, but the turbulence generated by the action of bottom friction on tidal currents acts against this, and may generate sufficient kinetic energy to maintain vertical mixing throughout the depth of the water column. During winter, the entire water

[1] School of Geography and Geosciences, University of St. Andrew's, St. Andrew's, Fife, KY16 9ST, Scotland, UK.

[2] Corresponding author; e-mail: j.scourse@bangor.ac.uk

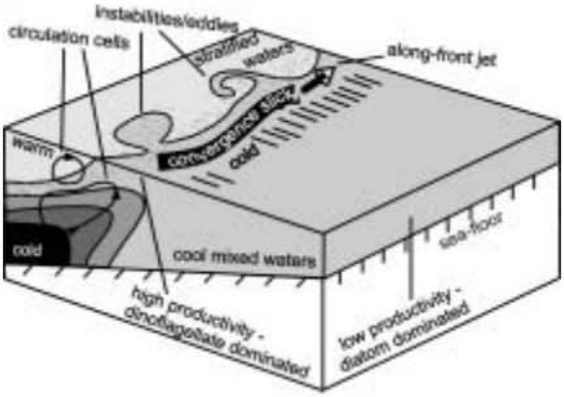

FIGURE 1. Schematic depicting the nature, dynamics, and biology of a tidal front (summer situation). Tidal fronts are seasonal phenomena common on high and mid-latitude continental shelves which occur at the juxtaposition of deeper, stratified, waters with shallower, mixed waters. The shallow, mixed, side has uniform temperature and density throughout, intermediate between the surface and bottom characterstics of the stratified side.

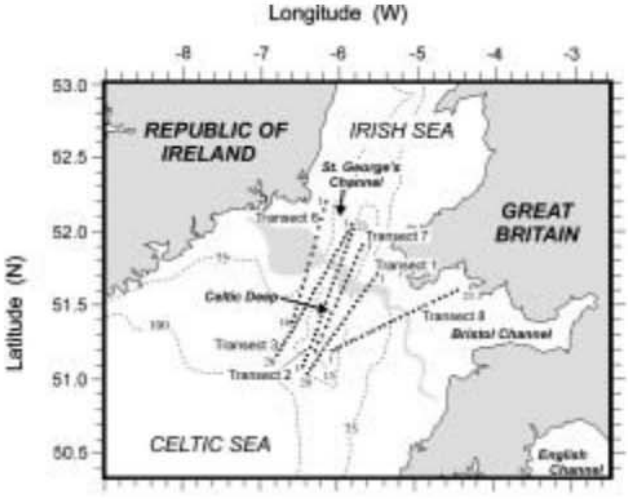

FIGURE 2. Location of study area showing the transects and CTD stations from which foraminiferal, sediment, and water samples were collected. Stippled area represents the mean summer position of the Celtic Sea front.

column is mixed with relatively uniform temperature, salinity, and density characteristics throughout. In early spring, when heat fluxes from the atmosphere to the sea surface, a warm surface layer develops. This layer is separated from the colder bottom waters by a sharp density gradient, the pycnocline, which restricts the exchange of heat and nutrients between the two water bodies (Fig. 1). In the Celtic Sea, where salinities are generally high throughout, the pycnocline generally coincides with the thermocline, defined as the sharp temperature gradient between the surface and bottom waters (Elliott and others, 1991). In autumn, as atmospheric cooling begins, the surface layer loses heat both upwards and downwards. Eventually the two layers become equal in temperature, the thermocline disintegrates and the whole water column re-mixes. Variations in tidal mixing and water depth result in some areas of the shelf becoming stratified while adjacent waters are mixed; the transition between the two is marked by a strong horizontal gradient known as a front.

The main tidal front in the study area is the Celtic Sea front extending between Britain and Ireland and curving southwards, at around 51°N, along the British coast. This front can be recognized in summer by temperature measurements across the boundary area and is recorded by satellite imagery which detects sharp, horizontal surface temperature gradients (Simpson and Bowers, 1979). The mixed zone is confined to the shallower (generally <100 m) inshore waters in the north and east of the study area, whereas the deeper water over the central and outer shelf stratifies during the summer months.

When discussing the biological oceanography associated with shelf sea fronts, it is important to distinguish between mixed, frontal, and stratified waters. The 'classical' phytoplankton cycle for seasonally stratified waters is characterized by a spring bloom followed by a subdominant autumn bloom. In winter there are few phytoplankton living because, although there is a high availability of nutrients, individuals are mixed below the euphotic zone and cannot photosynthesize. In spring, light input increases and the wind-mixed layer shallows until it no longer exceeds the critical depth (Sverdrup, 1953), the phytoplankton experience high levels of illumination, and a bloom is triggered.

Herbivorous zooplankton and bacterial blooms lag the phyoplankton blooms. Grazing pressure from zooplankton and the exhaustion of nutrients in the euphotic zone result in a low summer phytoplankton standing stock. The autumn bloom is attributed to a decrease in zooplankton numbers as a consequence of predation and the increased availability of nutrients due to wind-driven mixing. Diatoms comprise the majority of the spring bloom, while the summer population is dominated by dinoflagellates. Those areas characterized by year-round tidal mixing and frontal regions have a different biology. Holligan (1981) observed that fronts mark the landward limit of the spring bloom, which occurs only in stratified waters, while tidally mixed waters are dominated by relatively low numbers of diatoms. The frontal region consists of a low diversity, dinoflagellate population which has a single summer peak, rather than a biannual bloom, as does the subsurface phytoplankton maximum nearest the front (Fig. 1).

MATERIALS AND METHODS

SAMPLING

The samples used in this study were collected in the northeast Celtic Sea during two cruises aboard the *RV Prince Madog* in June–July 1995 and June 1996. Shipek grab samples were collected from 72 stations arranged along transects 1, 2 and 3 in 1995, and 56 stations along transects 6, 7 and 8 in 1996 (Fig. 2). The transects all intersected the Celtic Sea front in approximately a north–south direction except transect 8 which traversed the entrance to the Bristol Channel and the front from approximately west to east. Each Shipek grab sample was subsampled for foraminiferal and grain size analyses and, from transects 1–3, sediment geochemical analyses. Care was taken to ensure that only the surface ($\sim$0.5 cm) of each sample was subsampled. Samples

for foraminiferal analysis were preserved in ethanol, to which rose Bengal stain was added in order to discriminate between live and dead individuals. Samples for geochemical analysis were frozen. The temperature, salinity and density characteristics of the entire water column were also measured for each station using a Neil Brown Mk IIIb profiling conductivity, temperature and depth probe (CTD).

Sediment Analysis

The grain size samples were wet sieved through a 63 μm mesh and the retained sediment was dried at 105°C overnight in preparation for dry sieving. The larger fractions were sieved at 0.5Φ intervals and measured to an accuracy of 0.01g. A sedigraph (Micromeritics 5000ET) was used to measure grains of <100 μm in diameter. Samples were centrifuged with distilled water, treated with 10% hydrogen peroxide to remove organic matter, and then centrifuged again with distilled water. Calgon was used to deflocculate the samples, which were then dispersed in an ultrasonic bath for 15 minutes (Stein, 1985), followed by the use of a magnetic stirrer. The suspended solution was loaded into the sample cell and the X-ray intensity set to 700. Samples were analyzed for sizes between 3–100 μm and maintained at 32°C. Grain size parameters for each sample were calculated using a Fortran grain size analysis package (Jones, 1990). These include modal and mean grain size, sorting, skewness and kurtosis for both moments and Folks (Folk, 1966; Folk and Ward, 1957).

Geochemical Analysis

The samples for geochemical analysis ($CaCO_3$, inorganic carbon, organic carbon and nitrogen content) were thawed, sieved through a 500 μm sieve to remove the larger fragments, ground until the sediment had the consistency of flour, then weighed. The samples for organic carbon analysis were reacted with 100 μl of HCl and dried to remove all $CaCO_3$. Samples were then processed by a Carlo Erba NA-1500 carbon analyzer (Verardo and others, 1989). Samples were run in batches of up to 50, including control samples of Acetanilide, a National Bureau of Standards certified standard reference material for organic carbon/nitrogen microchemical analyses. The organic carbon and nitrogen contents were calculated using the data from the analyzer and the algorithm given in Verardo and others (1989). Inorganic carbon was calculated by subtracting organic carbon from total carbon, which was processed as above but without the decalcification step.

Foraminiferal Analysis

In preparation for microscopic examination, foraminiferal samples were washed through a 63 μm sieve and dried overnight. Flotation was carried out according to Meldgaard and Knudsen (1991) using carbon tetrachloride (CCl_4), which is considered appropriate for recent sediments; residues were checked for non-floating tests. A total of 52 samples were picked for 300 living and 300 dead individuals; identifications were based on a number of taxonomic sources (Haynes, 1973; Murray, 1971, 1991, 2000).

Statistical Analysis

Both live and dead foraminiferal data were analyzed using two different multivariate statistical techniques. Factor analysis involved the application of simultaneous Q- and R-mode analysis using a MINITAB program after Walden and Smith (1995). Data were prepared for analysis in the way prescribed by Imbrie and Kipp (1971), and any species which did not comprise at least 8% of one sample was eliminated before analysis. Data were input in the form of percentages. In addition, *Textularia bockii* and *Spiroplectammina wrightii* were grouped under the heading *Textilina* group because of their taxonomic and ecological affinity (Murray, 1979). All *Bolivina, Brizalina* and *Bolivinella* species were summed together into a *Bolivina* group, and all *Reophax* species were summed as a *Reophax* group. The input dataset used for the live factor analysis comprised 22 species or species groups; 13 were used for the dead analysis.

CCA is a useful complement to factor analysis because it examines each species individually and can help explain non-interactive inter-species associations (CCA does not consider inter-species interactions).

CCA was performed on a data set comprising both foraminiferal and environmental data and using the program (CANOCO, version 3.12, 1991) after ter Braak (1991). A detrended correspondence analysis (DCA) was automatically performed by CANOCO on the faunal data. In preparation for the analysis, those species which did not constitute 5% or more of at least one sample were removed from the species dataset. Species were not grouped for canonical correspondence analysis (CCA) and only those environmental variables which did not covary significantly were included in the environmental dataset. These included depth, temperature, % gravel, % sand, mean grain size, sorting (moments), skewness, and kurtosis (both calculated using moments and Folks), latitude and longitude. Percentage values were used for the species data and absolute numbers for the environmental data. To determine the exclusive individual contribution of each environmental variable to the analysis, a series of partial CCAs were carried out after Borcard and others (1992).

RESULTS

Environmental Gradients

The position of the tidal front was identified using temperature and salinity data from throughout the water column. Though this information is useful with regard to foraminiferal distributions in a qualitative way, for the purposes of the statistical analyses, only the bottom water temperature and salinity measurements were used. These, together with the position, depth, and remaining oceanographic data are given in Table 1.

Changes in bottom water temperatures across the area are shown in Figure 3a. These range from cooler stratified waters in the south (minimum 8.88°C) to warmer fully mixed conditions in the north (maximum 12.35°C). Isotherms illustrate that the stratified waters extend further north in the Celtic Deep bathymetric trough, suggesting that the subthermocline waters are fixed by depth in this area. Bottom

TABLE 1. Depth, position, water and sedimentary characteristics of each sampling station.

Sample:	Depth (m)	Bottom water		% Organic carbon	% Organic nitrogen	C/N ratio	Latitude N	Longitude W	S index °C	% Gravel	% Sand
		Temperature (°C)	Salinity PSU								
T1S01	64	12.27	34.9	1.17	0.23	5.09	51.68	5.49	0.0042	31.5	65
T1S02	67	11.95	34.97	0.31	0.06	5.17	51.65	5.56	0.1520	28.9	68.1
T1S03	68	11.49	35.01	0.24	0.04	6	51.61	5.61	0.1357	11.7	87.6
T1S06	87	10.17	35.38				51.5	5.77	0.5088	0.2	98.3
T1S07	86	10.1	35.38				51.46	5.82	0.5491	0	96.8
T1S09	91	9.9	35.36	0.52	0.06	8.67	51.39	5.92	0.6133	0	80.6
T1S14	103	9.61	35.36	0.86	0.1	8.6	51.22	6.16	0.6853	1.4	44.9
T1S17	102	9.41	35.34	0.69	0.09	7.67	51.11	6.31	0.7238	1.1	65.1
T1S19	101	9.56	35.37	0.25	0.03	8.33	51.04	6.41	0.6797	5.8	85.7
T2S01	98	9.41	35.34	0.14	0		51.05	6.44	0.7083	2.8	96.4
T2S03	104	9.25	35.3				51.14	6.38	0.7385	0	91.8
T2S07	115	9.33	35.33	1.09	0.13	8.38	51.32	6.27	0.7220	0.1	17.1
T2S11	115	9.34	35.32	0.41	0.06	6.83	51.49	6.18	0.7354	0	74.6
T2S14	115	9.73	35.21	0.34	0.04	8.5	51.63	6.1	0.6182	0	99.4
T2S16	111	9.53	35.32				51.71	6.04	0.6880	6.7	92.9
T2S19	105	9.95	35.32	0.35	0.04	8.75	51.84	5.96	0.5765	11.9	84
T2S20	102	9.84	35.23	0.21	0.03	7	51.88	5.93	0.4553	34.3	64.5
T2S21	105	10.65	35.12	0.13	0.03	4.33	51.93	5.9	0.2322	22.5	75.6
T2S22	93	11.58	34.89	0.45	0.06	7.5	51.97	5.87	0.0995	35.7	56.3
T2S23	95	11.61	34.91	0.27	0.03	9	52	5.85	0.0360	34.6	64.6
T3S01	98	11.6	34.89	0.27	0.04	6.75	51.97	5.86	0.0546	24.3	73.6
T3S03	109	10.23	35.16	0.17	0.03	5.67	51.91	5.93	0.2821	20.3	77
T3S05	108	9.71	35.24	0.22	0		51.84	6.01	0.6114	9.4	86.9
T3S07	115	9.69	35.27	0.15	0		51.77	6.08	0.5847	2.1	96.9
T3S10	109	9.75	35.25	0.31	0.05	6.2	51.67	6.19	0.5419	0	94.1
T3S11	99	10.1	35.15	0.26	0.04	6.5	51.63	6.22	0.5153	0	92.6
T3S13	96	9.46	35.27	0.21	0.03	7	51.57	6.29	0.7059	0	95.9
T3S15	96	9.3	35.32	0.39	0.05	7.8	51.5	6.37	0.7554	0	85.5
T3S16	101	9.32	35.32	0.35	0.06	5.83	51.46	6.4	0.7515	3.5	74
T3S17	96	9.3	35.31	0.31	0.04	7.75	51.43	6.44	0.7432	1.8	84.2
T3S19	88	9.38	35.27	0.27	0.04	6.75	51.36	6.51	0.7176	9.6	81.8
T3S23	92	9.25	35.26	10.17	0.02	8.5	51.23	6.66	0.7656	3.5	92.9
T6S02	75	11.82	34.92				52.11	6.2	0.0003	31.5	68.5
T6S06	82	11.58	34.96				51.86	6.28	0.0842	1.1	98.9
T6S08	71	11.02	34.96				51.77	6.32	0.2758	0.4	99.6
T6S10	71	10.28	35.05				51.66	6.37	0.3513	0.4	99.6
T6S12	81	9.09	35.22				51.42	6.47	0.6356	0	97.3
T6S14	93	8.88	35.22				51.53	6.42	0.7231	0	95.2
T6S16	93	8.89	35.23				51.33	6.5	0.7006		
T7S02	111	10.68	35.13				51.84	5.74	0.2707	53.7	46.3
T7S06	116	10.04	35.24				51.66	5.89	0.3753		
T7S10	110	9.73	35.25				51.5	6.03	0.5556	0	95.2
T7S16	114	9.73	35.35				51.22	6.29	0.5962	0	95.2
T8S01	106	9.82	35.35				51.17	6.17	0.6003	0	22.8
T8S02	104	9.85	35.35				51.19	6.11	0.5813	0	30.5
T8S05	90	10.36	35.29				51.24	5.9	0.4991	0	82.8
T8S08	82	10.49	35.24				51.29	5.69	0.4464	0	96.9
T8S09	79	10.59	35.24				51.31	5.63	0.4411	0	98.9
T8S10	76	10.75	35.24				51.33	5.56	0.4216	0	99.5
T8S13	71	11.05	35.17				51.39	5.32	0.1758	0.1	99.6
T8S16	64	11.46	35.02				51.44	5.08	0.1718	0	81.5
T8S20	49	12.27	34.67				51.51	4.75	0.1087	0.9	99
T8S21	41	12.35	34.6				51.53	4.66	0.0993	4.5	77.7

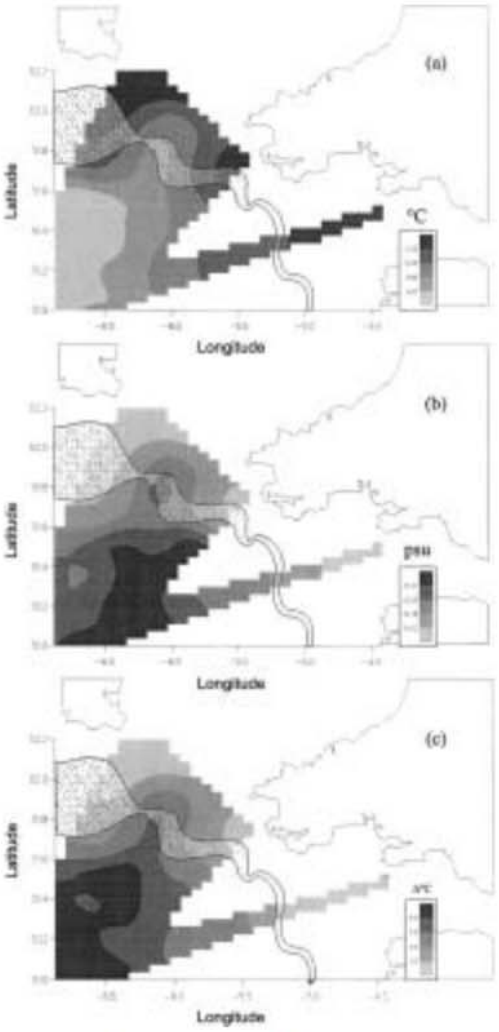

FIGURE 3. Distribution maps of (a) bottom water temperature (°C), (b) bottom water salinity (psu) and (c) stratification index, S-index (surface—bottom water Δ°C). Mean summer position of the Celtic Sea front shown.

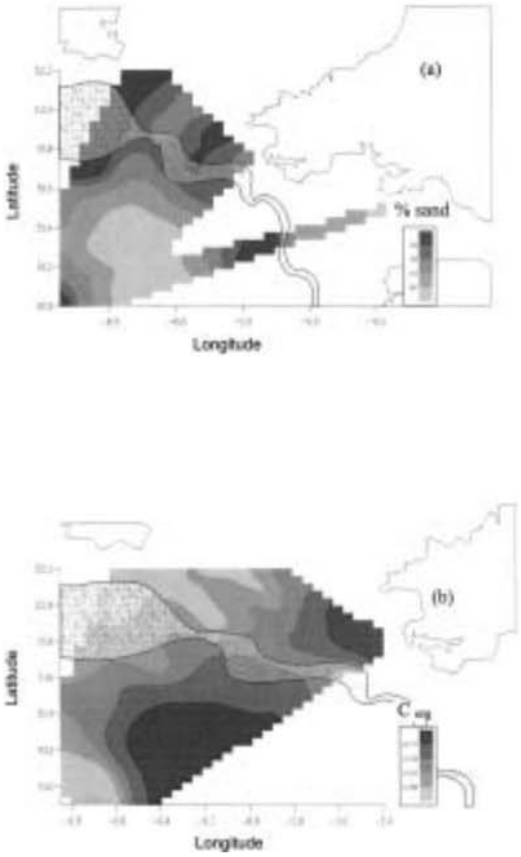

FIGURE 4. Distribution maps of (a) % sand, (b) % C_{org}. C_{org} data are not available for transect 8. Mean summer position of the Celtic Sea front shown.

water salinities are stable across the frontal region (Fig. 3b), but are lowest in the mixed St. George's Channel waters to the north and in the Bristol Channel, and higher in stratified waters.

Since no single variable provides a measure of the degree of stratification at a single site, the term "S-index" is defined here as the difference between bottom and surface water temperatures (Δ°C). The variability of S-index across the area is shown in Figure 3c. Mixed sites are those with S-index values less than 2 and stratified sites are those with an S-index greater than 6. Intermediate values indicate that a site is frontal.

The percentages of gravel, sand, silt and clay were determined for each sediment sample (Table 1). The distribution of % sand (>63 μm) is shown in Figure 4a. This demonstrates that the coarsest sediments lie in the north and northwest, while the finest lie to the south-east and at the end of transect 8. The relative contribution of gravel is highest in the mixed areas to the north, decreasing markedly through the frontal region. No gravel was recorded anywhere along transect 8, but there is a small increase in gravel content to the southwest. Sand content, by contrast, is relatively low in the mixed area to the north, high in the mid-frontal region, and highest in the west.

The distribution of organic carbon (Fig. 4b) demonstrates that surface water productivity, which is concentrated in the frontal zone (Tett and others, 1993) is not directly reflected in the underlying sediments. Other studies have indicated a direct coupling between chlorophyll maxima and organic carbon content of sediments in shelf settings (van Haren and Joordens, 1990). There is, instead, an east-west gradient, possibly due to advection of benthic fluff into deeper, more quiescent, basins. The inverse relationship in the distribution of organic carbon and % sand (Fig. 4) lends support to this hypothesis.

FORAMINIFERAL DISTRIBUTIONS

The percentage contribution of each species to both live and dead assemblages, and the densities of live and dead foraminifera per 10 cm^3 of sediment, are given in Appendices I and II. The total live and dead density distributions are shown in Figure 5 and for individual species in Figure 6. The greatest densities of live foraminifera occur in the area where mixed and frontal waters meet, and in stratified waters lying just beyond the frontal region. Stations along

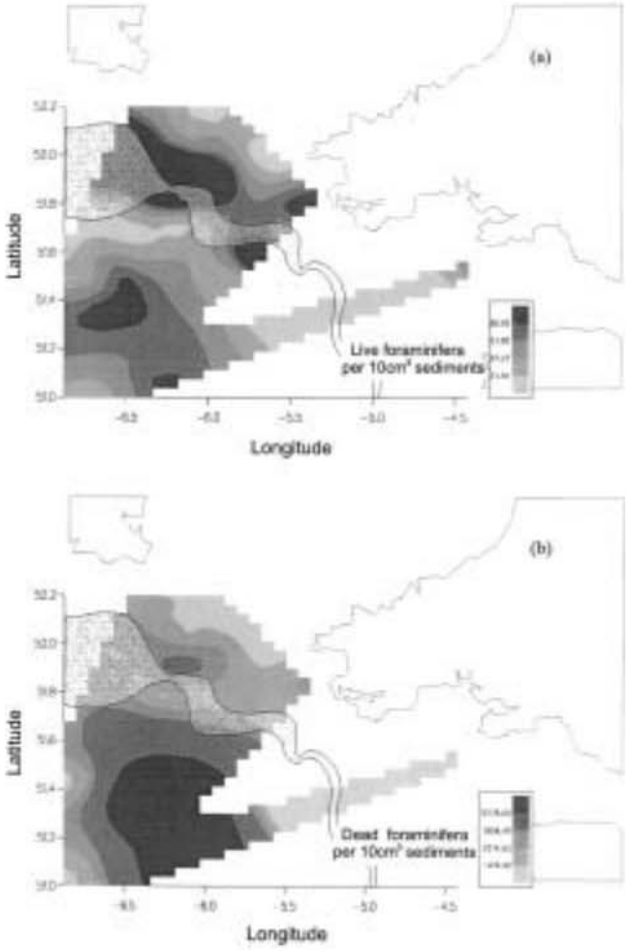

FIGURE 5. Distribution (in numbers of foraminifera per 10cm^3 sediment) of (a) live, and (b) dead foraminiferal densities. Mean summer position of the Celtic Sea front shown.

the entrance to the Bristol Channel, in mixed waters, and in the mid-frontal region show the lowest live densities.

As expected, the dead densities are up to 200 times greater than the live, but the live and dead distributions differ. The greatest dead densities are found in the Celtic Deep basin to the southeast; density decreases with increasing distance from this basin. The live data reflect only a "snapshot" of the foraminiferal distributions during summer conditions, and likely vary seasonally in response to factors such as the spring and autumn blooms. However, the dead distribution shows a strong inverse relationship to grain size % $>63\mu$m (Fig. 4a) suggesting that the difference between live and dead distributions might be controlled by sediment transport. Detailed comments on the distributions of individual species are included in Appendix III.

MULTIVARIATE STATISTICAL ANALYSES

Factor Analysis

The results of the R-mode analysis on the live data determine the characteristic species of each assemblage, while the Q-mode scores indicate the significance of each factor at each site. These scores have been mapped to show the area over which each assemblage is important (Fig. 7). The Q-mode scores have also been plotted against the measured environmental variables at the same sites to examine possible relationships; a derived factor is more likely to exhibit a relationship than any individual scores alone (Conradsen, 1993). Detailed comments on the factor analysis results of both live and dead datasets are included in Appendix IV. The distributions of the first four factor scores for the dead data, which account for over 84% of the total variance, are shown in Figure 8.

Canonical Correspondence Analysis

The summarized results of the CCA analysis of the live data are presented in Table 2. The sum of the unconstrained eigenvalues is the sum of the lengths of the maximized spread of species along hypothetical environmental gradients, and is effectively a detrended correspondence analysis (DCA; Hill and Gauch, 1980), while the sum of the canonical or constrained eigenvalues is the sum of a maximized spread along an environmental gradient, which is a linear combination of the measured environmental variables. By comparing the two, it is possible to ascertain how well the measured environmental variables explain the data. Given that the sum of the CCA eigenvalues is only two-fifths of the sum of the DCA eigenvalues, it is very likely that the most important controlling environmental variables were not measured. Only ~30% of the species data are explained by the measured environmental variables on the first three axes. The first and second axes are almost equally significant, the first explaining 12.6% of the variance, the second 11.1%. The third axis explains just 5.2% and the fourth only 3.1%. Only the first three axes are considered further.

To determine the exclusive individual contribution of each environmental variable to the analysis, a series of partial CCAs were undertaken (Borcard and others, 1992; Table 3). The percentage contribution can be calculated by comparing the eigenvalue of the partial CCA with the sum of the values of the main CCA. The contribution made by a particular variable may be greater than that shown because it covaries with other variables. This analysis indicates that the most significant individual contributions are made by latitude, depth, and longitude; i.e., location. Since these variables cannot, in themselves, be responsible for controlling species' distribution, it is clear that they are acting in this analysis as proxies for the true controlling parameters.

The environmental, species, and site scores produced in this analysis are given in Appendix V. The values for the first three axes have been converted to co-ordinates for biplots (Fig. 9). The environmental variables are represented by arrows whose length approximates their relative significance, and whose orientation reflects their relations with the explanatory axes, each other, the sites, and species. Since axes 1 and 2 explain similar amounts of the species variance they are comparable in length. Axis 3, however, is only half as important as axis 2. These demonstrate that the first axis is largely a function of mean grain size, skewness, latitude, and % gravel; the second axis, temperature, depth and longitude; and the third axis, % sand and sorting. Species are spread along the environmental gradients of which mean grain size and % gravel, temperature, and depth are the most

important. Species such as *Trochammina* sp., *Globotrochamminopsis pygmaeus, Deuterammina* (*Lepidodeuterammina*) *ochracea, Gavelinopsis praegeri, C. lobatulus*, and *C. fletcheri* occur optimally in northern sites with large proportions of gravel, while species such as *Stainforthia fusiformis* are found in much finer grained, southerly, sites. *Nonionella turgida, Bulimina marginata, Adercotryma wrighti* and *Hyalinea balthica* characterize cold, deep, southerly sites while *Q. seminulum, S. wrightii* and *Lamarckina haliotidea* prefer warmer sites. *Bulimina gibba* and *Eggerelloides scaber* show affinity for high % sand content.

The results of the analysis of the dead assemblage data are presented in Appendix VI and Table 4. Comparison of the sum of the canonical values with the constrained eigenvalues demonstrates that half of the variance can be explained by the measured environmental variables. While this is low, it does mean that these measured parameters are better at explaining the distribution of dead tests than the live. Only 41.4% of the variance is explained by the first four axes. The first and second axes explain similar amounts of the variance (16.7 and 12.3% respectively), while the third explains 10%. Since the fourth axis explains only 3%, only the first three axes are considered further.

Partial CCA analysis (Table 5) demonstrates that, as for the live, over half the explained variance is determined by covariance of the variables. Individually, the most important variable is latitude, but longitude, and skewness measured by moments are also important. The significance of latitude and longitude again suggests that these variables are acting as partial proxies, at least, for the actual environmental controls. The scores produced by the analysis for sites, species, and environmental variables are plotted in Figure 10. It is clear that depth, temperature, longitude, and latitude are the most significant explanatory variables. Depth and longitude influence the first axis, while % gravel, temperature, latitude and mean grain size influence the second. The third is a function of % sand and sorting.

Examination of the position of the various species relative to these gradients demonstrates some clear patterns (Fig. 10). Several species are arranged along the temperature gradient, from *H. balthica,* which characterizes the coldest temperatures, through *B. marginata, A. wrighti, G. praegeri, Q. seminulum* to *Elphidium magellanicum*. These species are also arranged along a gradient of increasing depth and decreasing grain size. Latitude, grain size, and % gravel all appear to be closely interrelated, and species such as *Gaudyrina rudis* and *Eponides repandus* have maxima in the most northerly, coarsest conditions, closely followed by *C. lobatulus, C. fletcheri* and *Ammonia batavus. B. gibba* and *E. scaber* reach optima in very high percentages of sand, while the *Bolivina* group prefers much finer substrates. Species arranged along the depth gradient include *S. fusiformis* in the deepest conditions, through *S. wrightii, T. bockii, Q. seminulum, Miliolinella subrotunda* to *Elphidium excavatum* in the shallowest.

The first axes of the both the living and dead analyses were subject to Monte Carlo permutations to test for significance. Both produced P-values of 0.01, demonstrating that these axes were significant.

DISCUSSION

Temperature and salinity measurements taken across the front in June–July 1995 and June 1996 record strong, temperature-driven, stratification in the Celtic Sea. The front marks the separation of mixed and stratified, cold and warm waters, high and low energy tidal currents, and is associated with high levels of productivity. It is known that these oceanographic features remain in place from mid-March to late-September (Elliott and others, 1991).

Though upwelling and downwelling resulting from along-front flows are difficult to measure (Hill and others, 1993), they are believed to profoundly influence productivity (James, 1978; Savidge and Foster, 1978). The weak circulation cells depicted in Figure 1 suggest that the seabed in the frontal region does not receive equal rates of debris and carbon flux from above (K. Horsburgh, pers. comm. 1999). It is likely, though unproven, that while the area directly beneath the convergence slick receives flux from above, some of the particulate matter becomes entrained by the flow between the circulation cells and is delivered instead southwards to the stratified area beyond the front. The seabed separating these two zones of deposition is, by contrast, deprived of detritus which is drawn away by the same flows.

The distribution map for organic carbon in the Celtic Sea (Fig. 4b) indicates that there is indeed a strong degree of pelagic-benthic decoupling between the surface waters and the seabed. Since productivity is centered around the frontal region, it might be expected that this would be reflected in the beneath-front seabed sediments. Instead, there is a clear east-west gradient which probably results from the redistribution of organic material to more quiescent areas. This interpretation is supported by the inverse relationship with % sand (Fig. 4a). The coarsest grain sizes are found in the north and the finest in the south, apart from a patch of coarse sediments in the extreme southwest. The hydrographic data, particularly temperature, accurately reflects the strength and distribution of stratification in the northeast Celtic Sea, but does not directly record the associated stratification dynamics which have been derived by other workers (cf. Hill and others, 1993). The sedimentary regime is clearly profoundly

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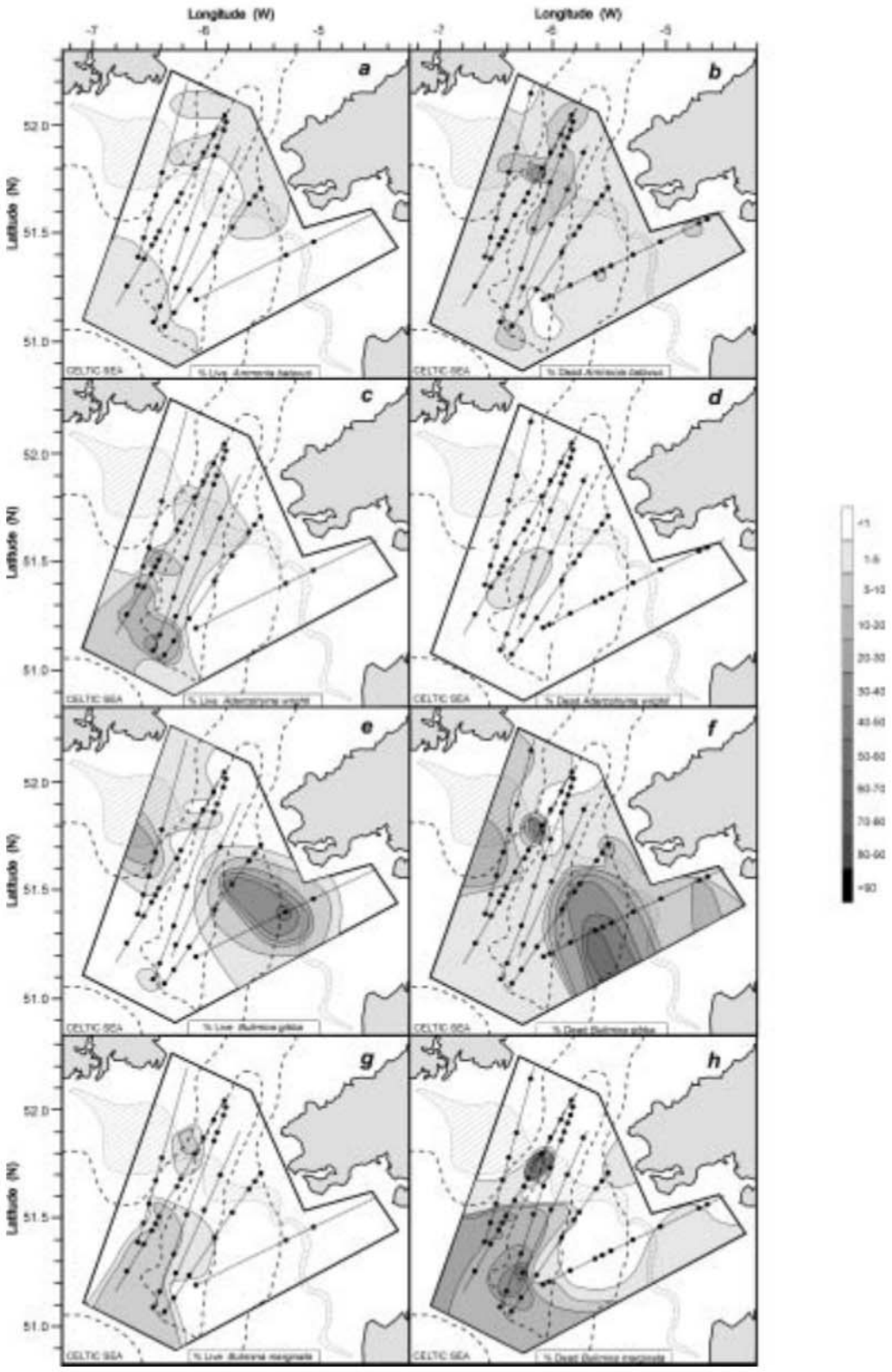
FIGURE 6. Distributions, in % frequency total live and % frequency total dead foraminifera, of (a) live *Ammonia batavus,* (b) dead *A. batavus,* (c) live *Adercotryma wrighti,* (d) dead *A. wrighti,* (e) live *Bulimina gibba,* (f) dead *B. gibba,* (g) live *Bulimina marginata,* (h) dead *B. marginata,* (i) live *Cibicides lobatulus,* (j) dead *C. lobatulus,* (k) live *Gavelinopsis praegeri,* (l) dead *G. praegeri,* (m) live *Hyalinea balthica,* (n) dead *H. balthica,* (o) live *Nonionella turgida,* (p) dead *N. turgida,* (q) live *Quinqueloculina seminulum,* (r) dead *Q. seminulum,* (s) live *Stainforthia fusiformis,* (t) dead *S. fusiformis,* (u) live *Spiroplectammina wrightii,* (v) dead *S. wrightii,* (w) live *Textularia bockii,* (x) dead *T. bockii.* Contours represent 1%, 5%, 10% and increments of 10% thereafter. These contour intervals are within the errors for the samples point counted for stations shown as black dots (e.g., Galehouse, 1971). Stations with low totals which raised the errors on the data above the 1% level for species with low % frequencies have been excluded from the analysis. Mean summer position of the Celtic Sea front shown.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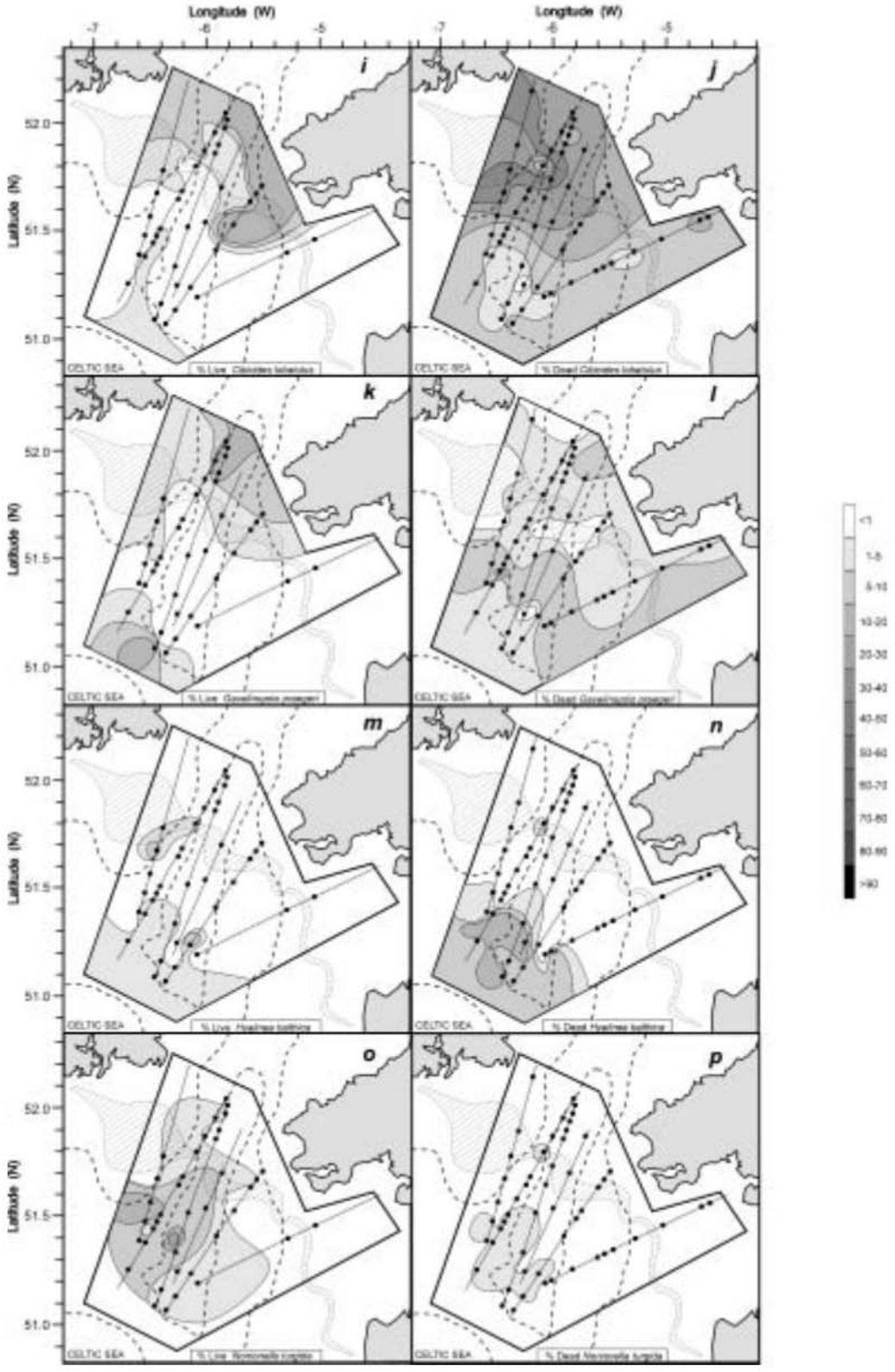

FIGURE 6. Continued

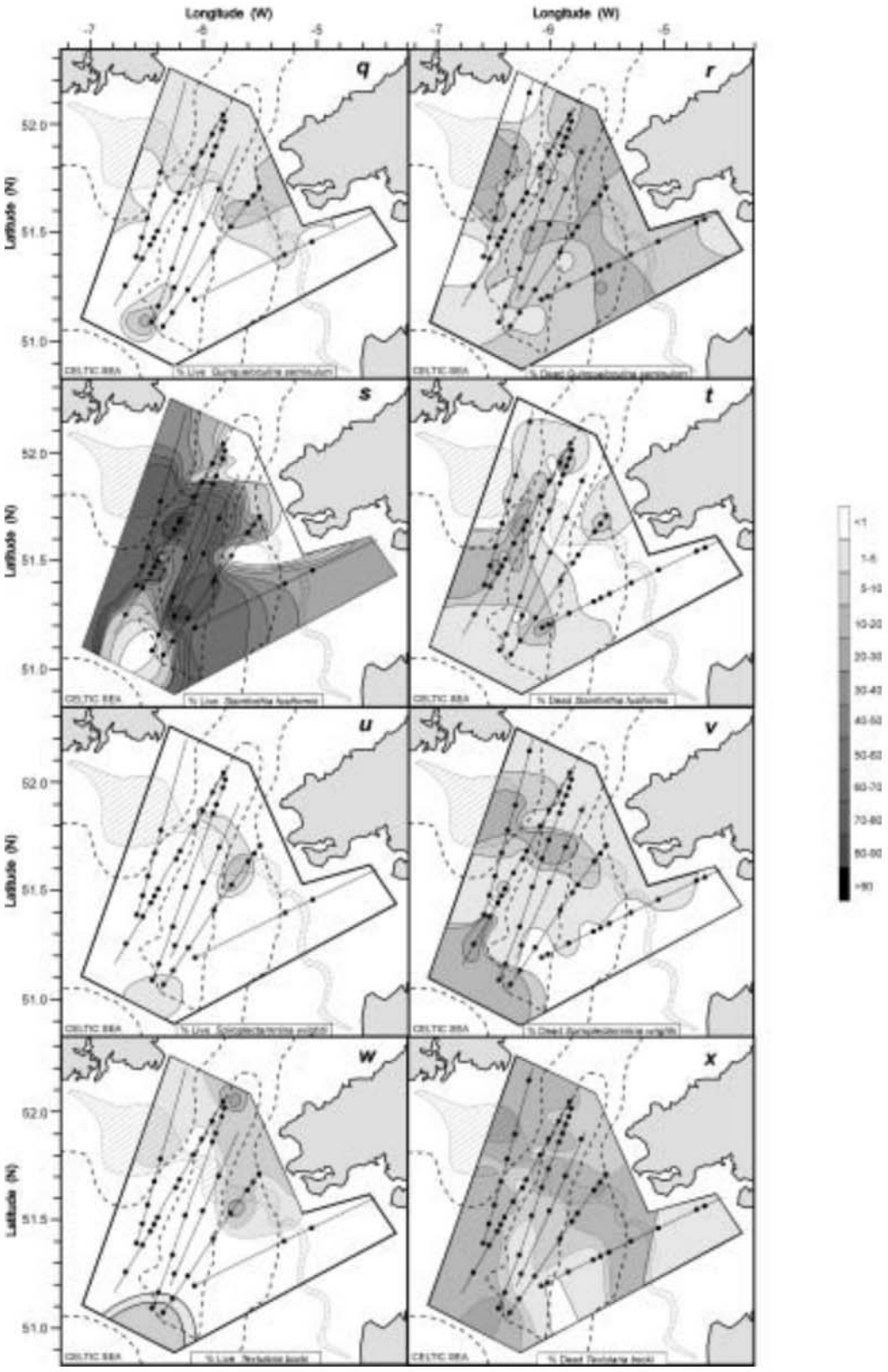

FIGURE 6. Continued

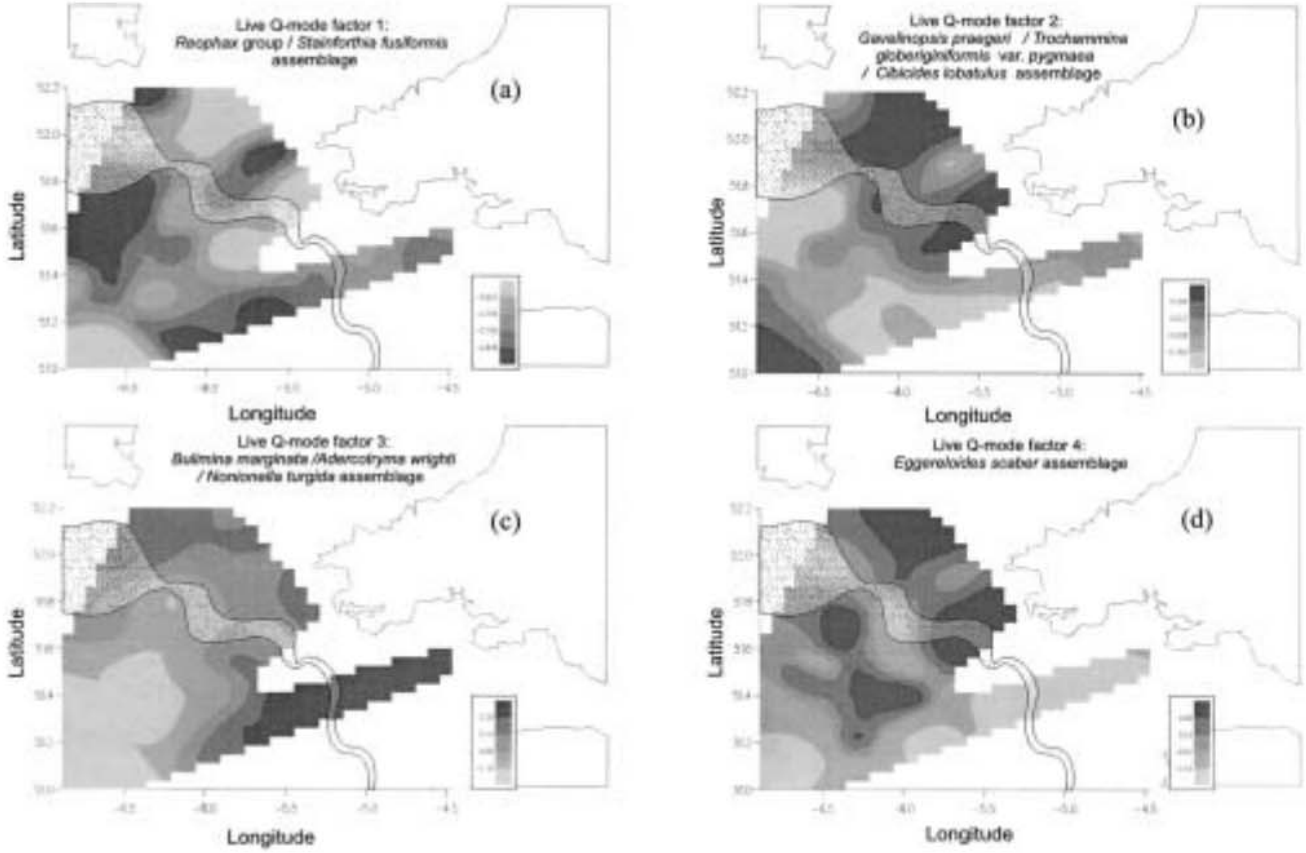

FIGURE 7. The mapped live Q-mode factor analysis scores for (a) factor 1: *Reophax* group and *S. fusiformis* assemblage, (b) factor 2: *G. praegeri, T. globeriginiformis* var. *pygmaea* and *C. lobatulus* assemblage, (c) factor 3: *B. marginata, A. wrighti* and *N. turgida* assemblage, (d) factor 4: *E. scaber* assemblage. Mean summer position of the Celtic Sea front shown.

influenced by the local oceanography, but the relationship is complex, and subject to reworking. Most significantly, the precise condition of the water column structure is not registered in the sediments directly beneath.

There are large differences between the live and dead distributions of some species (Fig. 6). This must be due either to the unrepresentative nature of the live distribution at the time of collection, or to *post-mortem* advection and differential test destruction. Variables such as grain size, sorting, and skewness which, like reworking, are a function of bed stress, have been measured, and so it should be possible to assess when reworking has influenced the distribution of a particular species. Though reworking is particularly vigorous in shelf environments, it seems reasonable, in this setting characterized by large seasonal variability, to speculate that some species' live distributions were not typical of the rest of the year, peak production being triggered by different environmental conditions. Other living/dead differences are a function of production and preservation (Boltovsky, 1991; Boltovsky and Totah, 1992; Loubere and others, 1993).

Initial comparison of the live and dead densities (Fig. 5) suggests active reworking, since the highest live densities are found in the region of the front whereas the dead are focused into the bathymetric basin in the southwest. The high live densities in the frontal region probably results from the high organic flux associated with the front (*e.g.,* Altenbach and Sarnthein, 1989). However, the individual species' distributions demonstrate that, for the majority of the most significant species, the hydrographic conditions of the area, particularly those during summer stratification, are consistently recorded. This supports Sturrock and Murray (1981), who found that Celtic Sea sediments consist of less reworked material than those in the western approaches to the English Channel. It is significant that species such as *S. fusiformis* and *N. turgida,* while constituting only a fraction of the dead assemblages, are nevertheless very significant indicators of frontal and stratified conditions respectively.

Factor analysis identifies a number of distinctive assemblages associated with the hydrographic conditions. These assemblages provide powerful tools for reconstructing the long-term dynamics of seasonal stratification. The mixed and mixed-frontal sites are typically dominated by dead tests of *C. lobatulus, T. bockii, S. wrightii, A. batavus* and *Q. seminulum.* Of these, only *C. lobatulus* is typical of a live mixed assemblage, which correlates with coarser sediments. Stratified and stratified-frontal waters are characterized by *B. marginata, H. balthica, Bolivina* group, *A. wrighti* and *N. turgida.* Factor analysis also suggests that *G. praegeri* should also be included in this group. However, the live distribution of *G. praegeri* shows that this species actually lives in mixed waters (Fig. 6k,l) so its inclusion in this

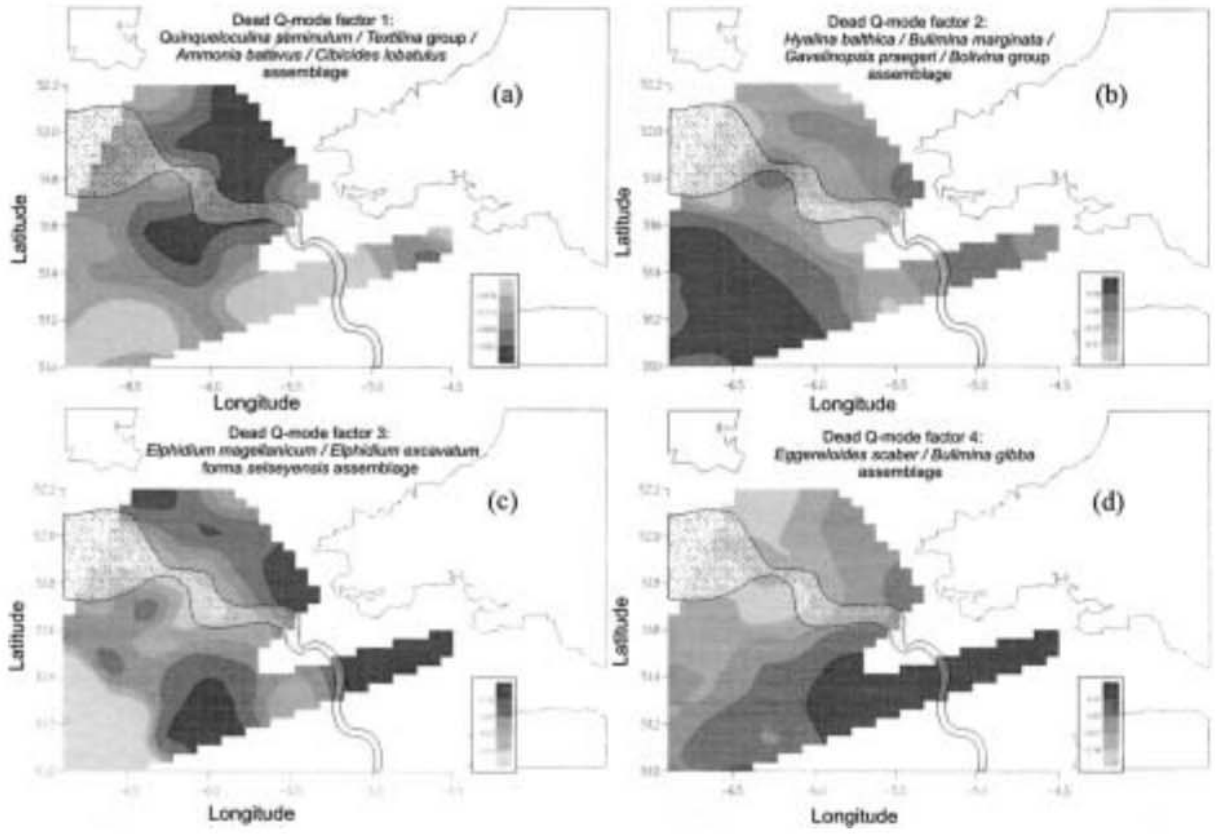

FIGURE 8. The mapped dead Q-mode factor analysis scores for (a) factor 1: *Q. seminulum, Textilina* group, *A. batavus* and *C. lobatulus* assemblage, (b) factor 2: *H. balthica, B. marginata, G. praegeri* and *Bolivina* group assemblage, (c) factor 3: *E. magellanicum* and *E. excavatum* forma *selseyensis* assemblage, (d) factor 4: *E. scaber* and *B. gibba* assemblage. Mean summer position of the Celtic Sea front shown.

group is probably a function of reworking. Precisely why this species should be so thoroughly decoupled from mixed waters, when a concave epifaunal species such as *C. lobatulus* is not, is difficult to explain; the hydrodynamic properties of the inflated *G. praegeri* test may be partly responsible. *N. turgida* and *A. wrighti* are included in this group, despite their rarity in the dead assemblages, because they are so firmly related to stratification. The area beneath the pervasive eddy in the north Celtic Deep (Fig. 8b) is also dominated by this assemblage, indicating that the regular incursion of stratified waters into the predominantly mixed area is being registered by the foraminiferal assemblages. The correlation of the live assemblage with temperature, salinity, S-index, and longitude show very clearly that this assemblage is directly related to stratification.

Factor analysis indicates that *S. fusiformis* and the *Reophax* group live in direct association with the front. This relationship was not established for the dead assemblages, however, because neither species preserves well, the former being underrepresented and the latter very rare. However, direct explanations for the association of both *S. fusiformis* and *Reophax* group with the front were not identified by statistical analysis; it is very clear from the poor correlations of several of the factor-derived assemblages with the measured environmental variables, and also from comparison of the magnitude of variability explained by unconstrained relative to constrained CA, that the main environmental controls were not directly measured. These missing variables may be oxygen concentration and food supply (cf. Nees, 1998). For commonly infaunal species like *S. fusiformis,* it is probable that it is the oxygen content of sediment pore waters rather than bottom water which is critical. Alve and Murray (1997), Caralp (1998), and Nees (1998) also suggest that the lability and nature of the food supply are significant.

TABLE 2. Summary of the CCA performed on the live data.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.31	0.28	0.13	0.07	2.48
Species-environment correlations	0.82	0.85	0.78	0.73	
Cumulative percentage variance of species data:	12.6	23.7	28.9	32	
Cumulative percentage variance of species-environment relation:	32.7	61.4	74.8	82.8	
Sum of all unconstrained eigenvalues (DCA)					2.48
Sum of all canonical eigenvalues (CCA)					0.96

TABLE 3. Results of the partial CCA performed on the live data.

Environmental variable	Sum of eigenvalues of partial CCA	% of the total explained variance exclusively explained by the environmental variable
depth	0.05	5.85
temperature	0.04	4.91
% gravel	0.04	4.18
% sand	0.04	4.18
mean	0.03	3.44
sorting	0.04	4.38
skew m	0.01	1.98
skew f	0.02	2.51
kurt m	0.02	2.71
kurt f	0.02	2.3
latitude	0.05	6.05
longitude	0.04	5.11
Sum of CCA eigenvalues	0.96	
Covariance		52.4

Nees (1998) identified three main food categories: fluffy aggregates which are easy to digest and produced during blooms (Jones and others, 1998); fecal pellets which are less nutrient-rich; and marine snow or particulate organic matter (POM), which is rained constantly but in small amounts. It is reasonable to assume that this full range of food types would be available across a frontal zone given the variability of the associated biology. The mixed waters are turbulent and well-oxygenated and are likely to contain a heavy suspended POM load with a strong lateral component. The frontal region is probably less well-ventilated and characterized by fluffy aggregates since bloom conditions occur here throughout the summer. The fully stratified region will, at least for the latter half of the summer, be poorly oxygenated and have a steady flux of POM. However, where the thermocline is shallow, dinoflagellates thrive, producing fluffy aggregates for at least part of the summer. During the winter months, fully mixed well-oxygenated conditions prevail in the area occupied by stratified water in the summer.

It is apparent that the effects of circulation cells have been recorded in the live data, in particular the *S. fusiformis-Reophax* group assemblage (live factor 1; Fig. 7a), which dominates in the mixed-frontal and the stratified-frontal transitional regions. These regions are separated by a low abundance "shadow", exactly as predicted for organic flux by cross-frontal circulation models. Perhaps even more significantly, the live density data (Fig. 5a) show a very similar pattern.

S. fusiformis is the most abundant live species in this area, appearing in almost every sample counted and constituting up to 66% live at some sites. It is not nearly as well represented in the dead assemblages though it reaches over 20% of the dead assemblage at some sites. There are some differences between the distribution of live and dead tests (Fig. 6s,t) but the broad features are similar: a heavy concentration of tests in the area of frontal and frontal-stratified transitional waters, and an absence along the Bristol Channel and in the fully stratified waters to the south.

The CCA results demonstrate that, when live, this species occurs in greatest abundances in well-sorted sediments, skewed towards fines and with low % sand content. Its dead distribution is linked to sorting and depth, which suggests reworking. Many workers have reported this species from fine-grained sediments (Collison, 1980; Conradsen, 1993). Murray (1983, 1986) also records a discrepancy between live and dead distributions in Lyme Bay. However, *S. fusiformis* is most often observed living in association with high levels of organic matter (*e.g.,* Alve, 1990, 1994; Alve and Murray, 1997; and Conradsen, 1993). This suggests that the association of *S. fusiformis* with muddy sediments may instead be a function of its affinity for organic matter, since these two parameters are linked (Cato, 1977). This is supported by the observation that it is not restricted to muddy habitats in the Celtic Sea, occurring also at some of the sandier sites which nevertheless contain organic detritus.

On the Porcupine Abyssal Plain, Gooday (1993) identified that species of *Stainforthia* (*Fursenkoina*) are opportunistic, able to exploit high levels of phytodetritus produced during spring blooms, and occur in low diversity, high dominance assemblages typical of such settings. This is also a characteristic of the Celtic Sea assemblages in which *S. fusiformis* dominates. A feature of such opportunistic foraminifera is their small size and thin-walled tests, adaptations which minimize reproductive energy requirement and permit rapid response to triggering events. Duijnstee and others (1998) demonstrate from a mesocosm experiment that *S. fusiformis* can reproduce at very small sizes when stressed, and Alve (1994) also suggests that their small size may also allow them to be easily transported to pioneer sites. A tolerance of low oxygen concentrations, even anoxia, is often a feature of bloom-responding foraminifera (Alve, 1990; Sen Gupta and Machain-Castillo, 1993). Bernhard and Alve (1986) demonstrated from nitrogen incubation experiments that *S. fusiformis* can survive anoxia, but that the species suffered some ATP damage, which suggests that it survived by becoming dormant.

Like other facultative anaerobes, *S. fusiformis* contains enzymes which allow it to survive without oxygen, but its survival is probably also a function of its maintenance of chloroplasts, which were observed in the Celtic Sea specimens. Chloroplasts are derived from ingested phytoplankton. Leutnegger (1984) proposed that foraminifera which maintain chloroplasts have evolved thin walls to permit light penetration for photosynthesis, suggesting that this is generally the function of symbionts in foraminifera. However, *S. fusiformis* often lives well below the depths to which light can penetrate (cf. Leutnegger, 1984) and which is also commonly infaunal. Similarly, Cedhagen (1991) reports chloroplasts in *Nonionella labradoricum* individuals living deep in the Norwegian Trench; though McFarland and Loew (1983) have shown that waves can focus flashes of high intensity light to great depths, Cedhagen (1991) suggests that the chloroplasts are probably heterotrophic and receive nutrients from their host and in return produce vitamins and lipids. Bernhard and Alve (1996) suggest that the chloroplasts may be a source of food enabling *S. fusiformis* to survive anoxia.

Alve (1994) found monospecific assemblages of *S. fusiformis* in Frierfjord, Norway, in samples from stratified highly organic waters polluted with paper mill waste. Like many of the Celtic Sea specimens, these were coated with a veneer of transparent mud-sized particles. Alve (1994) suggests that these may act as a barrier against harmful

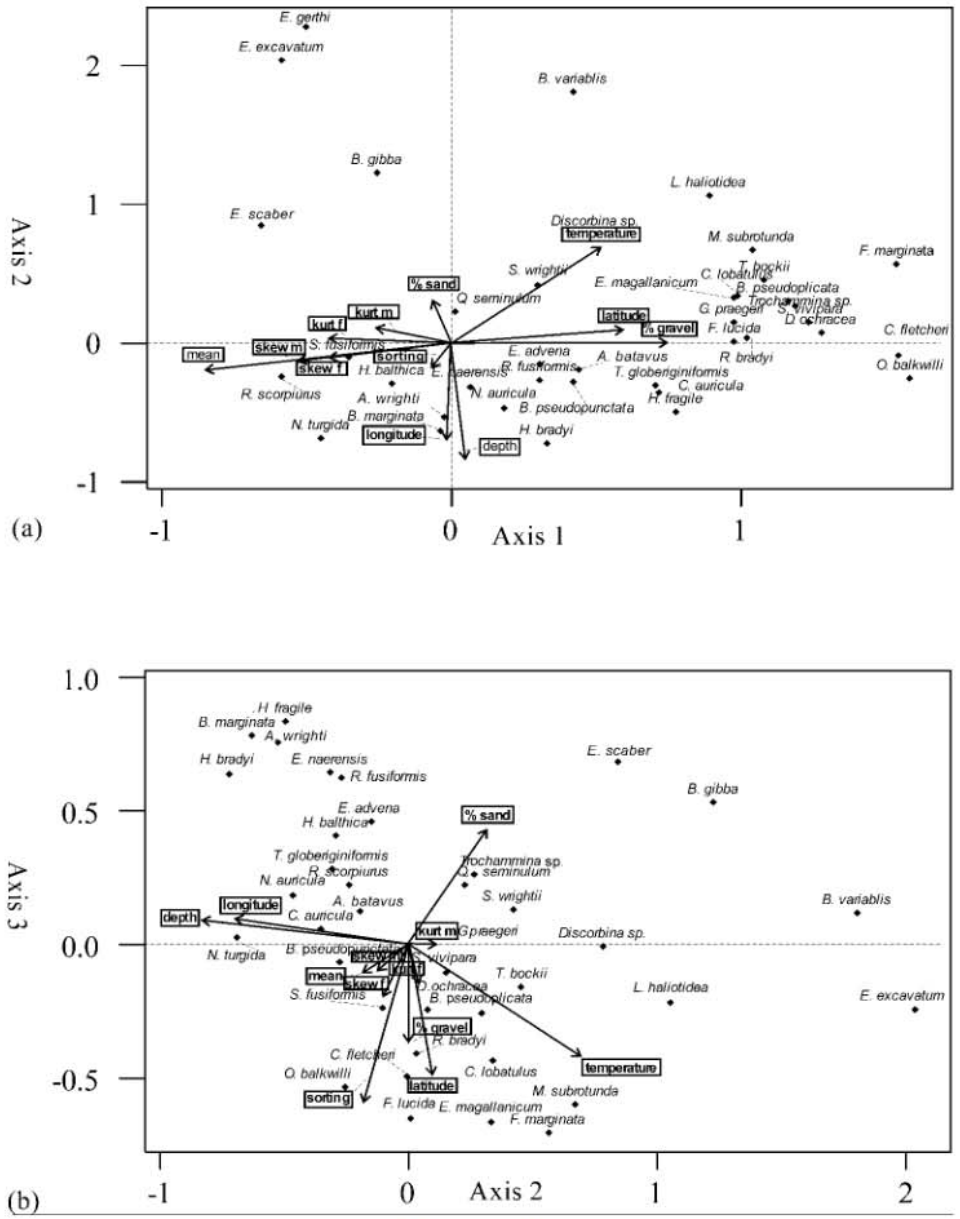

FIGURE 9. Species and environmental variable plot of the CCA on the live data (a) axes 1 and 2, (b) axes 2 and 3.

chemical compounds which are abundant in anoxic habitats, but they could alternatively be normal feeding 'cysts'. The species was also found living in Drammensfjord (Alve, 1990), having recolonized anoxic sediments, further confirming *S. fusiformis* as an opportunistic element.

An explanation for the distribution of *S. fusiformis* based on the theory of frontal circulation cells is probable since the areas in which this assemblage dominates are also those which receive advected phytodetritus from the surface front. The mixed-frontal zone receives organic matter directly

TABLE 4. Summary of the CCA performed on the dead data.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.26	0.18	0.16	0.04	1.54
Species-environment correlations	0.84	0.86	0.82	0.59	
Cumulative percentage variance of species data	16.7	28.4	38.4	41.4	
Cumulative percentage variance of species-environment relation	34.1	58	78.6	84.7	
Sum of all unconstrained eigenvalues (DCA)					1.54
Sum of all canonical eigenvalues (CCA)					0.75

TABLE 5. Results of the partial CCA performed on the dead data.

Environmental variable	Sum of Eigenvalues of partial CCA	% of the total explained variance exclusively explained by the environmental variable
depth	0.03	4.77
temperature	0.02	2.65
% gravel	0.01	2.39
% sand	0.01	2.52
mean	0.02	3.32
sorting	0.01	1.86
skew m	0.03	5.04
skew f	0.02	2.92
kurt m	0.02	3.58
kurt f	0.02	3.58
latitude	0.07	10.08
longitude	0.04	5.57
Sum of CCA eigenvalues	0.75	
Covariance		51.72

from the zone of convergence at the surface; the frontal-mixed zone also receives matter sourced from the convergence but which has become entrained in flows and delivered to the stratified side of the front. The same circulation theory proposes that the intermediate area is one of divergence, swept free of detritus. This is reflected in the faunal data which show a pronounced shadow in this area, not only for the *S. fusiformis* assemblage, but also in the density of the live foraminifera (Fig. 5a).

S. fusiformis is clearly an opportunistic species whose distribution is linked to the high flux of organic matter and low oxygen concentrations found in the frontal region. Though the preservation potential of the species is quite low, it is so abundant that it still leaves a sedimentary record. Alve (1994) has previously suggested the use of this species as a bloom indicator and, in the Celtic Sea, *S. fusiformis,* above all other species, indicates the position of the seasonal stratification front.

Factor analysis also defines a distinctive assemblage dominated by *B. gibba, E. excavatum* and *E. scaber* for the eastern part of the area and the Bristol Channel. The CCA indicates that this distribution is related to % sand content. *Q. seminulum,* often associated with sandier substrates, is also an important component of this assemblage.

CONCLUSIONS

Many of the faunal variations found in this study are clearly linked to the effects of tidal stratification. Four distinct assemblages have been identified by factor analysis of the live data: stratified, mixed, frontal and eastern. Of these, only the frontal assemblage was not identified by factor analysis of the dead data.

1) *Frontal assemblage:* this assemblage comprises the most abundant live species in the area, *S. fusiformis,* which is an opportunistic, facultative anaerobe, well-suited to the bloom-like conditions which exist in the frontal region. The majority of the *S. fusiformis* tests are subject to *post-mortem* destruction or transport, but nevertheless this species remains a significant part of the dead and, thus, fossil record.

2) *Mixed assemblage:* this assemblage is characterized by species which prefer coarser sediments such as *C. lobatulus, T. bockii, S. wrightii, A. batavus* and *Q. seminulum.* These species are not directly associated with mixed waters but high-energy conditions associated with tidal mixing. Most are epifaunal and this, combined with an association with strong currents, suggests that reworking may be significant. The dead assemblage constitutes robust, easily reworked, larger foraminiferal tests which is, in itself, indicative of the high peak bed stress vectors characteristic of the mixed zone.

3) *Stratified assemblage:* this assemblage includes *B. marginata, H. balthica, A. wrighti,* and *N. turgida.* Of these, *B. marginata* and *H. balthica* are over-represented in the dead assemblage, and *A. wrighti* and *N. turgida* under-represented, and this must have a bearing on their appearance in the fossil record. All species except *N. turgida* are known to tolerate low-oxygen conditions, though this species has been reported from sediments with high organic carbon content (Conradsen, 1993).

4) *Eastern assemblage:* this assemblage is dominated by *B. gibba, E. excavatum* and *E. scaber,* species which show an affinity for sandy substrates. However, they all show wide tolerance of a range of other environmental stresses, suggesting an opportunistic group able to colonize low competition niches.

These data confirm the inferences of Austin and Scourse (1997), and therefore gives independent support to their interpretation that the stable isotopic data also reflect this transition.

The study also identifies some interesting foraminiferal evidence for the mechanisms which deliver nutrients to frontal regions. The predicted cross-frontal transfer of nutrients is supported by the occurrence of stratified-type foraminifera in both the living and dead assemblages underlying the region of the pervasive eddy. The existence of surface converging circulation cells is also apparently recorded. The lowermost cell (Fig. 1) causes a divergence separating areas on the bed to which detritus is delivered, either by direct rain on the mixed side of this zone, or by entrainment into the circulation cells and the delivery to the stratified side. The scenario is captured by the distribution of the foraminiferal populations which are very abundant in the two receptive areas and sparse in between.

The *N. turgida* and *S. fusiformis* distributions highlight the significance of rarer thin walled elements in the fossil record whose poor preservation potential is probably a product of *in situ post-mortem* destruction rather than transfer out of the basin of deposition.

Statistical analyses indicate that some unmeasured environmental variables are important in controlling the foraminiferal distributions. The relations between these distributions and the hydrographic data indicate, however, that these variables are linked to seasonal stratification. We speculate that these variables probably include food supply and bottom water and pore water oxygen concentrations (cf. Gooday, 1993), which likely vary from mixed to stratified waters. These remain hypotheses for future field testing.

ACKNOWLEDGMENTS

The authors thank the captain and crew of the RV *Prince Madog* for assistance both during and after the research

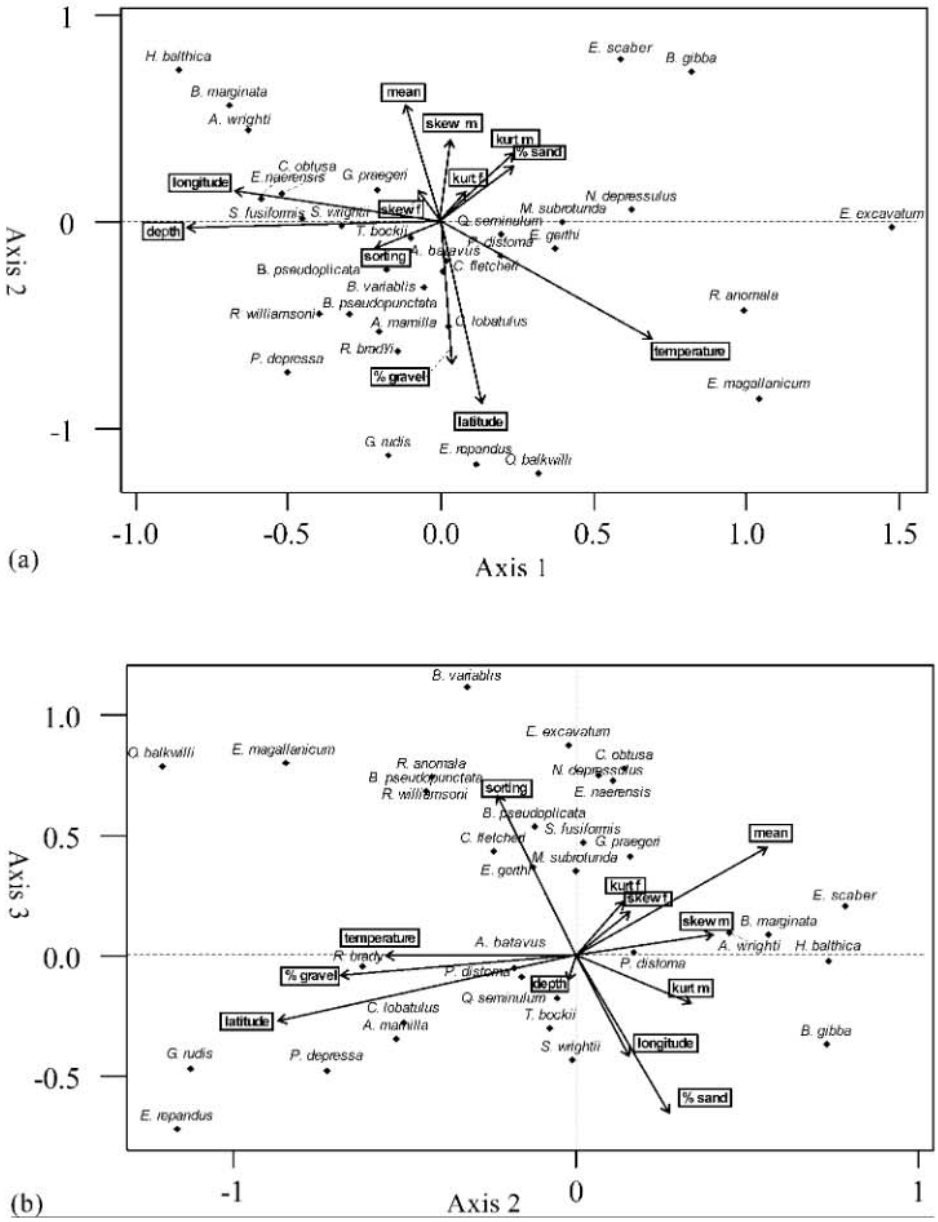

FIGURE 10. Species and environmental variable plot of the CCA on the dead data (a) axes 1 and 2, (b) axes 2 and 3.

cruises; Anne Hammerstein, Ian Pritchard, Emily Roberts, Iain McMyn, John McDonagh and Grant Fulton for their help at sea; Kevin Horsburgh for discussion of the dynamical aspects of stratification; Steve Juggins for help with the multivariate statistical work; and John Whittaker for taxonomic advice on the genus *Adercotryma*. John Murray provided useful critical comments on a draft of the manuscript. Karen Luise Knudsen is thanked for her advice on point counting statistics in foraminiferal analysis, and GAS wishes to thank her for her expertise in foraminiferal taxonomy. The careful and detailed comments of two anonymous referees were very helpful.

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Received 2 June 2000
Accepted 17 December 2000

APPENDIX I. Live foraminiferal percentage data for those species used in the statistical analyses and the density of foraminifera in each sample.

Live %	T1S01	T1S02	T1S03	T1S06	T1S07	T1S09	T1S14	T1S17	T1S19
Ammonia batavus	2	2	0	3	0	0	0	0	3
Adercotryma wrighti	0	0	2	0	5	0	0	15	18
Bulimina gibba	0	2	7	34	8	5	0	0	0
Bulimina marginata	0	1	0	0	0	1	2	0	7
Bolivina pseudoplicata	2	1	3	0	2	0	0	0	0
Bolivinellina pseudopunctata	1	2	2	0	0	0	0	0	0
Brizalina variabilis	0	0	0	0	0	0	0	0	0
Bolivina/Brizalina group	4	3	6	0	2	0	1	1	2
Cibicides fletcheri	2	0	1	0	0	0	0	0	0
Cibicides lobatus	12	10	4	18	0	0	0	0	0
Cancris auricula	5	6	4	0	17	1	0	5	6
Discorbinella sp.	0	0	0	0	0	0	0	0	0
Eggerella advena	0	0	0	0	2	0	0	0	2
Elphidium excavatum forma *selseyensis*	0	0	6	2	0	0	0	0	0
Elphidium gerthi	3	1	0	0	0	0	0	0	0
Elphidium magellanicum	0	0	0	0	0	0	0	0	0
Elphidium cf. *E. magellanicum*	13	4	0	0	0	0	0	0	0
Eggerelloides scaber	0	0	0	0	22	0	0	1	0
Epistominella vitrea	0	1	2	0	2	0	4	1	3
Fissurina lucida	0	2	0	0	0	0	0	0	0
Fissurina marginata	5	0	0	1	0	0	0	0	0
Gavelinopsis praegeri	6	3	2	1	2	0	0	0	8
Hyalina balthica	0	0	0	0	0	0	6	1	2
Haplophragmoides bradyi	0	0	0	0	0	0	0	4	0
Haplophragmoides fragile	0	0	0	0	0	0	0	0	0
Lamarckina haliotidea	0	0	0	0	0	0	0	0	0
Miliolinella subrotunda	4	2	0	2	0	0	0	0	0
Nonionella auricula	0	6	0	0	0	0	0	1	0
Nonionella turgida	0	2	0	0	2	1	3	27	5
Ophthalmidium balkwilli	0	3	0	0	0	0	0	0	0
Quinqueloculina seminulum	5	3	5	6	6	0	0	0	0
Rosalina bradyii	2	1	0	2	0	0	0	0	0
Reophax fusiformis	0	0	0	0	2	2	0	0	0
Reophax scorpiurus	0	0	1	0	8	7	0	2	5
Reophax group	0	0	2	1	9	10	0	2	5
Stainforthia fusiformis	8	29	32	0	9	11	81	34	15
Spirillina vivipara	0	0	0	0	0	0	0	0	0
Spiroplectammina wrightii	0	0	5	5	0	0	0	0	2
Textularia bocki	15	4	6	11	0	0	0	0	6
Textilina group	30	4	11	16	0	0	0	0	8
Globotrochamminopsis pygmaeus	1	1	3	0	3	0	0	3	7
Trochammina sp.	2	2	0	0	0	0	0	0	2
Deuterammina (*Lepidodeuterammina*) *ochracea*	1	1	2	0	0	0	0	0	1
Density per 10 cm^3	62.06	96.41	18.71	144.44	8.84	29.53	56.87	62.03	16.25
Count total (n)	331	376	263	299	129	378	327	290	260

APPENDIX I. Extended.

T2S01	T2S03	T2S07	T2S11	T2S14	T2S16	T2S19	T2S20	T2S21	T2S22	T2S23	T3S01	T3S05	T3S03	T3S07	T3S10
1	3	0	0	0	4	1	3	3	3	0	2	3	0	1	0
3	26	1	6	2	11	0	2	0	0	0	0	0	1	4	1
2	0	0	0	0	2	2	0	1	0	0	0	0	3	1	0
6	8	7	0	5	2	0	0	0	0	0	0	1	0	6	1
0	0	0	0	0	0	0	2	1	0	1	3	0	1	0	0
0	3	1	2	0	0	0	2	6	0	0	0	3	1	1	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	3	1	2	0	1	0	3	8	2	2	3	4	1	2	0
0	0	0	0	0	0	0	2	2	2	0	5	3	0	0	0
1	0	0	0	2	4	3	4	3	5	16	9	6	2	0	1
4	6	4	3	2	5	41	10	26	19	0	20	34	35	1	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	2	5	0	0	0	0	0	0	0	1	0	1
0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	4	0	2	1	0	0	2	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
0	5	0	2	0	0	0	0	0	0	0	0	0	0	1	1
21	2	0	0	2	5	0	0	1	1	0	0	0	1	5	1
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0
13	0	0	0	2	7	2	11	2	14	15	7	3	4	0	0
2	3	2	0	0	0	0	0	0	0	0	0	0	0	2	0
0	0	0	0	5	0	0	0	0	0	0	0	1	0	5	0
6	16	0	0	5	4	0	5	0	2	3	1	1	1	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
0	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0
5	8	24	19	2	4	1	0	0	2	0	0	1	12	7	1
0	0	0	0	0	1	0	5	1	0	2	3	0	2	0	0
10	3	0	0	9	9	0	3	2	1	2	2	1	1	2	1
0	0	4	0	0	0	1	2	4	0	0	4	3	2	0	0
1	1	0	2	23	2	1	0	0	0	0	0	2	2	0	0
0	2	0	3	0	4	0	0	0	0	0	0	2	1	1	1
1	3	0	5	23	7	1	0	0	0	0	0	4	3	1	1
3	4	53	56	14	5	37	2	6	17	0	1	8	16	60	90
2	0	0	0	0	0	0	5	4	2	4	1	3	1	0	0
1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
8	0	0	0	2	5	1	7	5	3	23	12	0	4	0	0
9	0	0	0	2	5	1	7	6	3	23	12	1	4	0	0
0	0	0	3	9	4	0	8	2	1	4	4	6	1	0	0
0	0	0	0	9	1	0	0	0	1	1	3	0	0	0	0
1	0	0	0	0	2	1	6	5	4	5	0	5	2	0	0
41.87	45.78	63.18	40.00	4.00	92.22	33.50	75.42	11.18	12.15	60.66	15.47	34.14	30.51	200.32	75.07
314	293	338	320	44	166	273	331	170	215	337	232	239	302	621	379

APPENDIX I. Continued.

Live %	T3S11	T3S13	T3S15	T3S16	T3S17	T3S19	T3S23	T6S02	T6S06	T6S08	T6S10
A. batavus	0	3	4	0	0	4	3	2	0	0	0
A. wrighti	0	0	9	4	5	12	11	0	2	0	0
B. gibba	3	0	2	0	0	0	0	11	2	2	13
B. marginata	0	0	7	1	2	8	6	0	0	0	0
B. pseudoplicata	0	0	0	0	0	0	0	0	0	0	0
B. pseudopunctata	1	1	0	0	0	0	0	0	0	0	0
B. variabilis	0	0	0	0	0	0	0	0	2	0	0
Bolivina group	1	1	0	0	0	2	2	0	2	1	0
C. fletcheri	0	0	0	0	0	0	0	0	0	0	0
C. lobatulus	0	0	1	0	0	1	0	3	2	2	0
C. auricula	2	5	6	5	2	5	10	0	0	0	0
Discorbinella sp.	0	0	0	0	0	0	0	0	0	4	0
E. advena	1	2	0	0	0	0	4	0	0	2	0
E. excavatum forma *selseyensis*	0	0	0	0	0	0	0	0	0	0	0
E. gerthi	0	0	0	0	0	0	0	0	2	1	0
E. magellanicum	0	0	0	0	0	0	0	8	0	0	0
E. cf. *E. magellanicum*	0	0	0	0	0	0	0	0	19	0	0
E. scaber	0	0	4	0	0	1	0	0	0	0	0
E. vitrea	0	5	0	0	0	0	2	0	0	3	0
F. lucida	0	0	0	0	0	0	0	0	0	0	0
F. marginata	0	0	0	0	0	0	0	0	0	0	0
G. praegeri	0	0	4	0	0	0	3	2	15	4	3
H. balthica	0	0	0	0	0	1	1	0	0	0	8
H. bradyi	0	0	1	0	0	1	2	0	0	0	0
H. fragile	0	0	0	0	0	0	2	0	0	0	0
L. haliotidea	0	0	0	0	0	0	0	0	8	0	0
M. subrotunda	0	0	0	0	0	0	0	0	0	0	0
N. auricula	0	0	0	2	5	8	4	0	0	1	0
N. turgida	4	6	14	8	2	5	13	0	0	0	0
O. balkwilli	0	0	0	0	0	0	0	0	0	0	0
Q. seminulum	0	0	0	0	0	0	0	0	2	0	0
R. bradyi	0	0	0	0	0	0	0	6	0	0	0
R. fusiformis	0	0	2	0	0	2	0	0	0	0	0
R. scorpiurus	4	0	20	0	2	0	0	0	0	0	0
R. group	4	0	21	2	2	2	0	0	0	0	0
S. fusiformis	78	64	15	71	73	44	25	63	10	65	67
S. vivipara	0	0	0	0	0	0	0	0	2	0	0
S. wrightii	0	0	0	0	0	0	0	0	2	0	0
T. bockii	0	0	0	0	0	0	0	3	19	2	0
Textilina group	0	0	2	0	0	0	0	3	21	3	0
G. pygmaeus	0	1	2	0	1	0	0	0	0	0	0
Trochammina sp.	0	0	0	0	0	0	0	0	0	0	0
D. ochracea	0	0	0	0	0	0	0	0	6	1	0
Density per 10 cm^3	29.34	11.50	31.03	81.41	76.94	67.64	57.00	8.27	3.84	30.89	33.92
Count total (n)	313	176	256	346	327	372	342	62	48	278	424

APPENDIX I.. Continued, Extended.

T6S12	T6S14	T6S16	T7S02	T7S06	T7S10	T7S16	T8S01	T8S02	T8S05	T8S08	T8S09	T8S10	T8S13	T8S16	T8S20
0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
2	4	0	0	3	3	1	0	0	0	0	0	0	0	0	0
2	0	0	0	1	0	0	0	0	3	35	17	57	43	19	20
0	2	0	0	0	0	2	2	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	7
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
3	3	2	0	0	5	0	0	3	4	0	7	2	2	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0	6	0	4	13	48	14
0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	2	0	0	0	3	0	0	1	3	12	7	0	11	7	4
3	0	2	0	8	1	0	0	0	1	0	0	0	0	0	0
0	0	0	5	0	0	0	0	0	0	0	2	0	0	0	0
0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	3	3	0	0	0	0	0	0	0	0	0	0	4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
11	10	9	0	5	8	5	31	11	9	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	5	0	0	1	0	0	33	0	5	2	4	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	2	0	0	0	0	0	0	0	3	0	0	0	0	0	2
6	6	6	0	2	7	0	0	1	7	0	0	0	0	0	0
6	8	6	0	2	8	0	0	1	10	0	0	0	0	0	2
62	67	70	70	61	67	88	59	79	32	47	57	34	24	23	18
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	5
0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	5
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
17.67	15.09	37.22	6.73	205.50	31.65	23.47	29.33	8.97	21.47	1.33	3.82	10.42	22.70	51.15	10.00
212	264	335	37	410	269	264	308	175	153	17	42	125	227	211	130

APPENDIX II. Dead foraminiferal percentage data for those species used in the statistical analyses and the density of foraminifera in each sample.

Dead %	T1S01	T1S02	T1S03	T1S06	T1S07	T1S09	T1S14	T1S17	T1S19	T2S01	T2S03
Ammonia batavus	3	4	4	3	3	3	0	4	7	4	3
Adercotryma wrighti	0	0	0	0	0	0	0	0	0	0	0
Asterigerinata mamilla	0	0	0	0	0	1	0	0	0	0	0
Bulimina gibba	8	4	5	34	38	27	2	0	0	0	0
Bulimina marginata	4	0	0	0	1	0	3	24	17	11	39
Bolivina pseudoplicata	3	1	1	0	0	2	8	4	2	0	4
Bolivinellina pseudopunctata	1	1	1	0	0	0	4	0	0	1	0
Brizalina variabilis	2	0	0	0	0	0	0	2	0	0	0
Bolivina/Brizalina group	7	3	3	0	0	4	17	8	3	2	6
Cibicides lobatulus	14	19	20	18	18	11	7	3	6	2	2
Cibicides fletcheri	3	0	0	0	2	0	2	0		0	2
Cassidulina obtusa	0	0	0	0	0	0	6	4	2	0	4
Elphidium excavatum forma *selseyensis*	5	3	7	2	2	5	0	0	0	0	0
Elphidium gerthi	2	2	2	0	2	6	3	0		0	0
Elphidium magellanicum	7	1	0	0	0	0	0	0	0	0	0
Elphidium cf. *E. magellanicum*	2	2	0	0	0	0	0	0	0	0	0
Eponides repandus	0	0	0	0	0	0	0	0	0	0	0
Eggerelloides scaber	0	0	0	0	0	0	1	2	0	2	2
Epistominella vitrea	1	0	0	0	0	0	8	6	2	0	1
Gavelinopsis praegeri	4	0	1	1	1	6	9	4	2	2	4
Gaudyrina rudis	0	1	1	0	0	0	0	0	0	0	0
Hyalina balthica	0	0	0	0	0	0	1	10	6	13	9
Miliolinella subrotunda	0	0	0	2	2	3	0	0	0	0	0
Nonion depressulus	0	0	0	0	0	0	0	0	0	0	0
Nonion turgida	0	0	0	0	0	0	2	2	0	0	1
Ophthalmidium balkwilli	0	0	0	0	0	0	0	0	0	0	0
Pyrgo depressa	0	0	0	1	0	0	0	0	0	0	0
Planorbulina distoma	1	2	0	6	2	0	0	0	0	0	0
Quinqueloculina seminulum	4	15	16	6	5	5	5	8	6	5	3
Rosalina bradyi	1	4	5	2	0	0	2	0	1	0	0
Rosalina anomala	2	0	0	0	0	0	0	0	0	0	0
Rosalina williamsoni	0	0	0	0	0	1	3	1	0	0	0
Stainforthia fusiformis	5	8	2	0	0	4	6	6	2	2	3
Spiroplectammina wrightii	2	4	6	5	3	2	0	1	19	18	1
Textularia bockii	6	13	20	11	12	8	5	3	15	28	8
Textilina group	8	17	25	16	15	10	5	4	34	46	9
Density per 10 cm^3	2760.00	1635.16	876.86	5200.00	8112.33	11025.00	17780.87	11242.78	3408.75	993.00	4851.56

APPENDIX II. Extended.

T2S07	T2S11	T2S14	T2S16	T2S19	T2S20	T2S21	T2S22	T2S23	T3S01	T3S03	T3S05	T3S07	T3S10	T3S11
3	5	3	3	8	8	3	3	7	9	7	5	0	2	2
1	4	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	0	1	3	0	0	0	0	0	2	0	0	3	2
0	4	3	0	1	0	2	0	0	1	0	0	0	4	5
28	18	0	0	0	0	0	0	0	0	0	0	58	2	0
3	0	0	0	0	1	4	2	3	3	2	3	3	3	3
2	0	0	0	0	0	3	2	0	0	0	0	0	1	0
2	0	0	0	0	0	0	4	0	0	0	0	0	0	0
8	0	1	1	0	2	8	8	3	5	3	4	5	4	4
4	12	27	35	32	26	14	14	26	24	27	32	2	28	24
1	0	0	0	4	2	2	8	0	4	9	3	1	0	2
6	0	0	0	0	0	0	1	0	0	2	0	2	0	5
0	2	0	0	0	0	3	1	0	0	0	1	0	0	0
0	1	0	0	2	0	2	1	2	1	1	0	0	0	2
0	0	0	0	0	0	3	2	0	1	0	0	0	0	0
0	0	0	0	2	0	0	3	0	4	2	2	0	0	0
0	0	0	0	0	1	0	0	5	0	0	0	0	0	0
1	2	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	3	1	0	1	2	0	3	3	5
7	3	0	2	2	2	5	5	2	1	4	4	4	2	4
0	0	0	0	2	2	0	0	2	0	0	0	0	0	0
5	1	0	0	0	0	0	0	0	0	0	0	4	0	0
0	2	0	0	0	0	0	0	0	0	0	1	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	2	5	0	0	0	0	0	0	0
0	1	0	4	2	0	0	0	1	0	0	1	0	0	0
0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
5	13	10	6	5	8	7	5	15	9	9	7	3	8	8
1	1	2	3	4	4	6	1	2	3	2	3	0	0	2
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	2	0	0	5	0	0	1	0	2	0	0
7	5	1	2	0	0	10	6	2	1	0	5	5	20	20
1	4	13	14	4	5	1	4	4	3	8	5	0	5	2
2	6	29	17	13	26	6	7	11	16	8	17	2	6	3
3	11	42	30	18	31	7	10	15	19	17	22	2	12	5
36874.77	9000.00	695.45	1205.56	2650.31	652.62	698.68	1725.91	213.43	340.00	1548.00	954.55	5961.29	71.15	2025.00

APPENDIX II. Continued.

Dead %	T3S13	T3S15	T3S16	T3S17	T3S19	T3S23	T6S02	T6S06	T6S08	T6S10	T6S12	T6S14
A. batavus	2	4	3	1	2	3	0	5	3	2	1	1
A. wrighti	0	0	0	0	1	0	0	0	0	0	0	0
A. mamilla	0	0	0	0	0	0	0	0	1	1	0	0
B. gibba	8	2	2	1	4	2	6	3	9	16	19	2
B. marginata	5	27	14	24	19	15	0	0	0	2	5	24
B. pseudoplicata	0	0	2	5	0	0	2	0	0	0	2	2
B. pseudopunctata	0	0	0	0	0	0	2	0	0	0	0	0
B. variabilis	0	0	0	0	0	0	0	0	0	0	0	0
Bolivina/Brizalina group	0	1	3	5	0	1	4	0	0	0	2	3
C. lobatulus	26	9	6	5	3	6	34	26	37	35	11	7
C. fletcheri	1	0	2	0	0	0	0	0	0	0	3	0
C. obtusa	3	2	2	2	0	0	0	0	0	0	2	1
E. excavatum forma *selseyensis*	2	0	0	1	0	0	2	0	0	0	0	0
E. gerthi	0	1	1	0	0	0	0	0	0	0	1	0
E. magellanicum	0	0	0	0	0	0	2	0	0	0	0	0
E. cf. *E. magellanicum*	0	0	0	0	0	0	2	0	0	0	0	0
E. repandus	0	0	0	0	0	0	0	0	0	0	0	0
E. scaber	0	0	0	0	0	2	0	0	1	2	0	0
E. vitrea	2	0	4	5	0	1	1	0	0	0	2	3
G. praegeri	2	9	7	10	4	3	1	0	2	0	9	9
G. rudis	0	0	0	0	0	0	0	0	0	0	0	0
H. balthica	0	0	0	0	11	9	0	0	0	0	0	2
M. subrotunda	0	0	0	0	0	0	3	0	0	0	0	0
N. depressulus	0	0	0	0	0	0	0	0	0	0	0	0
N. turgida	0	1	1	1	1	1	0	0	0	0	0	2
O. balkwilli	0	0	0	0	0	0	0	0	0	0	0	0
P. depressa	0	0	0	0	0	0	0	0	0	0	0	0
P. distoma	3	3	0	6	0	0	0	0	1	0	0	0
Q. seminulum	7	6	3	3	6	2	0	15	8	18	4	0
R. bradyi	1	0	0	0	0	0	1	1	0	0	0	0
R. anomala	0	0	0	0	0	0	6	0	0	0	0	0
R. williamsoni	0	0	1	0	0	0	0	0	0	0	0	0
S. fusiformis	11	6	29	15	6	4	2	1	1	0	10	14
S. wrightii	2	5	2	0	20	23	4	13	12	6	3	4
T. bockii	13	11	10	11	14	17	13	22	15	10	17	13
Textilina group	16	16	12	11	34	40	17	35	27	17	20	17
Density per 10 cm^3	5070.59	4311.27	8460.00	8131.76	2209.09	3090.00	267.00	52.95	357.86	910.08	2340.00	4032.00

APPENDIX II. Continued, Extended.

T6S16	T7S02	T7S06	T7S10	T7S16	T8S01	T8S02	T8S05	T8S08	T8S09	T8S10	T8S13	T8S16	T8S20	T8S21
1	4	7	3	2	0	1	2	3	5	3	4	4	5	4
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	1	3	0	0	0	0	0	0	0	0	0	0	0	0
2	3	2	4	0	1	2	26	60	42	42	28	8	12	5
24	0	0	9	47	4	5	0	0	0	0	0	0	0	0
2		0	0	0	1	5	3	0	0	0	0	3	2	0
0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
0	0	0	0	0	7	0	0	0	0	0	0	0	1	2
3	0	0	2	2	13	9	5	0	0	0	0	4	4	2
7	24	22	24	0	2	2	6	2	6	5	4	8	12	7
0	2	0	1	0	6	4	3	2	2	2	0	2	2	4
1	1	0	0	1	5	7	0	0	0	0	0	1	0	0
0	3	1	1	0	0	2	0	9	3	5	14	23	15	4
0	0	0	3	0	2	2	4	1	1	0	2	2	3	4
0	0	0	0	0	1	0	1	0	0	0	1	3	0	4
0	2	0	0	0	0	0	0	0	0	0	0	5	3	0
0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	2	0	2	0	0	3	4	12	4	2	1
3	0	0	1	1	5	4	0	0	0	0	0	0	0	0
9	5	3	5	0	9	7	8	2	0	0	2	5	4	3
0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	15	0	5	0	0	0	0	0	0	0	0
0	0	1	2	0	2	2	2	0	1	0	0	0	2	3
0	0	1	1	0	1	0	3	0	0	0	0	1	2	2
2	0	0	0	0	1	1	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	1	3	0	1	0	0	0	0	0
0	16	7	10	11	2	5	6	7	23	17	12	7	8	4
0	6	3	2	0	1	0	2	0	0	0	0	0	1	0
0	0	0	0	0	3	0	1	0	0	0	0	1	4	2
0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
14	0	0	4	0	14	13	3	0	0	0	0	2	0	2
4	3	14	3	1	0	0	3	0	1	0	0	2	1	0
13	9	19	9	3	3	1	4	4	9	12	13	4	3	4
17	12	32	12	5	3	2	7	5	10	13	14	6	4	4
5253.33	447.27	3810.00	4142.12	5578.67	33660.00	26067.69	8905.26	3881.25	4352.73	866.25	913.50	3272.73	451.38	7560.00

APPENDIX III. ENVIRONMENTAL AND TAXONOMIC NOTES ON INDIVIDUAL SPECIES

Ammonia batavus (Fig. 6a,b) constitutes a similar proportion of both live and dead assemblages, though the distributions are quite different. The largest live contribution of this species is found in the central part of the area and to the north. It is particularly concentrated in the stratified area to the southwest, but is completely absent from parts of the west and transect 8. Dead *A. batavus* is most abundant in the north and along transect 8. Correlation of the dead distribution with grain size and skewness, combined with the robust nature of the test, suggests that reworking is probable. Both live and dead individuals of *A. batavus* inhabit northerly sites and high % gravel according to the CCA. The live distribution is also related to temperature and the dead to mean grain size and skewness. *A. batavus* can tolerate great variability in temperature, salinity, and oxygen (Lutze, 1965; Risdal, 1964), which helps explain the live distribution.

Adercotryma wrighti was first identified in this study as *A. glomeratum,* but following the recent re-evaluation of Celtic Sea samples by Murray (2000), re-identified as *A. wrighti*; Brönnimann and Whittaker (1987) have distinguished between *A. glomeratum* (four chambers in the final whorl, three visible on each side), and *A. wrighti* (three chambers in the final whorl, three seen on the apertural and two on the antapertural side). It is probable that, in temperate waters, *A. wrighti* has been misidentified as *A. glomeratum. A. glomeratum* is often considered an Arctic indicator, and its distribution was interpreted by Williamson and others (1984) to correlate with lower temperatures. However, the recent consensus is that neither temperature nor substrate are the main controls (Alve and Nagy, 1986; Christiansen, 1958; Leslie, 1965; Schafer and Cole, 1974; Thiede and others, 1981), and it is probable that these subsequent studies relate to *A. wrighti* rather than to *A. glomeratum.*

A. wrighti (Fig. 6c,d) is distributed similarly in both live and dead assemblages but there is a large difference in the relative contribution made to each. Live *A. wrighti* can constitute as much as 10% of the total live assemblage, but dead it rarely exceeds 1%. There is a strong association between live occurrences of this species and stratified and frontal waters. CCA shows that the live and dead distributions of *A. wrighti* are related to cold water temperatures; live occurrences also associate with longitude, while the dead correlate with skewness. The increase in dead abundance along a skewness gradient indicates either reworking or long-term accumulation of tests pointing to an association with these conditions. A number of studies indicate that this species not only prefers high carbon flux, but can also tolerate the low oxygen levels often associated with such conditions (Alve and Nagy, 1986; Gooday, 1993; Austin and Sejrup, 1994). This is confirmed by Bernhard and Alve (1996), who concluded from nitrogen incubation experiments that the species is a facultative anaerobe, able to survive phases of anoxia, possibly by becoming dormant. These data suggest that the species is an opportunistic species; its small size is certainly appropriate to such a life strategy.

Live and dead distributions of ***Bulimina gibba*** (Fig. 6e,f) are similar. It is most abundant to the south and west but, most significantly, along transect 8 where it constitutes about a fifth of the live and dead assemblages. CCA shows a relationship between this species and coarser substrates with high % sand content. Though *Bulimina* spp. are widely regarded as low-oxygen tolerant (Sen Gupta and Machain-Castillo, 1993), *B. gibba* is not abundant in those parts of the Celtic Sea assumed to be oxygen deficient (*i.e.,* under stratified waters). It is rare or absent from the Celtic Deep basin. However, *B. gibba* appears to replace *B. marginata* in stratified samples in the west and east where the substrate is relatively coarse. This suggests that while *B. gibba* may be tolerant of low levels of oxygen depletion, its lower threshold levels are higher than for *B. marginata,* and so it is restricted to sandier substrates where infaunal oxygen levels are higher.

Live and dead specimens of ***Bulimina marginata*** also show similar distribution patterns, though this species constitutes a far greater proportion of the dead assemblage than the live (Fig. 6g,h). Both distributions reflect the area of stratified and frontal waters, except along the entrance to the Bristol Channel, where this species is rare or absent. In fully stratified waters, *B. marginata* is usually dominant in the dead assemblage. Interestingly, the position of the pervasive intrusion of stratified waters into the northern Celtic Deep trough is reflected in the distribution of this species. A relationship between *B. marginata* and depth is identified in both live and dead distributions by CCA. The live also show a relationship with temperature, hence stratification, and longitude. The dead are enriched in sites skewed towards fines, possibly the result of reworking. Though a large number of studies demonstrate that *B. marginata* prefers high organic fluxes and is able to tolerate low oxygen levels (Bandy and others, 1965; Risdal, 1963; Sen-Gupta and Machain-Castillo, 1993), in their experiments to test the response of various species to anoxia events through nitrogen incubation, Bernhard and Alve (1996) found that *B. marginata* had a poor survival rate. Other studies have drawn attention to the affinity of *B. marginata* for specific substrates (cf. Conradsen, 1993; Conradsen and others, 1994; Murray, 1986). This relationship probably derives from the fact that as organic content increases, grain size often becomes finer (Cato, 1977). Further evidence that *B. marginata* is associated with high levels of organic carbon is provided by Conradsen (1993), Conradsen and others (1994), and Qvale and van Weering (1985). *B. marginata* has also been reported from the stratified waters of the northern North Sea (Klitgaard-Kristensen and Sejrup, 1996).

Cibicides lobatulus never constitutes more than around 10% of the live assemblage but accounts for up to 20% of the dead at some sites (Fig. 6i,j). The distribution of live and dead *C. lobatulus* is the inverse of *B. marginata,* being highest in mixed and frontal waters. High values shift westward for the dead relative to the live, while dead values do not increase to the south as they do for the live. The contribution of *C. lobatulus* is least for sites along transect 8 and in the southern half of the area. CCA shows that both live and dead *C. lobatulus* are most abundant in the north, in warmer waters, and, for the dead only, in areas of high % gravel. As stratification is directly related to temperature, and the more northerly sites in this study are those which are mixed, this confirms *C. lobatulus* as a mixed assemblage indicator. This conclusion is supported by the almost complete consensus in the literature on the ecological preference of this largely epilithic species for fully oxygenated, high energy conditions and coarse-grained sediments (Murray, 1971; Conradsen, 1993; Hald and Steinsund, 1992; Klitgaard-Kristensen and Sejrup, 1996; Mackensen and others, 1985).

Eggerelloides scaber: CCA detected a strong relationship between this species and % sand. A relationship with mean grain size and skewness was also indicated for the dead assemblage, implicating reworking. Despite the grain size relationship, there is some evidence to suggest that substrate type is not the controlling variable. Murray (1986) reports it living in muddy sediments in Lyme Bay, and Alve and Nagy (1986) found it living in both coarse and fine-grained sediments in the Sandebukta branch of the Oslofjord. The latter authors found it tolerant of both high organic input and wood fibre pollution in Sandebukta, and suggest that its abundance might be related to low competition. Conradsen (1993) and Conradsen and others (1994) also find that it correlates positively with the organic content of sediments in the Kattegat and Skaggerak. In the Drammensfjord, Norway, it occurs in transitional waters between brackish and oxygen-depleted, suggesting that it is tolerant of moderately low oxygen concentrations. It is also found in the seasonally stratified waters of Breidangen, Oslofjord (Alve and Nagy, 1990) and close to a front in the Kattegat-Skaggerak (Conradsen and others, 1994). Lutze (1965) suggested that *E. scaber* is tolerant of temperature, salinity, and current variability, having found it living in the inflowing waters of the Danish Straits. De Stigter and others (1998) conclude that *E. scaber* is tolerant of low oxygen conditions but also suggest that it is a non-specific feeder. *E. scaber* probably has a poorer tolerance of low oxygen concentrations than some opportunists, but has compensated by developing an ability to withstand fluctuations in temperature, salinity, current velocity, and food supply explaining its abundance along the entrance of the Bristol Channel.

The live and dead distributions of ***Gavelinopsis praegeri*** are the inverse of each other (Fig. 6k,l). It is most abundant live in the mixed waters to the north and in the fully stratified waters away from the front, but dead it is most abundant in the transition between frontal and stratified waters and to the northeast. Live individuals are rare or absent along transect 8 but here dead specimens can contribute as much as 6% of some assemblages.

Live tests of ***Hyalinea balthica*** never account for more than 4.5% of the living assemblages but are well represented in the dead, where they can constitute as much as 17% of the total (Fig. 6m,n). Both distributions reflect the extent of stratified and mixed waters, except along the entrance to the Bristol Channel. CCA confirms that both live and dead distributions are related to temperature and hence stratification. The contours are much tighter for the dead, and abundance in-

creases evenly in a southwest direction, while the live are slightly more abundant in the west than in the frontal region. As with *B. marginata,* the distribution reflects the pervasive intrusion of stratified waters into the Celtic Deep trough. This feature is also reflected in the distribution of both living and dead *N. turgida* which, like *B. marginata* and *H. balthica,* also shows an affinity for stratified and frontal waters (Fig. 6o,p). Similarly, *N. turgida* is also rare or absent from the entrance to the Bristol Channel. Qvale and van Weering (1985) report an association between *H. balthica* and high sediment organic content, and Sen-Gupta and Machain-Castillo (1993) found the species abundant in oxygen minimum zones, both parameters associated with stratification. Though the abundance data on other bloom species, such as *S. fusiformis,* indicate that the flux of organic matter and oxygen concentrations are variable across the frontal region, this species shows a gradual and steady increase into stratified waters and records the area covered by the persistent eddy. So while it may tolerate low oxygen and prefer high organic flux, the precise environmental controls on this species are unclear, though the distributional data suggest factors linked to stratification.

Nonionella turgida: the strong similarity between the live and dead distributions of *N. turgida* suggest that this species is not easily reworked despite its poor representation in the dead (Fig. 6o,p). This may result from its infaunal occurrence in mainly muddy sediments (J.W.Murray, personal communication, 2000). The abundance of this species in the dead assemblage was too low to include in the CCA, but the same analysis of the live data places the optimum occurrence of this species in the relatively colder, deeper, stratified waters in the south characterized by fine-grained sediments. This is supported by Conradsen (1993), who found *N. turgida* living in association with *B. marginata* in fine-grained, high organic carbon sites. Though this suggests that this species may be tolerant of high carbon fluxes, Bandy and others (1965) reported that pollution from the Hyperion sewage outfall in California affected the *Nonionella* group unfavourably. Nevertheless, the distribution of *N. turgida* is strongly associated with stratification, demonstrating the potential significance of rarer species as paleostratification indicators.

Quinqueloculina seminulum makes important contributions to both live and dead assemblages in the Celtic Sea, but is more abundant in the dead. The highest live occurrences are in the east while the dead are concentrated in the frontal and mixed areas to the north and along the Bristol Channel entrance (Fig. 6q,r). The stratified intrusion is again highlighted by a positive anomaly in the live distribution. CCA relates maximal occurrences of dead *Q. seminulum* to shallower, warmer, sites, while the live are associated with high sand content in shallower sites. Despite the large dead/live distributional differences, the dead specimens show no relationship with sorting or skewness, suggesting that reworking is unlikely. Buzas (1993) describes *Q. seminulum* as an opportunist based on an *in situ* experiment in a shallow site in which *Q. seminulum* was the first species to recolonize following disturbance. Murray (1991) describes it as a phytodetrital feeder. It is therefore possible that this species, like *A. batavus,* can tolerate a wide range of conditions.

The distributions of ***Spiroplectammina wrightii*** and ***Textularia bockii*** are very similar (Fig. 6u–x), and it has been suggested that these species should be lumped together (Murray, 1979). Both contribute significantly to the dead assemblage but are less well represented in the live. This may be the result of the dense agglutinated tests obscuring the pink staining of live individuals. However, despite the low numbers of live specimens identified, the distribution seems comparable to the dead; the species is abundant in the north in mixed and frontal waters but also in the south in fully stratified waters well away from the frontal region. Numbers are low for the intermediate area and along the entrance to the Bristol Channel. CCA shows that both live *S. wrightii* and *T. bockii* inhabit warmer sites with coarser sediments. They are found dead in the shallower sites in well-sorted sediments. Some *post-mortem* transport is plausible given their epifaunal habitat (Murray, 1991). Murray (1986) observed *T. bockii* living in shelly sand, and Klitgaard-Kristensen and Sejrup (1996) found it living in coarse-grained sediments associated with strong currents in the northern North Sea. Conradsen (1993) defined an assemblage consisting of *T. bockii* with *C. lobatulus* and *G. praegeri,* which correlated with coarse grain sizes. It seems likely that these species distributions, when living, are related to coarser sediments as might be expected given their epiphytic/epilithic life-strategy (Murray, 1991; Vilks and Deonarine, 1987). However, other unknown variables must also be influential since they do not thrive in similar substrates along the entrance to the Bristol Channel.

APPENDIX IV. DETAILS OF FACTOR ANALYSIS RESULTS

Live Data

The first four live factors account for over 80% of the variance. The most important of these is defined by the *Textilina* group (0.98), *Reophax* group (−0.97), and *S. fusiformis* (−0.86). The latter two are negatively correlated to this factor, so that where the Q-mode scores are most negative these species are most significant. Live factor 1 is therefore most significant in the frontal-stratified zone, along much of transect 8, and in parts of the mixed area (Fig. 7a). This is the most significant of the live assemblages and accounts for 58% of the variance in the data.

The second live factor assemblage accounts for 11% of the variance and is defined by *G. praegeri* (0.74). *G. pygmaeus* (0.67), and *C. lobatulus* (0.62) are subdominant. These species are positively correlated to factor 2, so the most positive Q-mode scores indicate where this assemblage is most important. The area of dominance is located in the mixed and mixed/frontal zones (Fig. 7b), but also in the fully stratified waters to the south. This assemblage is not significant along transect 8. This factor has a negative correlation ($R^2 = 0.44$) with Φ indicating that this factor is associated with coarser sediments.

B. marginata (−0.71) is the defining species of live factor assemblage 3, with *A. wrighti* (−0.61) and *N. turgida* (−0.49) subdominant. These species are negatively correlated with factor 3, and are therefore dominant in the stratified and stratified-frontal waters in the center of the area, but absent along the entrance to the Bristol Channel (Fig. 7c). This assemblage accounts for just 7.7% of the variance, but correlates with several environmental variables, including bottom water temperature ($R^2 = 0.532$), salinity ($R^2 = 0.338$) and S-index ($R^2 = 0.676$). As the dominant species are negatively correlated to the Q-mode scores, these correlations indicate that this assemblage is most significant at southerly stratified sites characterized by relatively lower temperatures and higher salinities.

The fourth factor assemblage accounts for just 4.5% of the variance, but does not correlate with any of the environmental variables. The defining species, *E. scaber,* is negatively related to the factor (−0.39). This assemblage is most abundant along transect 8 and in the south of the area (Fig. 7d).

Dead Data

The defining species of the most significant of the dead assemblages, accounting for over 58% of the variance, is *Q. seminulum* (−1.66), with *Textilina* group (−1.27), *A. batavus* (−1.2) and *C. lobatulus* (−1.12) subdominant. These species are most important in the mixed and mixed-frontal region (Fig. 8a), but excluding the area of pervasive stratification in the northern Celtic Deep. There are no significant correlations between this factor and any of the measured environmental variables.

Dead factor assemblage 2, which accounts for 13% of the variance, is defined by *H. balthica* (0.63) with subdominant *B. marginata* (0.56), *G. praegeri* (0.53) and *Bolivina* group (0.54). This assemblage dominates in stratified waters, including the northern Celtic Deep (Fig. 8b), and correlates with a number of environmental variables, including temperature ($R^2 = 0.396$), % clay ($R^2 = 0.483$) and mean grain size ($R^2 = 0.331$). As this assemblage is positively related to the Q-mode factor scores, this indicates that it is most important in cooler sites characterised by fine sediments and high % silt content.

E. magellanicum (0.51) characterizes dead factor assemblage 3, along with *E. excavatum* forma *selseyensis* (0.25) and *Bolivina* group (0.27). This assemblage explains over 7% of the variance and, as it is positively correlated to the Q-mode scores, is prominent along most of transect 8 and in the mixed area to the north (Fig. 8c). There were no significant correlations between this assemblage and any of the measured environmental variables.

Dead factor assemblage 4 accounts for 5.8% of the variance and is characterized by *E. scaber* (0.49), with subdominant *B. gibba* (0.47) and *Q. seminulum* (0.44). This assemblage is positively related to the Q-mode scores and is most significant in the eastern part of the area (Fig. 8d).

APPENDIX V. Results of the CCA on the live foraminiferal and the environmental data.

Live CCA Scores	Axis 1	Axis 2	Axis 3	Axis 4
Ammonia batavus	0.44	−0.19	0.23	0.28
Adercotryma wrighti	−0.02	−0.53	0.76	0.3
Bulimina gibba	−0.26	1.23	0.53	−0.21
Bulimina marginata	−0.04	−0.63	0.78	0.24
Bolivina pseudoplicata	1.16	0.3	−0.25	0
Bolivinellina pseudopunctata	0.42	−0.27	−0.06	0.3
Brizalina variabilis	0.42	1.81	0.22	0.51
Cibicides fletcheri	1.61	0	−0.49	0.22
Cibicides lobatulus	0.99	0.34	−0.43	−0.11
Cancris auricula	0.72	−0.35	0.05	0.28
Discorbinella sp.	0.5	0.78	0	−1.09
Egerella advena	0.3	−0.25	0.46	−0.03
Elphidium excavatum forma *selseyensis*	−0.58	2.04	−0.24	1.49
Elphidium gerthi	−0.5	2.27	−1.43	1.24
Elphidium magellanicum	0.97	0.33	−0.66	−0.05
Elphidium cf. *E. magellanicum*	0.98	1.19	−0.54	−0.25
Eggerelloides scaber	−0.66	0.84	0.69	−0.25
Epistominella vitrea	0.06	−0.31	0.65	0.19
Fissurina lucida	0.98	0	−0.65	−0.97
Fissurina marginata	1.54	0.56	−0.7	−0.4
Hyalina balthica	−0.21	−0.29	0.41	0.28
Haplophragmoides bradyi	0.33	−0.72	0.64	0.18
Haplophragmoides fragile	0.77	−0.5	0.83	−0.17
Lamarkina haliotidea	0.89	1.06	−0.21	0.12
Miliolinella subrotunda	1.04	0.67	−0.6	0.14
Nonionella auricula	0.18	−0.47	0.19	0.67
Nonionella turgida	−0.45	−0.69	0.02	0.28
Ophthalmidium balkwilli	1.59	−0.26	−0.53	0.41
Quinqueloculina seminulum	0.01	0.23	0.23	−0.36
Rosalina bradyi	1.02	0.03	−0.41	−0.03
Rosalina fusiformis	0.31	−0.27	0.63	−0.55
Gavelinopsis praegeri	0.98	0.14	0	−0.09
Reaphax scorpiurus	−0.59	−0.24	0.23	−0.06
Stainforthia fusiformis	−0.35	−0.11	−0.24	−0.08
Spirillina vivipara	2.24	0.25	−0.1	0.17
Spiroplectammina wrightii	0.3	0.42	0.13	−0.47
Textularia bockii	1.08	0.46	−0.16	−0.19
Globotrochamminopsis pygmaeus	0.7	−0.31	0.28	−0.15
Deuterammina (*Lepidodeuterammina*) *ochracea*	1.28	0.07	−0.24	−0.01
Depth	0.04	−0.84	0.09	−0.22
Temperature	0.52	0.69	−0.41	−0.08
% gravel	0.75	0	−0.36	−0.06
% sand	−0.06	0.32	0.43	−0.29
Mean grain size	−0.85	−0.19	−0.1	−0.05
Sorting (moments)	−0.07	−0.18	−0.59	0.49
Skewness (moments)	−0.53	−0.13	−0.09	−0.05
Skewness (folks)	−0.42	−0.1	−0.2	0.05
Kurtosis (moments)	−0.26	0.12	0	−0.24
Kurtosis (folks)	−0.43	0.03	−0.15	0.06
Latitude	0.6	0.09	−0.49	−0.14
Longitude	−0.01	−0.7	0.1	−0.28

APPENDIX VI. Results of the CCA on the dead foraminiferal and the environmental data.

Dead CCA Scores	Axis 1	Axis 2	Axis 3	Axis 4
Ammonia batavus	0.01	−0.18	−0.05	−0.07
Adercotryma wrighti	−0.63	0.44	0.09	0.43
Asterigerinata mamilla	−0.2	−0.52	−0.34	0.24
Bulimina gibba	0.82	0.73	−0.36	0.28
Bulimina marginata	−0.69	0.56	0.08	−0.18
Bolivina pseudoplicata	−0.22	−0.12	0.54	0.19
Bolivinellina pseudopunctata	−0.3	−0.44	0.68	0.14
Brizalina variabilis	−0.05	−0.32	1.12	0.58
Cibicides lobatulus	0.02	−0.5	−0.28	0.03
Cibicides fletcheri	0	−0.24	0.44	0.14
Cassidulina obtusa	−0.52	0.14	0.78	0.42
Elphidium excavatum forma *selseyensis*	1.47	−0.02	0.88	−0.57
Elphidium gerthi	0.38	−0.12	0.37	0.13
Elphidium magellanicum	1.04	−0.85	0.8	−0.36
Elphidium cf. *E. magellanicum*	0.5	−0.87	0.45	−0.34
Eponides repandus	0.11	−1.16	−0.72	0.59
Eggerelloides scaber	0.59	0.78	0.21	−0.46
Epistominella vitrea	−0.59	0.11	0.73	0.28
Gavelinopsis praegeri	−0.21	0.16	0.42	0.15
Gaudyrina rudis	−0.17	−1.13	−0.47	0.11
Hyalina balthica	−0.86	0.74	−0.01	−0.36
Miliolinella subrotunda	0.4	0	0.35	0.08
Nonion depressulus	0.63	0.06	0.75	−0.03
Ophthalmidium balkwilli	0.32	−1.21	0.79	0.08
Pyrgo depressa	−0.5	−0.73	−0.47	−0.05
Planorbulina distoma	0.19	−0.16	−0.08	0.18
Quinqueloculina seminulum	0.19	−0.05	−0.18	0.08
Rosalina bradyi	−0.14	−0.62	−0.04	0.06
Rosalina anomala	0.99	−0.42	0.74	0.1
Rosalina williamsoni	−0.4	−0.44	0.68	0.22
Stainforthia fusiformis	−0.45	0.02	0.47	0.15
Spiroplectammina wrightii	−0.33	−0.01	−0.43	−0.21
Textularia bockii	−0.09	−0.07	−0.3	−0.16
Depth	−0.83	−0.02	−0.1	0.28
Temperature	0.69	0.56	0	−0.02
% gravel	0.03	−0.69	−0.08	0.03
% sand	0.24	0.27	−0.65	−0.38
Mean grain size	−0.12	0.57	0.45	0.37
Sorting (moments)	−0.18	−0.23	0.67	−0.09
Skewness (moments)	0.02	0.41	0.08	0.41
Skewness (folks)	−0.07	0.16	0.18	0.04
Kurtosis (moments)	0.24	0.34	−0.19	0.4
Kurtosis (folks)	0.08	0.14	0.23	0.05
Latitude	0.13	−0.87	−0.27	−0.02
Longitude	−0.68	0.16	−0.42	0.25