



The distribution of agglutinated foraminifera in NW European seas: Baseline data for the interpretation of fossil assemblages

John W. Murray and Elisabeth Alve

ABSTRACT

Assemblages composed entirely of agglutinated foraminifera occur in a restricted range of modern environments: where carbonate dissolution is prevalent, e.g., marshes, deep shelves or ocean depths below the carbonate compensation depth. Fossil agglutinated assemblages undoubtedly come from a wider range of environments than these modern analogues. Natural post-depositional or diagenetic dissolution of carbonate foraminiferal tests in original dead assemblages (ODAs) leads to the formation of residual agglutinated assemblages. Simulating this process experimentally by treating modern ODAs with dilute acid gives rise to acid-treated assemblages (ATAs). This paper provides a synthesis of previous work on 261 samples and provides new data on a further 87 samples. Investigated environments range from marginal marine marshes and estuaries through fjord and shelf seas to deep sea. The pattern of species diversity in ATAs follows the same pattern as that for ODAs and living assemblages: there is a progressive increase in diversity from marginal marine to deep sea. Because agglutinated foraminifera are normally only a small component of ODAs, the ATAs provide a much more reliable guide to species and generic distributions. Although the faunal distribution patterns are well defined in terms of broad environment, it has proved difficult to account for individual distributions using the available data on abiotic environmental factors. In NW European seas, *Miliammina* is confined to intertidal to shallow subtidal marginal marine environments but elsewhere it is common on deep shelves (e.g., off Antarctica). In summary where evolution can not explain the absence of calcareous taxa, ATAs fill the no-analogue gap and provide baseline data that can be used to interpret the ecology of fossil agglutinated assemblages.

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INTRODUCTION

The palaeoecological interpretation of fossil assemblages of agglutinated foraminifera is dependent on comparison with modern analogues. However, modern living and dead assemblages with exclusively organo- and ferro-agglutinated walls (Banner et al. 1991) are found only in environments where the water is under-saturated in carbonate. In the modern world such conditions occur especially on high intertidal marshes and in the deep sea below the calcite compensation depth but also occasionally in fjords (Loch Etive, Scotland, Murray et al. 2003) and on deep continental shelves (Larsen shelf, Antarctica, Murray and Pudsey 2004). However, it is unlikely that all fossil agglutinated assemblages come from this limited range of modern analogues. This raises two possibilities regarding fossil agglutinated assemblages. Alternative 1: they lived in or were predominant in a wider range of environments than at present (i.e., discrepancy induced by evolution and changing climate and palaeogeography, e.g., Nagy et al. 2010). Alternative 2: that some of them are secondary assemblages derived from original assemblages that included calcareous forms (as suggested by Scott et al. 1983). The primary aim of this paper is to fill the no-analogue gap in modern data by exploring the second alternative. This, in turn, should shed light on the first alternative.

A simple way to approach this problem is to simulate the natural processes of carbonate dissolution by experimentally dissolving original dead assemblages (ODAs) to obtain residual acid-treated assemblages (ATAs) from a wide range of modern environments. Our studies to date have shown that ATAs retain a considerable amount of ecological information (see Table 1 for source references and references with ecological information). A further advantage of studying ATAs is to provide much more reliable data on the distribution of agglutinated species; the latter are commonly heavily outnumbered by calcareous forms in ODAs, and consequently it is difficult to obtain a statistically reliable sample. We use dead rather than living assemblages because the present study is not ecologically process-oriented. The assemblages living at the site at the time of collection are influenced by patchiness and seasonality whereas the time-averaged dead assemblages, even though they may include exotic forms, reflect longer-term conditions and the potential fossil assemblages. The data for agglutinated foraminifera in this paper are based on >63 µm size fraction for all environments except deep sea where >125 µm

was used. These cutoffs should be borne in mind if the size fraction used for fossil material is greater than the reference information presented here especially for species diversity and species abundance.

This study is the first to synthesise the distribution of agglutinated taxa in environments ranging from intertidal, through shelf seas, to deep sea for the NE Atlantic margin. It includes data on 87 new samples together with data from work previously completed. In addition, the aims of this study are:

- To establish patterns of species diversity for ATAs with respect to major environments.
- To compare these ATA species diversity patterns with the ODAs and also with live patterns (summarised in Murray 2006).
- To determine the distribution of taxa with respect to broad environments; to determine ecological controls.
- To determine the role of local transport in modifying agglutinated assemblages.

MATERIAL AND METHODS

Altogether 348 samples are considered (Table 1). The majority (261) are from our previous studies (Figure 1). In addition, there are 55 new samples from southern England temperate brackish estuaries with bordering marshes (Christchurch and Poole Harbours, Beaulieu, Exe and Hamble estuaries), 25 from Norwegian fjords (shallow, 35-150 m: outer Lyngdalsfjord, Frierfjord, and Kragerø basin and outer Oslofjord; deeper than 400 m: Sørfjord, Hardangerfjord), four from the Skagerrak and three from the continental shelf Muck and Stanton deeps off Scotland (shelf deeps). All samples, representing the surface 1 or 2 cm of sediment, were stained with rose Bengal. In each case the >63µm living (stained), ODA and ATAs have been studied separately. The aim of acid treatment is to make it easier to pick sufficient agglutinated tests by removing the calcareous forms. The ATAs were prepared by dissolution in dilute acetic acid (pH 2.0-2.5). In the case of the deep fjord samples, the ODAs were rich in agglutinated tests so acid treatment was not necessary as sufficient tests could readily be picked. For consistency with the ODA data, ATA assemblages comprise dead tests only.

Tubular tests were not counted because they fragment during sampling and processing and give unreliable numbers. In some cases the multilocular test readily breaks into fragments (e.g., *Reophax moniliformis*, *Hormosinella guttifer*) so only those individuals with three or more chambers were

Table 1. Sources of data.

| Environment | Location | Samples | Source reference | Other related references; environmental information |
|--|----------------------|---------|------------------------|--|
| Marsh | S Norway | 10 | Murray and Alve, 1999b | Alve and Murray, 1999; Murray and Alve, 1999a |
| | S Sweden | 1 | Murray and Alve, 1999b | Alve and Murray, 1999; Murray and Alve, 1999a |
| | Denmark | 3 | Murray and Alve, 1999b | Alve and Murray, 1999; Murray and Alve, 1999a |
| | Exe estuary, UK | 3 | new | Murray, 1980 |
| | Christchurch, UK | 1 | new | |
| | Hamble, Beaulieu, UK | 11 | new | Horne et al., 2004 |
| | | | | |
| Marginal marine (excluding marshes) | S Norway | 59 | Murray and Alve, 1999b | Alve and Nagy, 1986; Alve and Murray, 1999; Murray and Alve, 1999a |
| | S Sweden | 36 | Murray and Alve, 1999b | Alve and Murray, 1999; Murray and Alve, 1999a |
| | Denmark | 24 | Murray and Alve, 1999b | Alve and Murray, 1999; Murray and Alve, 1999a |
| | Exe estuary, UK | 7 | new | Murray, 1980, 1983 |
| | Poole, UK | 15 | new | Humphreys, 2005 |
| | Christchurch, UK | 18 | new | Murray, 1968 |
| | Hamble estuary, UK | 8 | Alve and Murray, 1994 | Murray and Alve, 2000b; Alve and Murray, 2001 |
| | | | | |
| Fjord | S Norway | 4 | Alve and Murray, 1995a | |
| | S Norway | 8 | new | |
| | W Norway | 17 | new | Alve et al., 2011 |
| | Scotland, Loch Etive | 6 | Murray, et al., 2003 | |
| | | | | |
| Shelf seas | North Sea | 21 | Alve and Murray, 1995a | Murray, 1985, 1992 |
| | Southern UK | 54 | Murray and Alve, 2000a | Murray, 1970, 1979, 1986 |
| | | | | |
| Shelf deeps | Skagerrak | 18 | Alve and Murray, 1995a | Alve and Murray, 1995b, 1997 |
| | Skagerrak | 4 | new | |
| | W Scotland | 3 | new | Murray, 2003a, b |
| | | | | |
| Slope | NE Atlantic | 17 | Murray and Alve, 1994 | |
| | | | | |
| | Total | 348 | | |

counted towards the ATAs (following the practise of Murray and Alve 1999a).

Environmental data have been compiled from the sources listed in Table 1. In addition, the sea floor flux of organic matter has been calculated for shelf seas and the deep sea (see below). For shelf seas, all samples are from beneath areas of summer thermocline except for four samples from the southern North Sea (#3445, #3446, #3454, #3456). Fjords commonly have an estuarine water circulation but are distinguished from e.g., British estuaries by their silled basins, water stratification and sometimes by the presence of low oxygen or anoxic bottom waters. The examples here are all from oxic bottom water conditions.

Non-metric Multi-dimensional Scaling (MDS), principal component analysis, and species diversity calculations have been performed using Primer v.6.1.6 (Clarke and Gorley 2006). The MDS technique plots samples in two-dimensional space 'such that the relative distances apart of all points are in the same rank order as the relative dissimilarities (or distances) of the samples, as measured by some appropriate resemblance matrix calculated on the (possibly transformed) data matrix.' (Clarke and Gorley 2006, p. 75). For MDS the faunal data were transformed using square root and resemblances calculated using the Bray Curtis method. For the multivariate analysis (principal component analysis and MDS) of the abiotic fac-

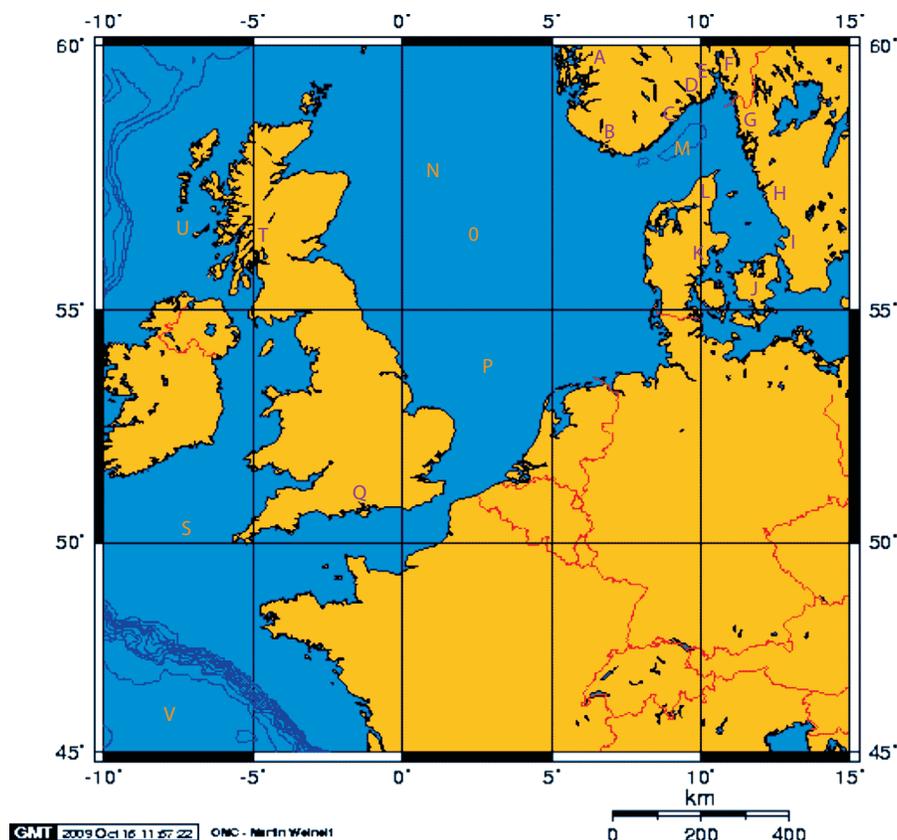


FIGURE 1. Map of the study area with localities. A. Hardangerfjord, B. Lyngdalsfjord, C. Isefærifjord; Kvstadkilen; Dype Holla, Lyngør; Tøkersfjord, Lyngør; Hasdalen; Kilsfjord, D. Kragerøfjord, E. Tjøme; Borre; Sandebukta, F. Bunnefjord; Hunnebotn, G. Hålkedalskilen; Tjärmö; Finnsbobukten; Gullmarsvik; Hafstensfjord, H. Kungsbackafjord, I. Jonstorp, J. Kildehuse; Kalundborg, K. Vejle Fjord; Havhuse (Kalø Vig); Vosnæs Pynt, (Kalø Vig), L. Løgstør; Valsted; Frederikshavn, M. Skagerrak, N. Forties, O. Ekofisk, P. Southern North Sea, Q. Hamble; Beaulieu; Christchurch; Poole; Exe, R. Channel, S. Celtic Sea, T. Loch Etive, U. Muck and Stanton Deeps, Scotland, V. NE Atlantic (only partially shown - see Murray and Alve 1994 for details).

tors plus sea floor organic flux the data were normalised prior to analysis. Species diversities have been calculated using Fisher alpha (Fisher et al. 1943 and the information function, $H(S) (=H'(\ln))$, (Shannon 1948; Hayek and Buzas 1997).

Figure 1 was prepared from www.aquarius.ifm-geomar.de. Coloured images of species were taken using AxioVision Release 4.7.2 at the Natural History Museum, London. For each specimen, successive images were taken at different focal depths from the highest level downwards. These images were then merged using Auto-Montage 4.0 to give the sharpest image. The system works best on larger individuals, and it is difficult to achieve really sharp images of very small individuals. However, the results are images that show the natural colour and texture of the tests (although a few, such as *Miliammina fusca*, which was previously coated in gold, look more yellow than nor-

mal). The figures were compiled using Adobe Photoshop CS4. Some images show specimens stained with rose Bengal but such individuals were not included in the assemblage counts (based on dead only).

Sea Floor Organic Flux

Data on the average sea surface primary production per day are now available from satellite imagery (NEODASS) and from these data the annual rate is readily calculated. Primary production by plankton in the surface waters of the ocean and marginal seas is consumed by organisms as food or by bacterial decay during its descent through the water column. The amount of organic carbon that reaches the sea floor is termed the sea floor organic flux (Kaminski et al. 1999). In a classic study of the relationships between primary and export production, Berger et al. (1988) discussed previous attempts to quantify the downward flux of

organic material and proposed various equations for its calculation at different water depths. They also concluded that the coastal regions of the oceans and sub-polar regions account for 50% of the total production and more than 80% of the flux of organic material to the sea floor. Altenbach et al. (1999) used Berger et al. equation 12 in their calculations of flux rates (F) for the eastern Atlantic Ocean. The factors are water depth in m (labelled z by Berger and D by Altenbach) and annual primary production (PP) as $g C_{org} m^{-2} yr^{-1}$. Equation 12 is: $F(D)=9PP/D + 0.7PP/D^{0.5}$. An alternative equation (11) for shallower waters is $J(z)=6.3*PP/z^{0.8}$. However, the results differ by only 2-3% for water depths down to 200 m so, in the present study, equation 12 has been used throughout to calculate the C_{org} flux to the sea floor at investigated sites. In coastal areas the presence of suspended sediment causes the determination of PP to be less accurate so satellite data for these areas (A-L, Figure 1) have not been included. An example of this is found in Tilstone et al. (2005).

Data on average daily sea surface primary production are available for the years 1998 to 2005. For the shelf sea areas away from the influence of suspended sediment there is remarkably little variation in the pattern of values from one year to another. The 2005 data were used for this study. Rather than calculate the values for each precise data point a general value has been taken for each main area, shelf sea (M-V, Figure 1: North Sea Forties and Ekofisk, Skagerrak, outer Celtic Sea, Scotland shelf deeps all $146 g C_{org} m^{-2} yr^{-1}$; central Celtic Sea $219 g C_{org} m^{-2} yr^{-1}$) and for the deep sea ($73 g C_{org} m^{-2} yr^{-1}$). However, for each sample the sea floor organic flux has been determined according to water depth using equation 12 as noted above. This general approach to determining sea floor organic flux is justified because the foraminiferal data represent an average of decades of foraminiferal accumulation so there is no point in making comparisons with a precise value based on a single observation of the sampling spot.

Although the primary production of coastal areas cannot be reliably determined due to the masking effects of suspended sediment, in such areas the main food source for benthic foraminifera is likely to be the benthic flora of diatoms, bacteria and cyanobacteria together with organic detritus derived from marine or terrestrial plants or degradation products. Whereas in shelf seas and deep sea areas the most variable environmental parameter is likely to be the sea floor organic flux, in shal-

low waters there is greater variation in abiotic factors such as temperature, salinity and energy from waves and/or water currents.

Taxonomy

Where necessary we have revised the taxonomy of our previous studies. Type material was examined in the Natural History Museum, London, and reference examples of '*Labrospira jeffreysii*' (Williamson) and *Trochammina bullata* Höglund were provided from the Höglund Collection in Aarhus University, Denmark. Altogether, there are 92 named agglutinated species. Notes on individual taxa are given in the taxonomic list.

RESULTS

The entire data set including both previously published and new samples are in Appendix 1 and 2.

Species Diversity

Plots of Fisher alpha against H(S) are similar for ATAs and ODAs although the range is somewhat extended for the latter (Figure 2). There is a significant positive linear correlation between the ATAs and ODAs for both diversity indices but the correlation is stronger for Fisher alpha ($R^2 = 0.778$) than for the information function ($R^2 = 0.485$, Figure 3). There is a progression from low diversity in marsh and marginal marine, through shelf seas, shallow fjord, shelf deeps and Skagerrak, deep fjord >500 m and deep sea (Figure 4). See Table 2 for the distribution of diversity values for each environment together with the mean and standard deviation. Overall, there is an increase in diversity with water depth: deeper than 500 m alpha is >5. Deeper than 100 m H(S) rarely goes below 1.0.

Non-metric Multi-dimensional Scaling (MDS)

Samples that plot close together have similar faunal composition; those that plot far apart are different. Because the faunas of marginal marine marshes and estuaries are fundamentally distinct from those of the shelves, we have presented MDS of these data as separate plots (Figures 5, 6).

Marsh and estuary. When individual geographic areas are plotted separately there is varying degree of overlap (indicating local differences) of the estuaries (Exe, Christchurch, Poole, Hamble in England; shallow waters around Oslofjord, Kattegat and Skagerrak in Norway, Denmark and Sweden) and relatively little overlap with the field for marshes. The overall picture becomes even

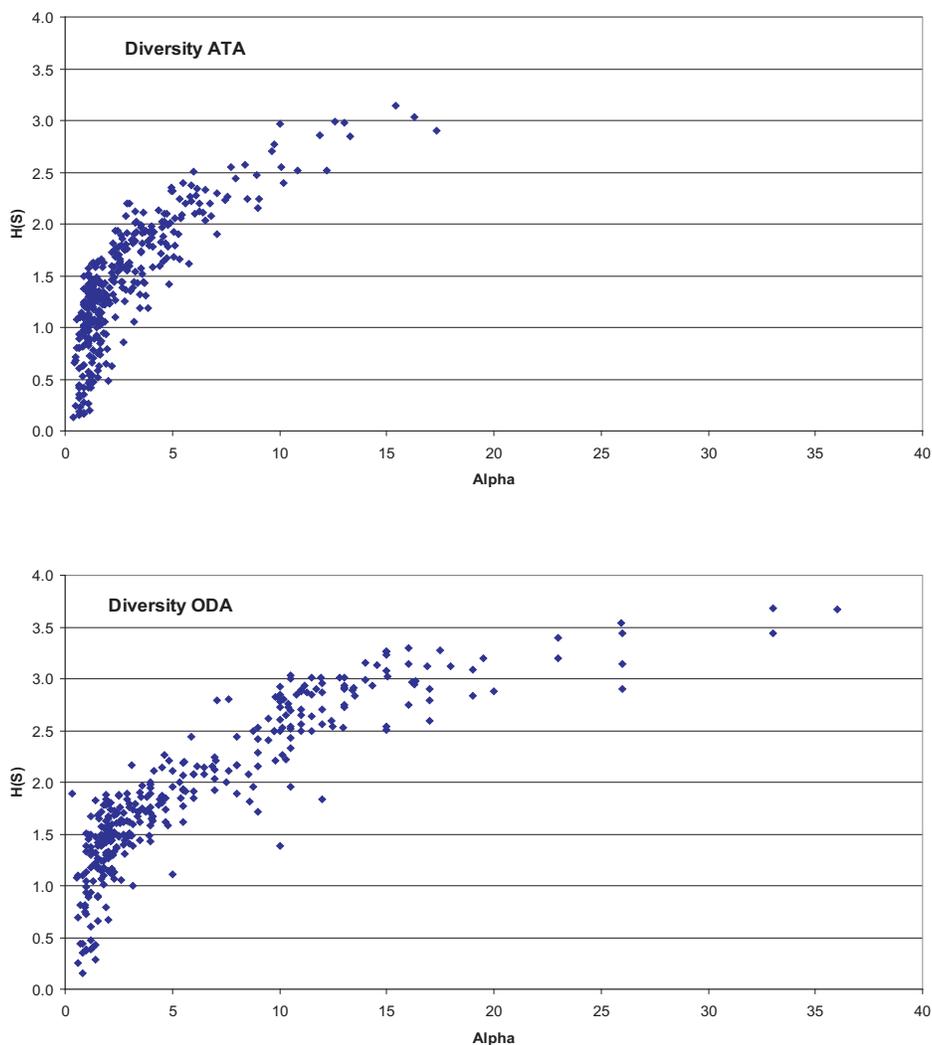


FIGURE 2. Species diversity of ATAs and ODAs.

clearer when the data are plotted as marsh (M), estuary <3 m deep (E) and ≥ 3 m deep (E*) (Figure 5). This is a reflection of the fact that many of the marsh taxa are confined to marsh habitats.

Shelf seas to deep sea (Figure 6). Overall, the ATA faunal composition of the main study areas are reasonably distinct although there is some overlap with the Channel/Celtic Sea (CC), the southern North Sea (NS) and the Scottish shelf deeps (MD). The Skagerrak field (SK) includes outer Oslofjord (OF) and outer Lyngdalsfjord (YL). Loch Etive (Et) is more closely similar to the UK shelf seas than the deep Hardangerfjord (H). The latter lies between SK and the deep sea (NE) with one sample overlapping the latter.

Depth Distributions of Species

Because our data set extends from intertidal to deep sea (4250 m) we have been able to determine the depth distributions of species (ranges) within those extremes. These are summarised in Table 3. There is a progressive change in faunal composition with increasing depth but there are no obvious depth-related boundaries. However, there are some differences in relative abundance in the various environments. For instance, *Adercotryma wrighti* reaches abundances of nearly 60% on shelf seas at depths of 100-130 m whereas in Hardangerfjord and the deep sea it never exceeds 16%.

Distribution by Environment and Geography

The distribution patterns are presented by environment (Figure 7, species; Figure 8, genera)

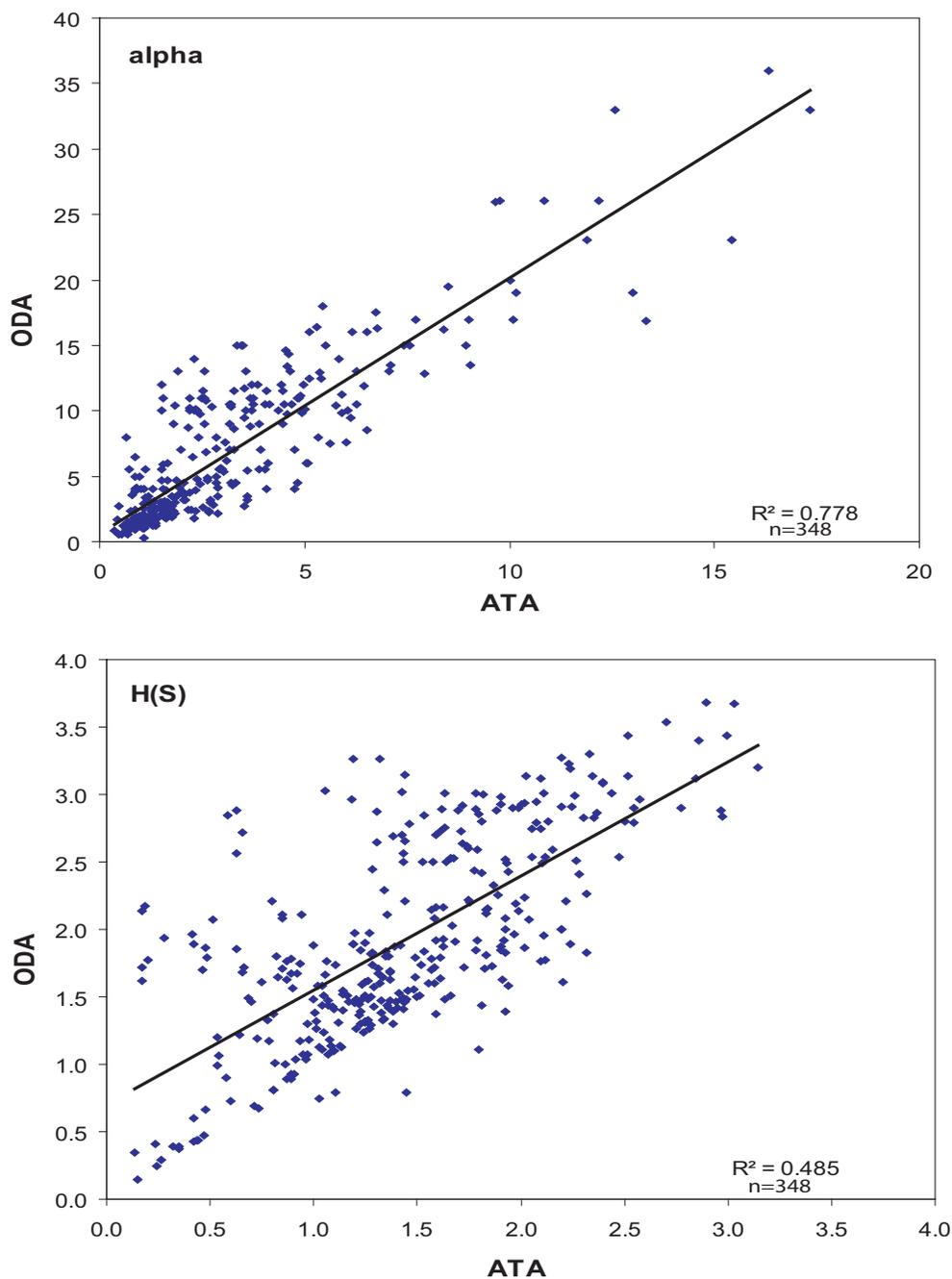


FIGURE 3. Correlation of alpha and correlation of H(S) for ATAs and ODAs.

and by geography (Figure 9). The shallow water areas (<6 m) around Oslofjord, Skagerrak and Kattegat are treated as marginal marine (estuarine) here as they are brackish.

There is a clear progression of species from marsh to deep sea (Figure 7.2). Typical marsh species such as *Jadammina macrescens* and *Trochammina inflata* also occur in adjacent non-

vegetated intertidal flats. Likewise, some intertidal taxa are present in low abundance on marshes. The faunas of shelf seas, shelf deeps and shallow fjord (Etive) have much in common. Those of the deep Hardangerfjord overlap the shelf seas and deep seas. The pattern for genera is somewhat different (Figure 8) because some span a broad spectrum of environments (e.g., *Haplophrag-*

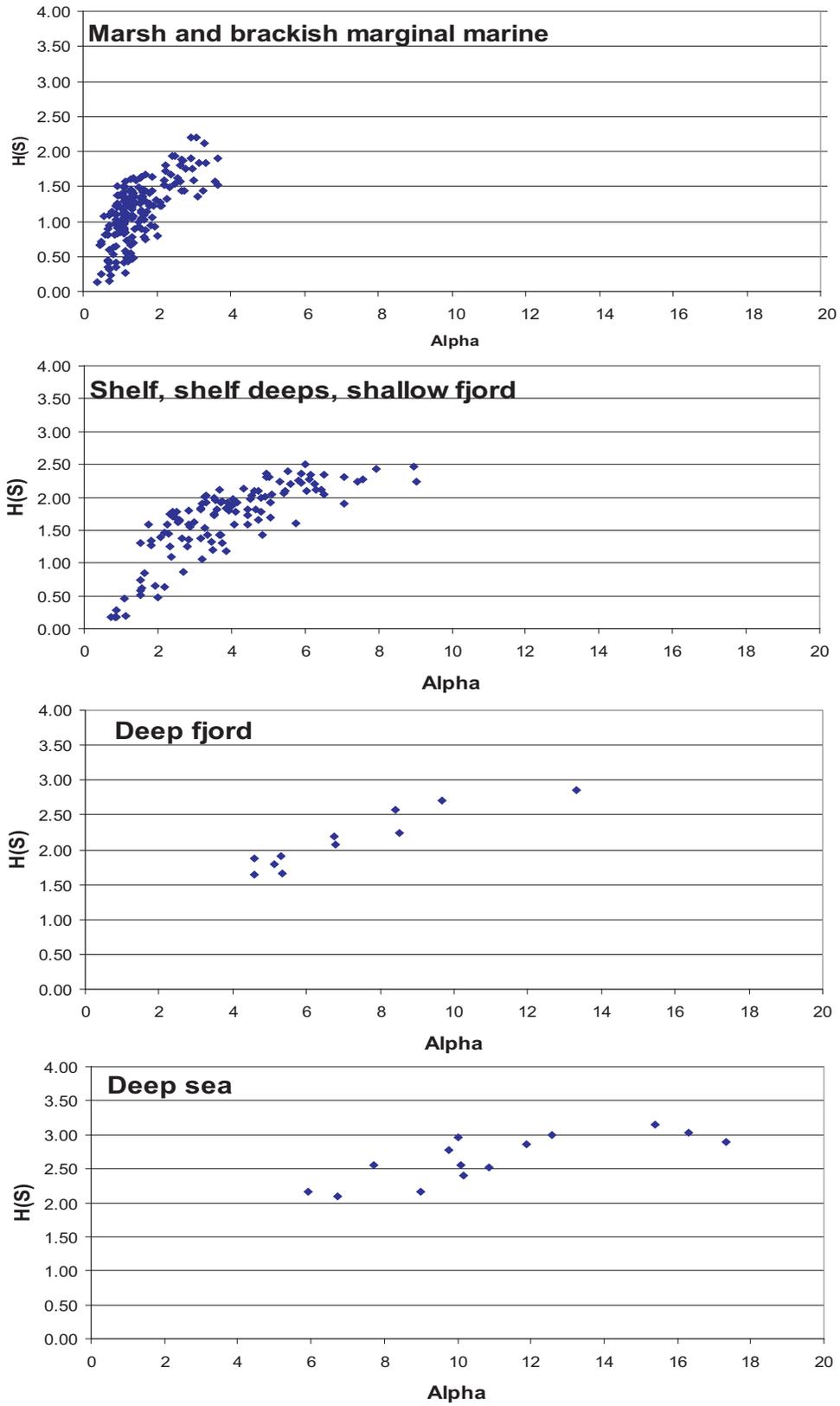


FIGURE 4. ATA species diversity for different environments.

Table 2. Summary of diversity values for ATAs. The comparative data on living assemblages are from Murray (2006, Table 8.1) and * Alve et al. 2011.

Values $\geq 10\%$

| Fisher alpha | Marginal marine | | Fjord | Shelf seas | Shelf deeps | >500 m | |
|-----------------|-------------------|-----------------------|-------|---------------|----------------|---------------|-------------|
| | Brackish marsh | Lagoons, estuaries | | | | Deep fjord | Deep sea |
| n | 29 | 167 | 18 | 75 | 25 | 8 | 16 |
| mean | 1.03 | 1.51 | 4.71 | 3.22 | 5.30 | 8.01 | 11.186 |
| st. dev. | 0.53 | 0.69 | 2.13 | 1.38 | 1.49 | 2.64 | 3.25 |
| | % | % | % | % | % | % | % |
| ≤ 1 | 66 | 18 | | 5 | | | |
| 1.1-2.0 | 24 | 64 | 6 | 16 | | | |
| 2.1-3.0 | 10 | 13 | 33 | 23 | | | |
| 3.1-4.0 | | 5 | 6 | 29 | 24 | | |
| 4.1-5.0 | | | 11 | 17 | 24 | | |
| 5.1-6.0 | | | 17 | 6 | 20 | 25 | 6 |
| 6.1-7.0 | | | 11 | 3 | 16 | 25 | 6 |
| 7.1-8.0 | | | 6 | 1 | 12 | | |
| 8.1-9.0 | | | | | 1 | 25 | 6 |
| 9.1-10.0 | | | 6 | | | 12 | 18 |
| 10.1-11.0 | | | | | | | 18 |
| 11.1-12.0 | | | | | | | 6 |
| 12.1-13.0 | | | | | | | 18 |
| 13.1-14.0 | | | | | | 12 | |
| 14.1-15.0 | | | | | | | |
| 15.1-16.0 | | | | | | | 6 |
| 16.1-17.0 | | | | | | | 6 |
| 17.1-18.0 | | | | | | | 6 |

| Information function | Marginal marine | | Fjord | Shelf seas | Shelf deeps | >500 m | |
|-------------------------|-------------------|-----------------------|-------|---------------|----------------|---------------|-------------|
| | Brackish marsh | Lagoons, estuaries | | | | Deep fjord | Deep sea |
| n | 29 | 167 | 18 | 75 | 25 | 8 | 16 |
| mean | 1.00 | 1.18 | 1.83 | 1.50 | 2.03 | 2.28 | 2.66 |
| st. dev. | 0.37 | 0.41 | 0.54 | 0.56 | 0.34 | 0.41 | 0.43 |
| | % | % | % | % | % | % | % |
| <0.50 | 14 | 8 | | 9 | | | |
| 0.51-1.0 | 21 | 23 | 6 | 9 | | | |
| 1.01-1.50 | 65 | 48 | 28 | 16 | 16 | | |
| 1.51-2.0 | | 19 | 11 | 56 | 12 | 25 | |
| 2.01-2.5 | | 2 | 50 | 9 | 72 | 38 | 25 |
| 2.51-3.0 | | | 6 | | | 38 | 62 |
| 3.01-3.5 | | | | | | | 12 |

| Alpha for live assemblages | | | | | | | * |
|----------------------------|-----|-----|-----|-----|--|------|------|
| mean | 1.1 | 1.7 | 2.4 | 8.6 | | 7.6 | 12.3 |
| st. dev. | 0.7 | 1 | 1.9 | 4.9 | | 1.92 | 6.2 |

| H(S) for live assemblages | | | | | | | * |
|---------------------------|------|------|------|------|--|------|------|
| mean | 1.10 | 1.08 | 1.39 | 2.37 | | 2.30 | 2.68 |
| st. dev. | 0.49 | 0.47 | 0.58 | 0.63 | | 0.38 | 0.64 |

moides, *Reophax*, *Cribrostomoides*, *Adercotryma*, *Eggerelloides*, *Portatrochammina*). Superimposed on the environmental controls on distribution there is also a geographical component. Although most

species are found throughout the geographic range of their environment (Figure 9) some are more restricted. For instance, the marsh species *Tiphotrocha comprimata* is confined to Norway and

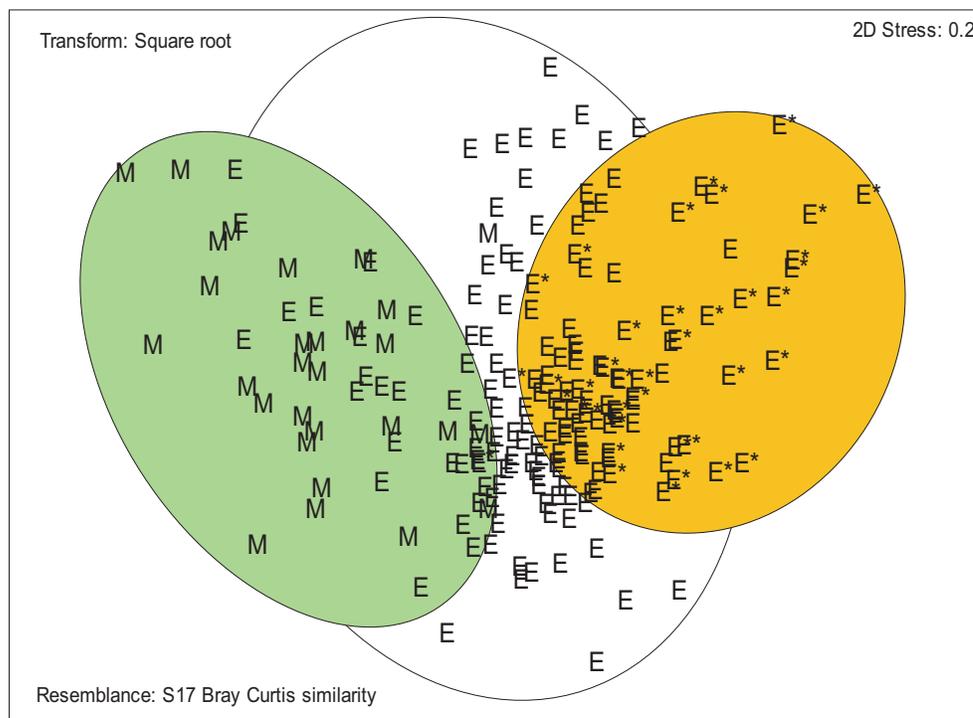


FIGURE 5. MDS plot of ATA data for marginal marine environments. M = marsh (green ellipse), E = estuary 0-3 m deep (uncoloured ellipse), E* = estuary ≥ 3 m deep (yellow ellipse). Ellipses are drawn to emphasize closeness between samples from similar environments.

Balticammina pseudomacrescens has yet to be found in the marshes of Sweden and Denmark. *Ammotium cassis* is absent from Britain. *Liebusella goesi* is rare in shelf seas and most abundant in deeper water (Norwegian fjords, Skagerrak and shelf deeps off Scotland) but not on the continental slope.

Controls on Distribution Patterns

As many data as possible have been gathered on environmental parameters. This includes our own measurements made at the time of sampling and data from the literature (Appendix 1 and 2). Unfortunately, there is not a complete environmental data set for every sample. Data on maximum bottom water temperatures are more complete than those on minimum values and this is true also for salinity. As noted above, the sea floor organic flux is calculated from satellite imagery in those areas away from the coast where suspended sediment is minimal or absent. Nevertheless, some useful conclusions can be drawn about the relationships between environmental parameters and the foraminiferal assemblages.

Principal component analysis and MDS plots of marsh and shallow water environments (Appen-

dix 1, marginal marine; Figures 10, 11) show a large scatter of points with marsh samples occupying a distinct field which slightly overlaps that of the rest of the samples and which seems primarily determined by water depth. Otherwise, there are no clear correlations between different geographic areas and the environmental variables.

For shelf seas, down to about 300 m, the C_{org} shows a wide range of 8-38 g C_{org} m⁻² yr⁻¹ which narrows to 6-23 and 2.7-5.2, respectively, for shelf deeps and deep fjord, and to 0.9-2.1 g C_{org} m⁻² yr⁻¹ in the deep sea (Figure 12). There is a positive linear correlation between water depth and maximum temperature ($R^2 = 0.5051$) and hence between sea floor organic flux and maximum temperature ($R^2 = 0.5819$), and a weak positive correlation between sea floor organic flux and sediment grain size ($R^2 = 0.2953$). Multivariate analysis of the abiotic factors plus sea floor organic flux shows a clear pattern (Figure 13). The vectors for the environmental parameters on the PCA plot show that the primary control on the deep sea (D), Skagerrak (SK) and Hardangerfjord (H) is a combination of water depth and maximum temperature. These areas are also separated from one another

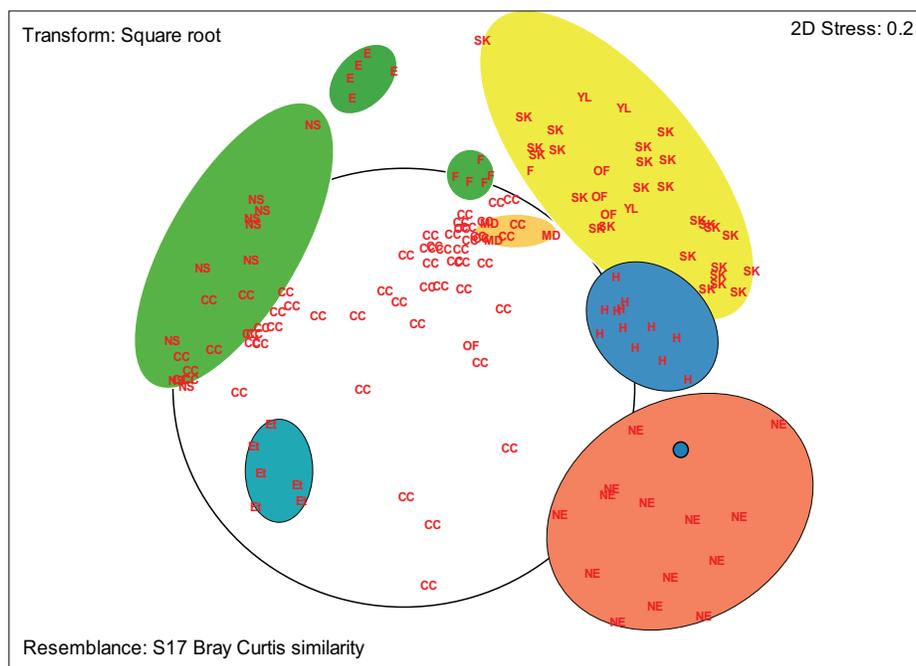


FIGURE 6. MDS plot of ATA data for shelf and deep sea. Major fields are coloured except for CC which is outlined. All the North Sea areas are green. E Ekofisk; Et Etive; MD Muck and Stanton deeps; F Forties; CC Celtic Sea and Channel; NS North Sea; H Hardanger; YL outer Lyngdalsfjord; SK Skagerrak, including Kragerø; OF outer Oslofjord; NE deep sea - NE Atlantic. Ellipses and circles are drawn to emphasize closeness between samples from similar environments.

by sediment grain size differences. The shelf sea environments are separated primarily on their sediment characteristics and to a lesser extent on sea floor organic flux (finer sediment and lower sea floor organic flux in the Forties (F) and Ekofisk (Ek) areas of the North Sea than in the Celtic Sea (C)).

DISCUSSION

There is abundant evidence of syndepositional dissolution of calcareous tests in certain modern environments including both terrigenous and carbonate sediments (for example, marshes: Jonasson and Patterson 1992; De Rijk and Troelstra 1999; Fatela et al. 2009; shallow water: Green et al. 1993; Murray and Alve 1999a; Berkeley et al. 2007; fjord: Alve and Nagy 1986; Murray et al. 2003; shelf seas: Murray 1989; shelf deeps: Alexandersson 1979; enclosed seas: Exon 1972; deep sea: Schröder 1988). This manifests itself in calcareous tests having an etched surface (Murray 1967; Murray and Wright 1970; Peebles and Lewis 1991; Fatela et al. 2009), breakage or loss of later chambers (Murray and Alve 1999a; Moreno et al. 2007) and a higher abundance of agglutinated tests in the dead assemblages than could be accounted for by differential production between

species (Murray and Alve 1999a). Dissolution may be caused by corrosive bottom waters (Alexandersson 1979), or sediment pore waters where the metabolic decay of organic matter in the top few cm leads to lowered pH (Reaves 1986; Walter and Burton 1990), or destruction through bacterial activity (Freiwald 1995). Moreno et al. (2007) point out that foraminifera secrete magnesian calcite that is chemically heterogeneous and structurally disordered, and these factors play a role in its reactivity. They calculated the solubility index using a model based on pure calcite but noted that the index for magnesian calcite may be slightly different. In their Portuguese estuary, where the index is zero, calcareous tests are abundant, but where it is negative dissolution takes place, and calcareous tests are either low in abundance or absent altogether. However, it is relatively rare in modern environments for there to be total dissolution loss of calcareous taxa. The exceptions are marshes and the deep sea at depths greater than the lysocline. Dissolution may also take place during sediment burial through subsidence, as part of the processes of fossilisation and finally weathering of deposits exposed at outcrop following uplift.

Table 3. Summary of the depth distributions of species in ATA assemblages.**Marginal marine***Ammobaculites balkwilli* intertidal to 6 m.*Ammoscalaria runiana* intertidal to 6m, mainly between 3-5.5 m.*Ammotium cassis* 2-6 m*Ammotium salsum* mainly 0-5 m; 54 m in Loch Etive (transported?)*Balticammina pseudomacrescens* only intertidal.*Haplophragmoides wilberti* mainly intertidal.*Miliammina fusca* intertidal to 6 m. All records >10m are from Loch Etive (down to 140 m, probably through transport).*Jadammina macrescens* mainly intertidal; transported into slightly deeper water (2 m).*Reophax moniliformis* mainly <2m, common to 6 m.*Trochammina inflata* mainly <1 m.*Tiphotrocha comprimata* mainly <1 m.**Shelf seas – deep sea***Adercotryma glomeratum* 100-4250 m.*Adercotryma wrighti* 35-4250m. Abundant 100-130 m.*Ammodiscus gullmarensis* 20-500 m.*Cribostrumoides jeffreysii* mainly shallower than <2000 m. Abundant <150 m.*Cribostrumoides crassimargo* mainly shelf, occasionally shelf deep and deep sea (4250 m).*Cribostrumoides nitidus* shallowest at 100 m; deepest 1815 m*Cribostrumoides subglobosus* shallowest 290 m; deepest 4250 m.*Cuneata arctica* mainly 0-100 m; deepest 483 m probably due to downslope transport.*Cystammina pauciloculata* rare, 1806-3678 m.*Deuterammina ochracea* rare in estuaries (probably transported in), shelf seas and shelf deeps.*Eggerella europea* 50- 1500 m.*Eggerelloides medius* mainly <800 m.*Eggerelloides scaber* mainly <150 m.*Eratidus foliaceus* rare on shelf and deep sea.*Glomospira gordialis* rare on shelf, deeps and deep sea.*Haplophragmoides bradyi* 50-2000 m; abundant 50-900 m.*Haplophragmoides sphaeriloculus* mainly >2900 m.*Hormosinella guttifer* rare in shelf deeps and deep sea.*Lagenammina arenulata* 300-4250 m.*Leptohalysis catella* common on muddy shelf, rare in shelf deeps.*Liebusella goesi* rare on shelf and shelf deeps, shallow and deep fjords.*Morulaepecta bulbosa* mainly <150 m.*Portatrochammina murrayi* 17-4250 m; abundant 50-1800 m.*Psammosphaera fusca* rare on shelf and shelf deeps.*Recurvoides trochamminiforme* from 48 m - ~2000 m; highest abundance 50-400 m.*Reophax bilocularis* very rare in shelf deep and deep sea.*Reophax fusiformis* shelf, and rarely shelf deep.*Reophax micaceus* shallow and deep fjords, shelf deeps, deep sea.*Reophax scorpiurus* 45-300 m.*Repmanina charoides* shallow and deep fjord, shelf deeps, deep sea.*Saccammina socialis* shallowest 98 m; deepest 4250 m.*Spiroplectammina biformis* common in shallow fjords, present in shelf deeps, deep fjords and deep sea.*Textularia earlandi* intertidal to 500 m.*Textularia kattedagensis* 50-500 m.*Textularia skagerakensis* 50-1100 m.*Trochammina subturbinatus* mainly >500 m.*Trochamminopsis quadriloba* from 48 m - ~2000 m; highest abundance 300-700 m.

The original dead assemblages (ODAs) not only represent the accumulation of tests derived from successive live assemblages over a period of years or decades but also the results of any post-mortem modification, especially transport of tests. As the ATAs are based on ODAs they also show such features. This chain of reasoning affects their species diversity and patterns of distribution. There is also some destruction of agglutinated tests,

especially those that are poorly cemented and therefore fragile (Schröder 1988; De Rijk and Troelstra 1999; Fatela et al. 2009). In our study some *Miliammina fusca* tests were sufficiently fragile to collapse during mounting (see also Culver et al. 1996). *Leptohalysis* is also fragile, and some individuals may be destroyed during sample processing (e.g., Murray et al. 2003). Similarly, agglutinated tubular foraminifera become broken

during sample collection and processing; we have therefore excluded them from assemblage counts. In arctic fjords, shelf seas and deep sea, early diagenesis destroys many agglutinated tests (Barmawidjaja et al. 1992; Majewski and Zajączkowski 2007; Hald and Steinsund 1996; Wollenburg and Kuhnt 2000). According to Schröder (1988) *Reophax scorpiurus* is considered to have low fossilisation potential while *Hormosinella distans*, *Eratidus foliaceus*, *Psammosphaera fusca*, *Glomospira gordialis*, *Ammolagena clavata*, *Karrerella apicularis*, *Nodellum membranaceum*, *Ammobaculites filiformis*, *Haplophragmoides sphaeriloculus*, *Cribrostomoides subglobosus* and *Adercotryma glomeratum* show progressively greater preservation potential. However, Kuhnt et al. (2000) disagreed with Schröder's conclusions as they consider habitat preference to be equal in importance to wall structure. They point out that many Cretaceous and Palaeogene deep-sea agglutinated assemblages are formed of small infaunal taxa. Increased preservation in coastal settings where relatively high sediment accumulation rates cause rapid burial below the redox cline in the sediment seem to promote preservation of agglutinated forms as it slows down organic matter degradation (discussion in e.g., Alve 1996; Berkeley et al. 2007).

Species Diversity

Our first study showed that deep sea ATAs, like the ODAs from which they were drawn, have high diversity (Murray and Alve 1994). Our subsequent studies in a wide range of environments have confirmed that ATAs provide much information on species diversity even when only a few agglutinated individuals are recorded in the ODA. The progressive increase in species diversity of ATAs from low in marginal marine environments to high in the deep sea (Figure 2, Table 2) is comparable with that both of ODAs (Figure 2) and living assemblages (see Murray 2006, figure 8.4.). Of course, the fields differ to some degree and the range of species diversity in ODAs is greater not only than that of the ATAs but also that of the living assemblages from which they were drawn. The consequences are apparent from the statistics: the means and standard deviations of alpha and H(S) are comparable (Table 2, N.B. shelf deeps were included with shelves by Murray 2006).

Modern calcareous forms have three basic wall structures: calc-agglutinated, porcelaneous, hyaline. We pose the question: do any of the calcareous groups mimic the diversity pattern of the

whole assemblages? It is unlikely that this would be true of calc-agglutinated or porcelaneous forms as both are restricted to a limited range of environments, the former to normal marine shelf seas and upper bathyal, and the latter mainly to shallow water normal marine or hypersaline environments – elsewhere they are rare. Since the majority of taxa in most modern environments have hyaline walls (Murray 2006) it follows that they are highly likely to mimic the diversity of the whole assemblage.

These observations are important from a practical point of view. If the non-calcareous agglutinated and hyaline components of an assemblage both individually mimic the diversity of the whole assemblage then a study carried out on just one or the other subset in fossil material should suffice to give enough diversity information to help determine the original environment.

Distribution Patterns

Unlike calcareous foraminifera, agglutinated forms occupy the full range of brackish/marine/hypersaline environments, from almost supratidal to the deepest ocean. However, with the exception of marshes, agglutinated foraminifera are minor elements of most modern foraminiferal assemblages. The limited literature giving details of agglutinated species ecology is summarised in the Taxonomic notes and comments on species ecology listed below.

In this study, the MDS plots show the similarities and differences between the various environments. Because marshes have a distinct fauna they are readily separated from the adjacent non-vegetated flats (Figure 5). For subtidal areas, the limited overlap of the North Sea with the Channel/Celtic Sea shows these areas to be faunally distinct (Figure 6), perhaps partly due to finer sediment and lower organic flux in the Forties and Ekofisk areas of the North Sea than in the Celtic Sea. Likewise, Loch Etive has little in common with the Norwegian fjords (Lyngsdalsfjord, Oslofjord or Hardangerfjord). The deeps on the Scottish shelf and the Skagerrak are quite similar and there is a progression from the Skagerrak to Hardangerfjord to the deep sea, which partly reflects increasing water depth. Also, the Skagerrak and Hardangerfjord have finer (muddy) substrates than the deep sea (which although muddy contain sand-size planktonic foraminiferal tests). The environmental parameters we have available are not comprehensive enough to explain the faunal differences we record between the investigated areas. However,

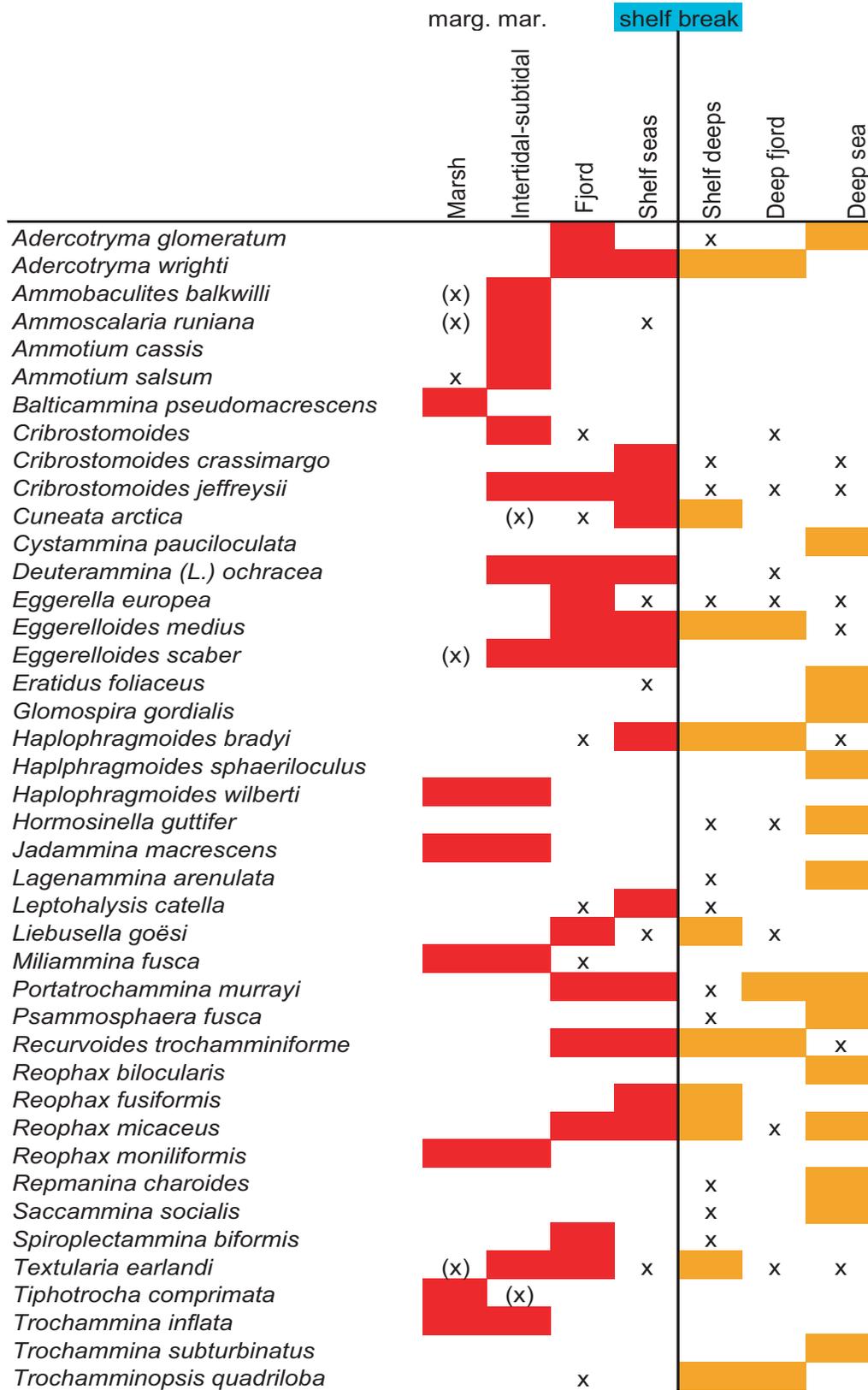


FIGURE 7. Distribution of ATA taxa by environment, 1. Species arranged alphabetically by genus, 2. Species in order of occurrence. Red and orange = $\geq 10\%$; x = $< 10\%$. (x) indicates tests interpreted to be transported.

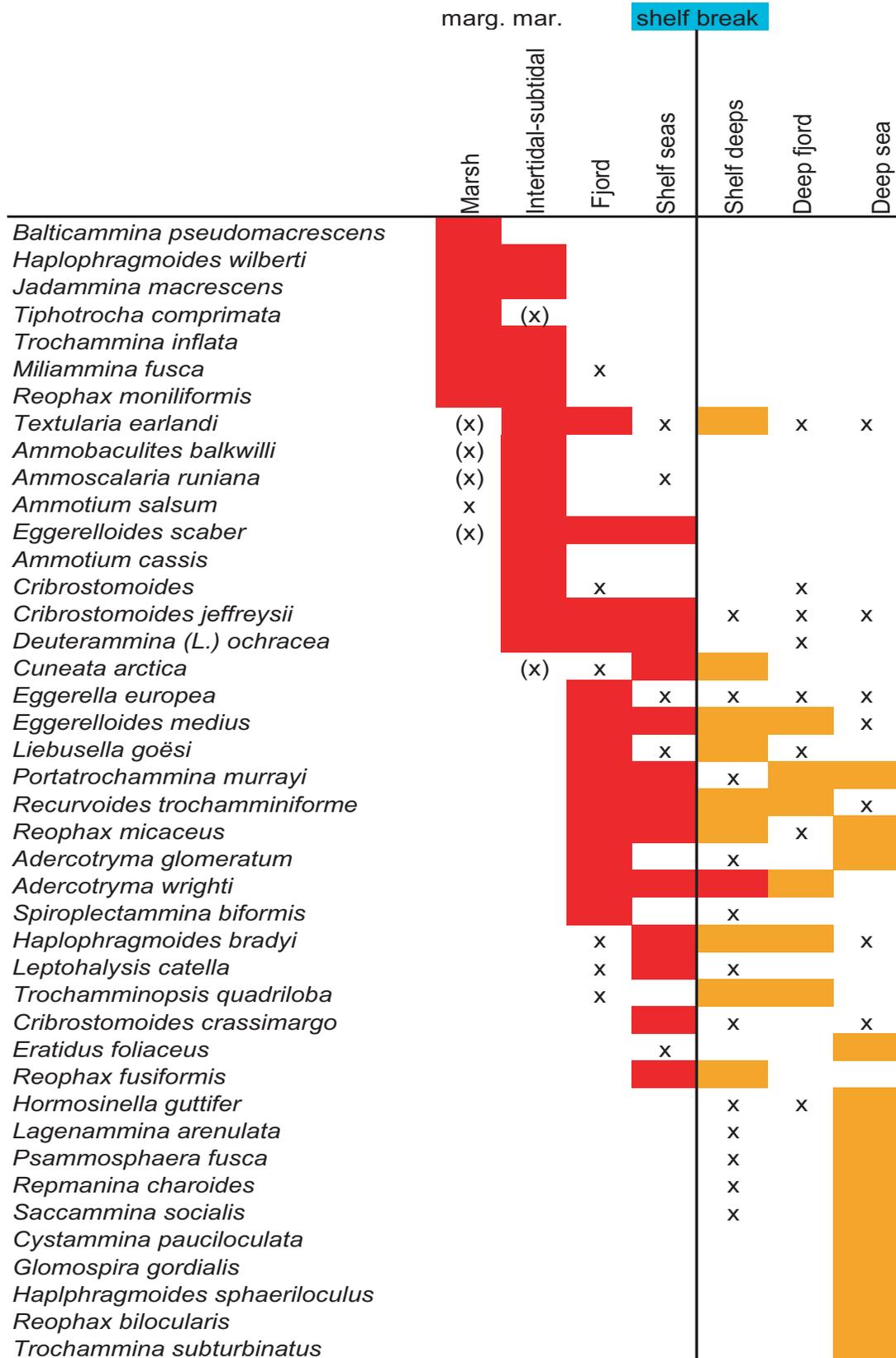


FIGURE 7 (continued). (Part 2.)

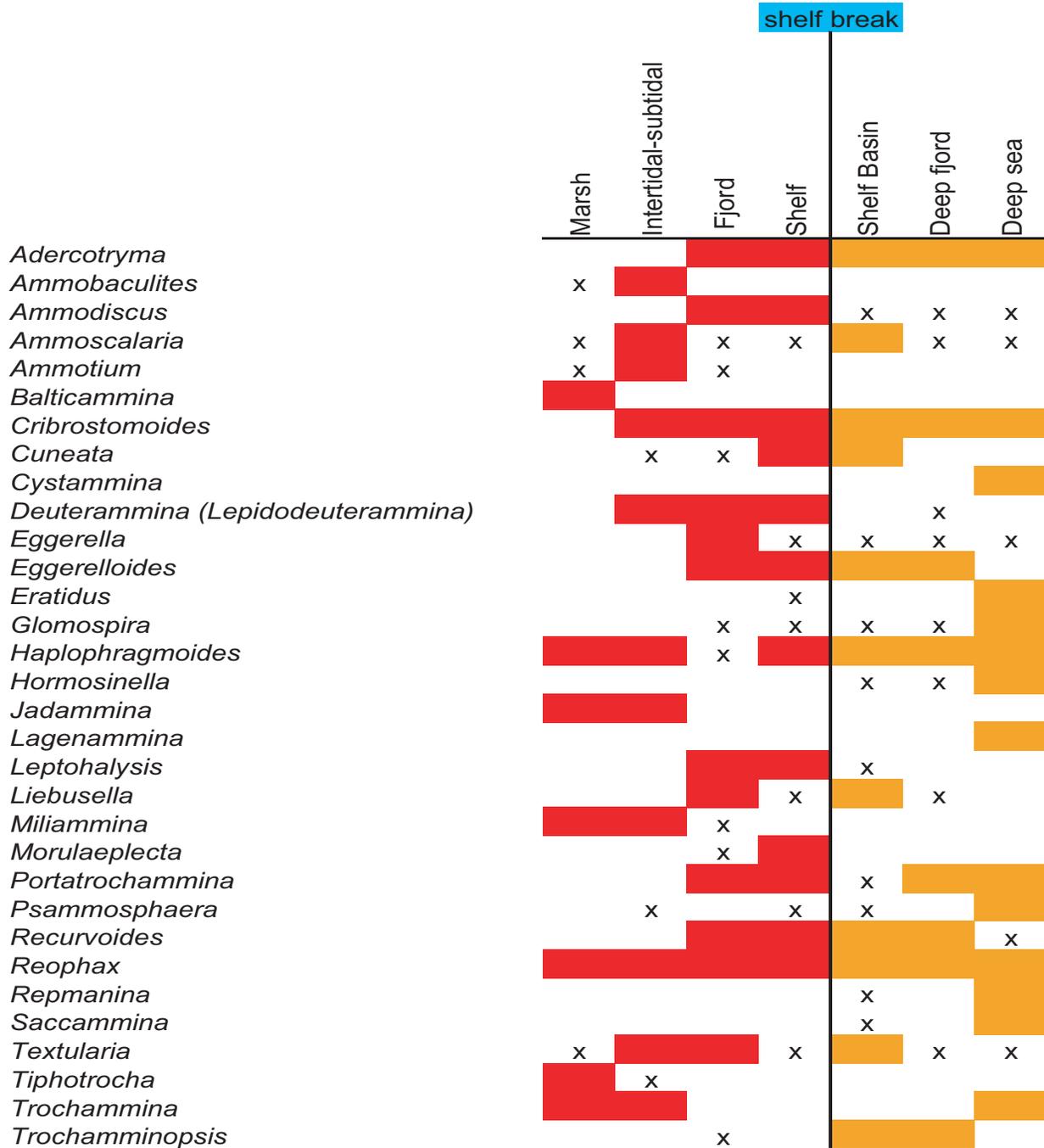


FIGURE 8. Distribution of ATA genera by environment, 1. Arranged alphabetically, 2. In order of occurrence. Red and orange = $\geq 10\%$; x = $< 10\%$. (x) indicates tests interpreted to be transported.

the relationship with broad environments is very clear (Figures 7, 8). Overall, the data show that even if only the agglutinated components of the assemblages from these areas are considered, their composition reflects differences in environmental characteristics.

The distributions of species and genera fail to reveal any clear depth-related boundaries but there is a progression in faunal change with increasing water depth from shore to deep sea (Figures 7-9). A similar environmental distribution of agglutinated foraminifera exists on the NW Atlantic margin (Schafer et al. 1981).

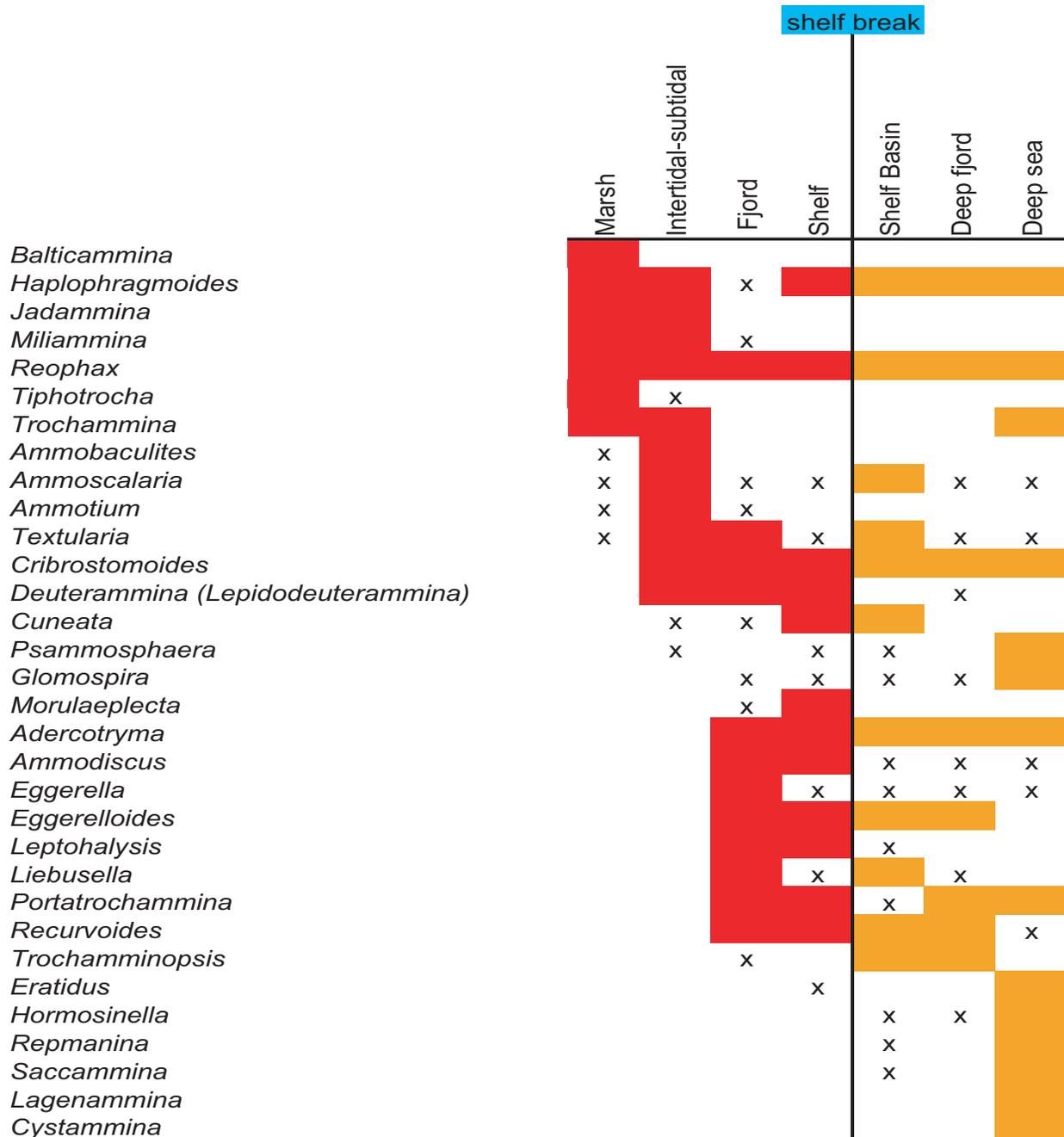


FIGURE 8 (continued). (Part 2.)

Figure 14 compares live distributions for the study area (based on Murray 2006, and web appendix tables 192-196 therein) with those described here for the main species in the ATAs. It should be noted that the relative abundance of agglutinated species is often low in live assemblages where they may be heavily outnumbered by calcareous forms. This partly accounts for the differences between live and ATA for fjord, shelf seas,

shelf deeps and deep fjord. Misidentifications may also widen the range of certain species (it is e.g., not likely that *Eggerelloides scaber* or *Trochammina inflata* live in the deep sea). It is immediately apparent that there is some localised transport of marsh taxa into adjacent intertidal flats (e.g., *Jadammina macrescens*), to a smaller extent, transport from intertidal flats onto marshes (e.g., *Textularia earlandi*), and downslope transport of

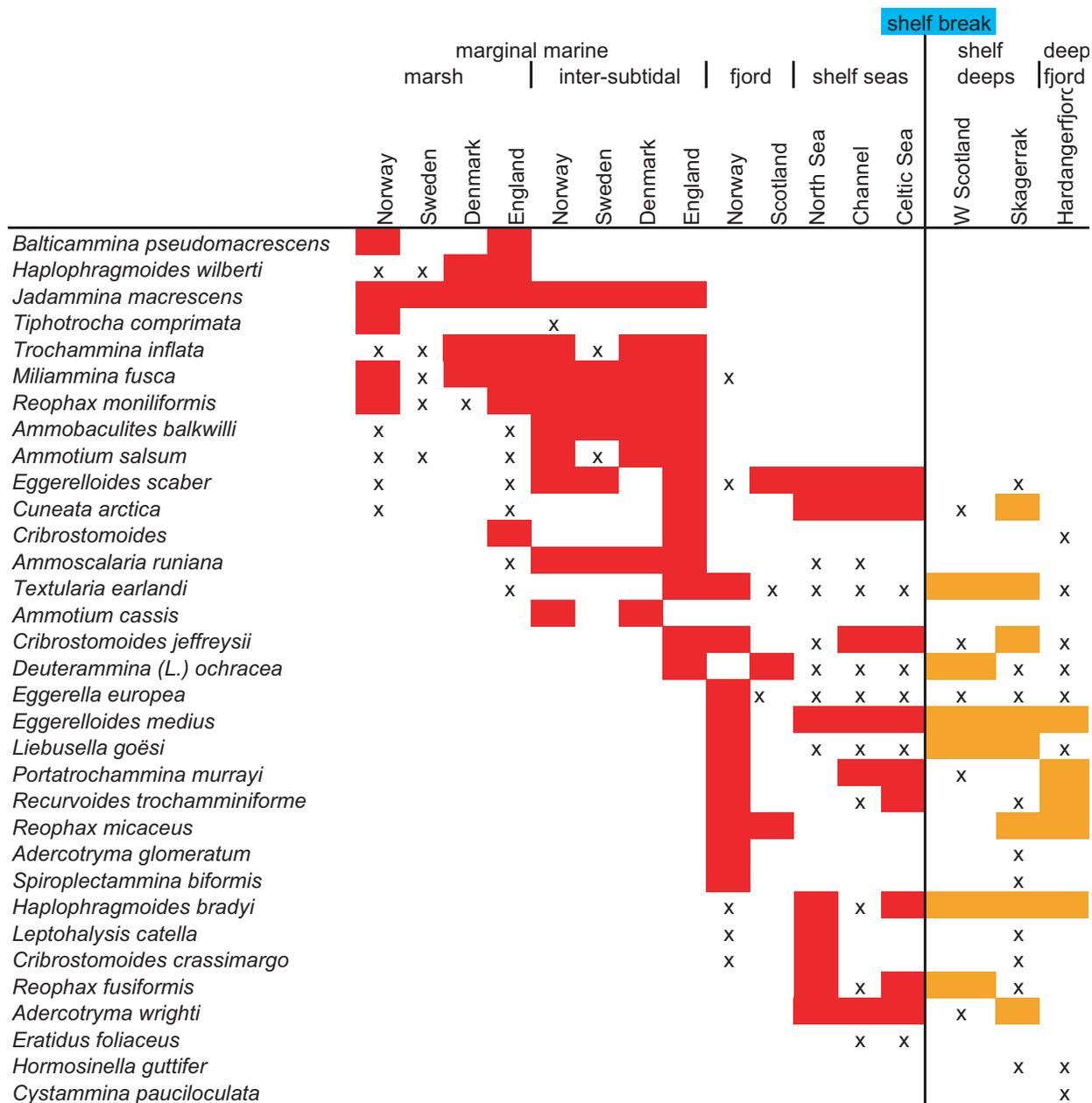


FIGURE 9. Geographic distribution of ATA taxa. Red and orange = $\geq 10\%$; x = $< 10\%$.

shelf taxa (Table 3). *Cribrostomoides jeffreysii* and *Deuterammina (L.) ochracea* are common in intertidal and fjord ATAs. The former has recently been recorded live along the Norwegian Skagerrak coast (Alve, unpublished data), otherwise they are yet not recorded living in the present study environments.

Balticammina pseudomacrescens, *Haplophragmoides wilberti*, *Jadammina macrescens* and *Trochammina inflata* are cosmopolitan species restricted to marshes (Murray 2006). In tidal areas these species show distinctive patterns of distribu-

tion that are controlled mainly by elevation but also by salinity (see Patterson 1990; De Rijk 1995). The marshes around the Skagerrak, Oslofjord and Kattegat are essentially non-tidal with water level changes due primarily to barometric pressure and wind stress. The difference in elevation between the marsh front and the landward limit is often only a few tens of cm. *Balticammina pseudomacrescens* occurs only on the landward and higher parts of the marsh with a cover of dry leaf litter indicating infrequent flooding (Murray and Alve 1999a). These marshes are very reliable indicators

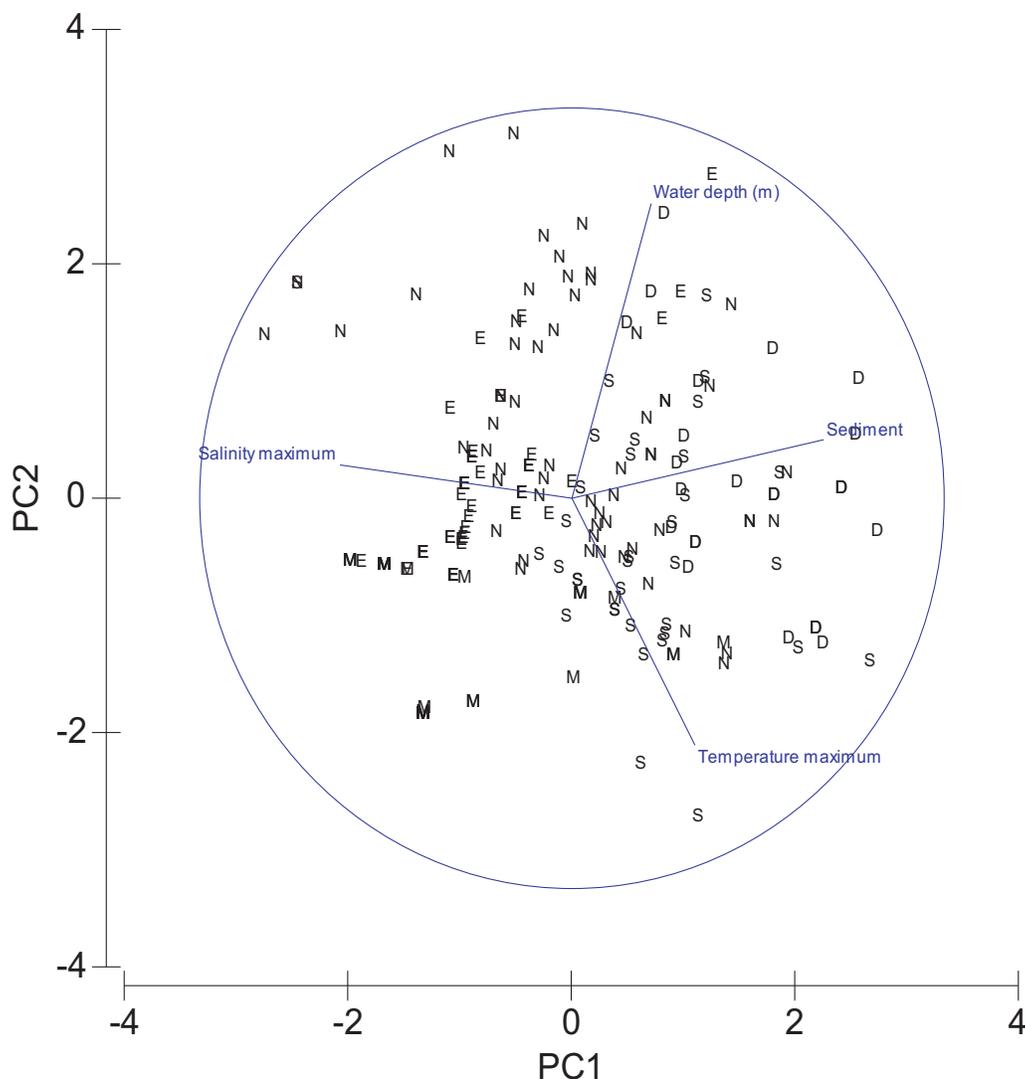


FIGURE 10. Principal component analysis of marginal marine environments. M = marsh for all areas; remainder intertidal-subtidal, N = Norway, S = Sweden, D = Denmark, E = England.

of the upper limit of sea level and probably also of salinity (Alve and Murray 1999a).

Although *Miliammina fusca* has a restricted distribution in our study area being confined to marsh, intertidal and to a lesser extent in shallow fjord (Figure 7) the genus *Miliammina* is also common in deep shelf sea environments off Antarctica (Murray and Pudsey 2004). Based on DNA analysis and wall structure, Habura et al. (2005) conclude that *Miliammina fusca* is descended from a calcareous miliolid. The wall structure is considered not to be typical of agglutinated taxa. However, from an ecological perspective it behaves like an agglutinated form.

Ammotium cassis is absent from Britain because of the absence of suitable non-tidal envi-

ronments. *Eggerella europeae* has not previously been reported living in the study area but recent data show it is common subtidally along the Norwegian Skagerrak coast (Alve, unpublished data). There are difficulties in distinguishing between *Reophax fusiformis* and *R. micaceus*, and this probably accounts for the disparity between the live and ATA distributions. The total (live plus dead) assemblages of Baffin Island fjords range in depth from ~215 to 708 m. They are ice covered for up to 10 months per year, and the bottom sediment is >85% silt plus clay. *Textularia earlandi* is dominant in fjords north of Lat. 68°N while *Spiroplectammina bififormis*, *Adercotryma glomeratum* (which may really be *A. wrighti* as their illustrations show only three chambers) and *Cuneata arctica* dominate in

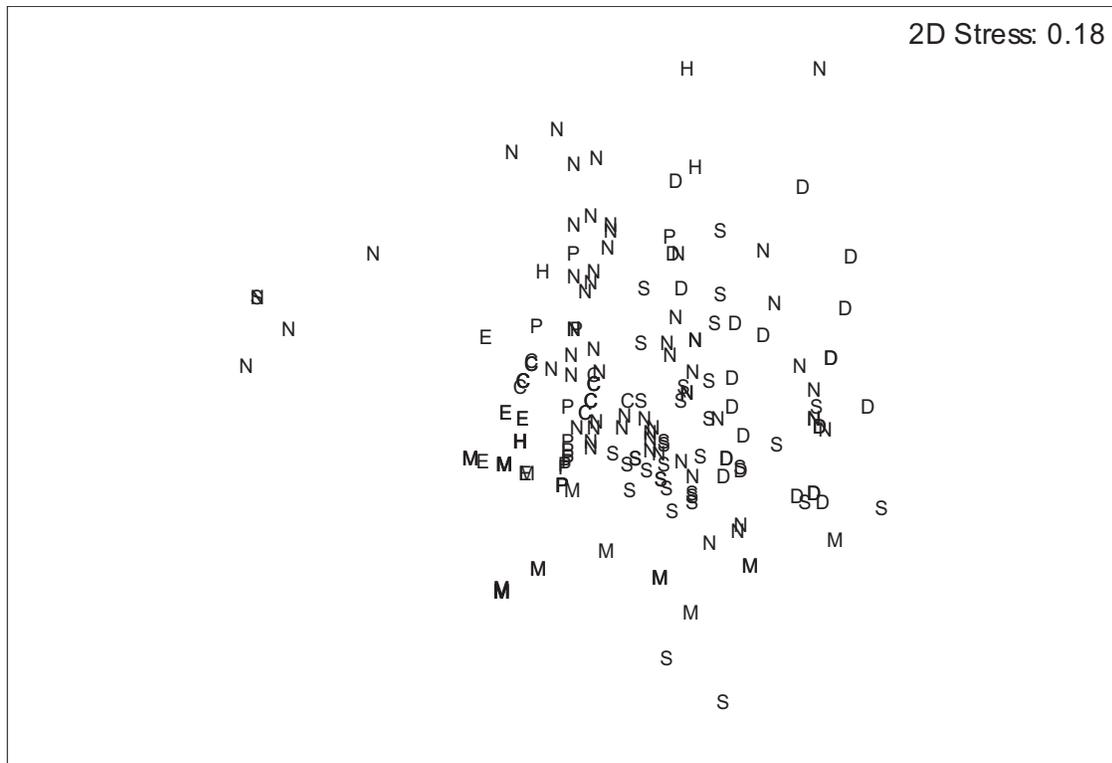


FIGURE 11. MDS plot of marginal marine environments. The data were normalised; resemblance based on Euclidian distance. See Figure 13 for locality details.

those fjords south of Lat. 70°N (Schafer and Cole 1986). Similarly, Corner et al. (1996) found live *Adercotryma glomeratum* and *Spiroplectammina biformis* to be indicative of inner fjord at depths of 26-124 m in Tana, Norway.

Hardangerfjord is of particular interest because although it reaches bathyal depths (850 m) its connection with true deep sea is across a continental shelf (<200 m) and also shallow sills (140 m) within the fjord system. Nevertheless, there are some living continental slope to deep-sea species present including *Ammolagena clavata*, *Ammoscalaria tenuimargo*, *Cribrostomoides subglobosus*, *Haplophragmoides sphaeriloculus*, *Hormosinella guttifer*, *Hyperammina laevigata*, *Lagenammina arenulata* and *Lagenammina tubulata*, and these were perhaps introduced as propagules (Alve et al. 2011). In the ATAs discussed here most are present at less than 5%, and the maximum for any species is 7%. From the estimated sea floor organic flux (2.5 gCm⁻² y⁻¹) this area is comparable with that of the continental slope.

On the Newfoundland, Canada, upper slope (500 m) live *Adercotryma glomeratum*,

Spiroplectammina biformis and *Cribrostomoides jeffreysii* are found in the seasonally variable, cold Labrador Current water mass while *Earlandamina bullata* (given as *Trochamminella*) are more common in mid-slope NADW and in mixed NADW and NSOW at 2000 m together with *Eratidus foliaceus* (given as *Ammomarginulina*) (Schafer and Cole 1982). According to Schmiedl et al. (1997) in the eastern South Atlantic live *Lagenammina*, *Psammosphaera* and *Reophax* are related to sandy sediments in areas of bottom currents but this is not obviously so in our study area.

A comparison of >150 µm stained (living) foraminifera in the axis of a Portuguese submarine canyon and those on the adjacent continental slope shows low standing crops (<30 individuals 10 cm⁻²) from 332-4969 m in the canyon, and higher values at 307 and 1000 m on the slope (140 and 40 individuals 10 cm⁻²) with just a few individuals at 4798 m. Arboresecent agglutinated taxa are more abundant on the slope and almost absent from the canyon except at 4969 m. The distributions in the canyon were attributed to harsh physical factors such as high bottom currents especially in the upper and middle canyon (Garcia et al. 2007).

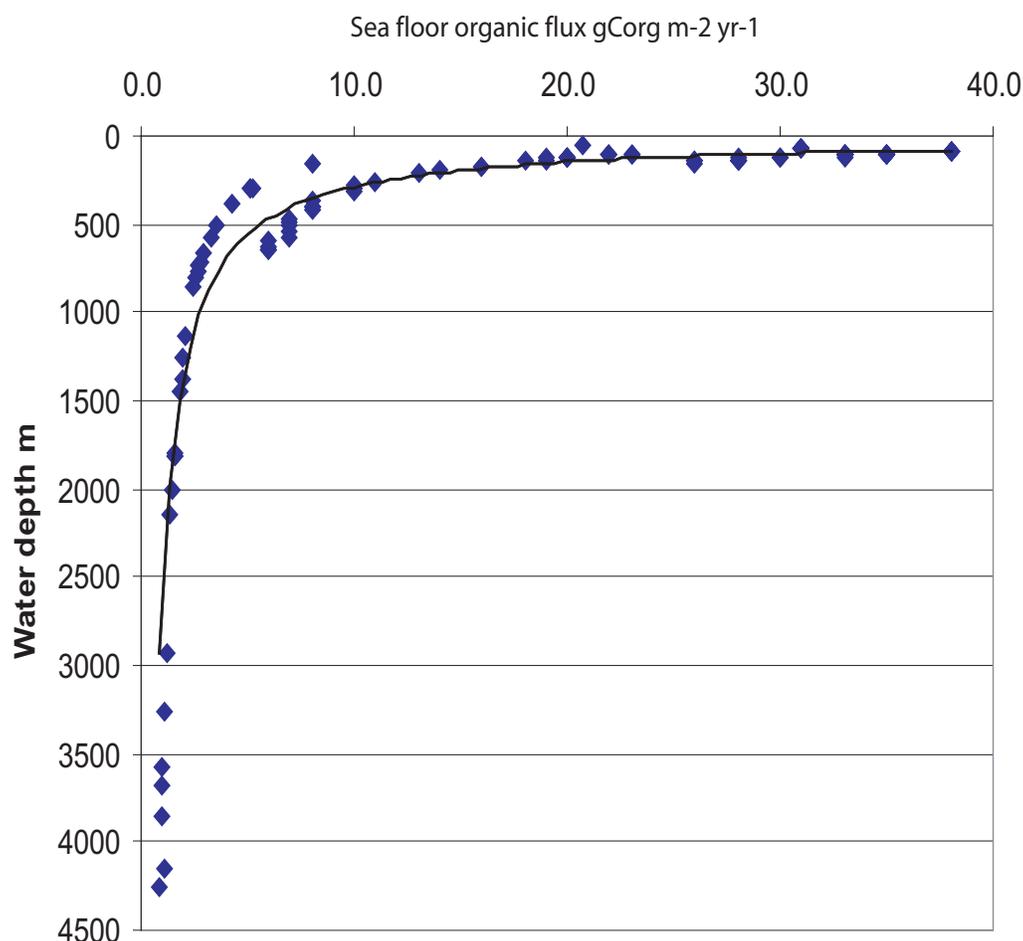


FIGURE 12. Correlation between water depth and sea floor organic flux.

Samples from terraces in the upper and middle canyon have larger standing crops dominated by calcareous infaunal species. The presence of fragile agglutinated taxa such as *Crithionina hispida* is taken as evidence of the absence of sediment disturbance by physical factors. The lower canyon faunas are more similar to those of the adjacent slope, dominated by agglutinated forms including *Reophax* and *Lagenamma* with low phytodetritus and most organic material present is refractory (Koho et al. 2007). According to Van der Zwaan et al. (1999) there is a correlation between uniserial agglutinated forms (their *Reophax* spp.) and Mn: remobilisation of Mn leads to reduced number of *Reophax*.

In 1985 Jones and Charnock proposed a morphogroup model based on samples from the UK continental margin, and this model has been widely

used for the interpretation of palaeoecology of ancient sediments. However, it is now known that the original model needs some revision, and the present large data set will provide an excellent opportunity to do this.

Relationships between Live, Dead and Acid-treated Assemblages

Where agglutinated foraminifera dominate living assemblages, as in some shallow water areas around the Skagerrak-Kattegat, the main species is the same in live, dead and acid-treated assemblages; for instance, dominance of *Balticamina pseudomacrescens*, *Haplophragmoides wilberti*, *Miliammina fusca* or *Jadammina macrescens* (Murray and Alve 1999b). However, in a few cases the living assemblage has a dominant species different from that of the dead and ATA, e.g., live

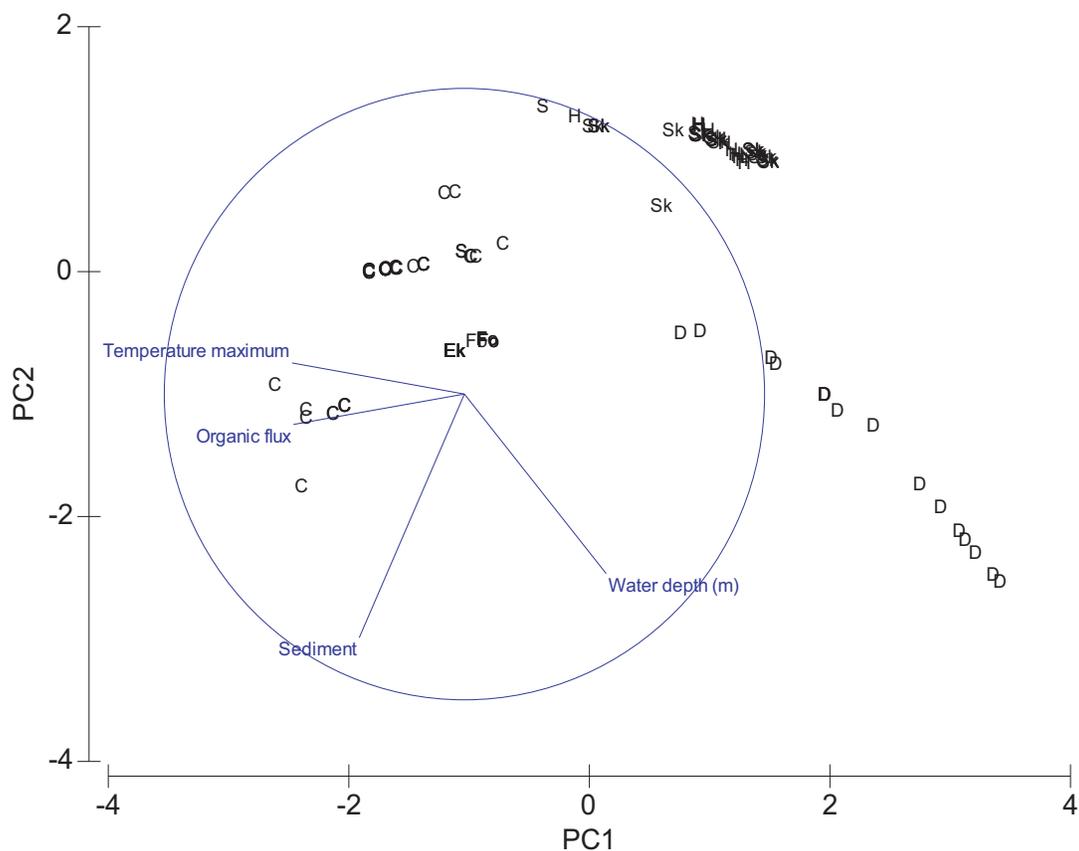


FIGURE 13. Principal component analysis of shelf to deep sea environments. C = Celtic Sea and Channel, N = North Sea, Ek = Ekofisk, Fo = Forties, Sk = Skagerrak, H = Hardangerfjord, D = deep sea.

dominant *Miliammina fusca* leading to *Jadammina macrescens* or *Trochammina inflata* dominated ODA or ATA. This is probably due to a bloom in the dominant living species at the time of sampling. In this same area, seven different calcareous ODAs give rise to *Miliammina fusca* ATAs making this the most ubiquitous shallow water species representing environments ranging from marsh edge to water depths of 6 m (limit of sampling) with a wide range of temperatures and salinities.

In the North Sea many living and dead assemblages are dominated by the opportunistic species *Stainforthia fusiformis*. Following dissolution, these give rise to a variety of ATAs dominated by: *Adercotryma wrighti* (given as *A. glomeratum*), *Cuneata arctica* (given as *Clavulina obscura*), *Eggerelloides medius* or *E. scaber*, *Morulaepecta bulbosa*, *Reophax fusiformis* or *Leptohalysis catella* (but the latter is unlikely to be well preserved due to its fragility, Alve and Murray 1995a). *Elphidium excavatum* ODAs give rise to *Eggerelloides scaber* ATAs. In the Skagerrak shelf deep *Pullenia osloensis* ODAs give rise to *Textularia earlandi* ATAs (given as *T. tenuissima*), *Stainforthia fusiformis* ODAs

give rise to one or other *T. earlandi*, *Eggerelloides medius*, *Haplophragmoides bradyi* or *Trochamminopsis quadriloba* ATAs (given as *T. pusillus*).

The English Channel and, to a lesser extent, the Celtic Sea both experience strong bottom currents. Consequently, many of the agglutinated taxa adopt a clinging or attached mode of life. Such forms comprise >70% of ATAs from the western Channel and >40% from the Western Approaches (areas of strong tidal currents) and lower values in those parts of the Celtic Sea least affected by such currents. Whereas there are three distinct inner shelf sea ODAs, they all give rise to a single *Eggerelloides scaber* ATA that Murray and Alve (2000a and 2000b) interpreted as indicating that the ODAs are better discriminators of subtle environmental differences than the ATAs in this instance. However, the more tranquil outer shelf sea areas each have distinctive ODAs, which are reasonably well preserved in the ATAs.

In the deep-sea NE Atlantic all the ODAs are essentially calcareous, and the dominant genus is *Cassidulina*. In the ATAs trochamminids are abundant ($\geq 30\%$) in the majority of samples. The situa-

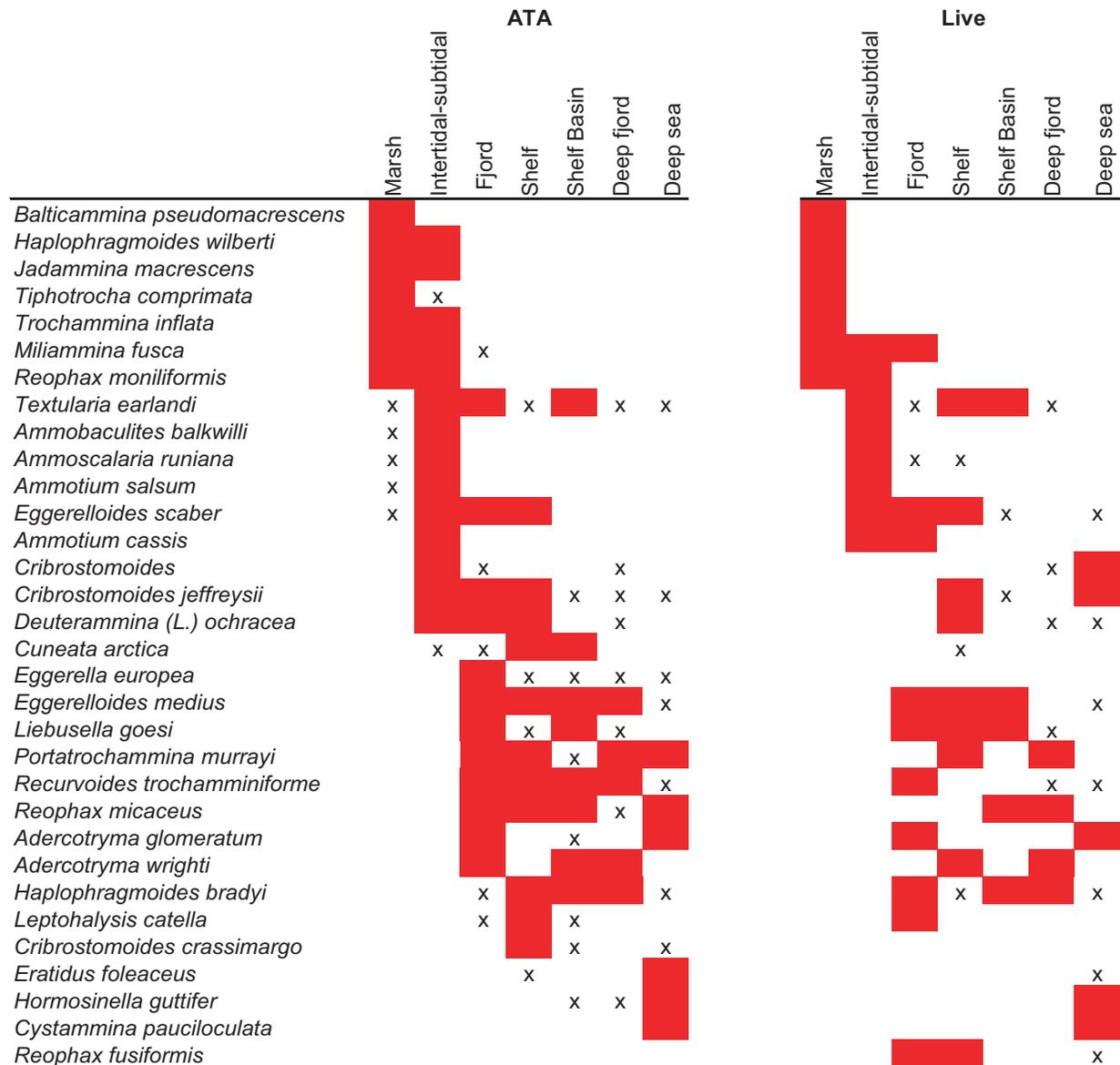


FIGURE 14. Comparison of live and ATA distributions in the NE Atlantic (live data based on Murray 2006). Red fields indicate abundance $\geq 10\%$; x = $< 10\%$.

tion is similar on the Newfoundland slope (Schafer et al. 1981). Genera occurring with localised abundances $> 10\%$ in the present deep sea samples include *Haplophragmoides*, *Reophax*, *Trochammina*, *Cribrostomoides*, *Psammosphaera*, *Glomospira*, *Adercotryma*, *Portatrochammina*, *Eratidus*, *Hormosinella*, *Repmanina*, *Saccammina*, *Lagenammina* and *Cystammina* (Figure 8.2). There is a broad pattern of distribution with respect to water depth. Tube fragments are most abundant on the continental slope and rise and sparse from the deeper basin. They are particularly abundant off

NW Africa that may be related to nutrient-rich upwelling (Murray and Alve 1994).

CONCLUSIONS

Acid treated assemblages of agglutinated foraminifera (ATAs) show patterns of species diversity that mimic those of the original dead assemblages (ODAs) and those of the living assemblages; all show a progression from low to high diversity with passage from marginal marine through shelf seas to deep sea.

There is a clear progression in the distribution of species and genera from marginal marine to

Table 4. Published SEM micrographs of species from the study area. A = Alve, M = Murray.

| Species | Published illustrations - SEM |
|--|---|
| <i>Adercotryma glomeratum</i> | M & A, 1994, pl. 1, fig 1 |
| <i>Adercotryma wrighti</i> | A & M, 1995a, pl. 1, figs 1, 2 (as <i>A. glomeratum</i>); M & A, 2000a, pl. 1, figs 1, 2; M, 2003a, figs 2.1, 2.2 |
| <i>Ammobaculites balkwilli</i> | M & A, 1999a, pl. 1, figs 1-5; M & A, 1999b, fig. 2I |
| <i>Ammoscalaria pseudospiralis</i> | M, 2003a, fig. 2.3 |
| <i>Ammoscalaria runiana</i> | M & A, 1999b, fig. 2M |
| <i>Ammotium cassis</i> | M & A, 1999b, fig. 2V |
| <i>Ammotium salsum</i> | M & A, 1999b, fig. 2J |
| <i>Balticammina pseudomacrescens</i> | M & A, 1999b, fig. 2A-C |
| <i>Buzasina ringens</i> | M & A, 1994, pl. 1, fig 2 |
| <i>Clavulina obscura</i> | A & M, 1995a, pl. 1, fig. 3 |
| <i>Cribrostomoides jeffreysii</i> | M & A, 1994, pl. 1, fig. 3; M & A, 2000a, pl. 1, figs 6-8; M, 2003a, fig.2.5 |
| <i>Cribrostomoides subglobosus</i> | M & A, 1994, pl. 1, figs 5, 6 |
| <i>Cribrostomoides</i> sp. A | M & A, 2000a, pl. 1, figs 9-12 |
| <i>Cribrostomoides</i> sp. | M & A, 1994, pl. 1, fig 4 |
| <i>Cuneata arctica</i> | M & A, 2000a, pl. 1, figs 13, 14; M, 2003a, fig. 2.6 |
| <i>Cystammina pauciloculata</i> | M & A, 1994, pl. 1, fig 7 |
| <i>Deuterammina (Deuterammina) rotaliformis</i> | M & A, 2000a, pl. 2, figs 21-23; M, 2003a, figs 2.7, 2.8 |
| <i>Eggerella europea</i> | M & A, 2000a, pl. 1, figs 15-17; M, 2003a, fig. 2.9 |
| <i>Eggerelloides medius</i> | A & M, 1995a, pl. 1, figs 4, 5; M & A, 2000a, pl. 2, figs 16-17; M, 2003a, fig. 2.10 |
| <i>Eggerelloides scaber</i> | A & M, 1995a, pl. 1, figs 6, 7; M & A, 1999b, Fig. 2K; M & A, 2000a, pl. 2, figs 14-15; M, 2003a, fig. 2.11 |
| <i>Eggerelloides</i> sp. | A & M, 1995a, pl. 1, figs 8, 9 |
| <i>Eratidus foliaceus</i> | M & A, 1994, pl. 1, fig 9 |
| <i>Glomospira gordialis</i> | M & A, 1994, pl. 1, fig 10 |
| <i>Haplophragmoides bradyi</i> | A & M, 1995a, pl. 1, figs 10, 11; M & A, 2000a, pl. 2, figs 9, 10; M, 2003a, figs 3.1, 3.2 |
| <i>Haplophragmoides sphaeriloculus</i> | M & A, 1994, pl. 1, fig 11 |
| <i>Haplophragmoides wilberti</i> | M & A, 1999b, fig. 2D, E |
| <i>Haplophragmoides</i> sp. 1 | M & A, 2000a, pl. 2, figs 7, 8 |
| <i>Haplophragmoides</i> sp. 2 | M & A, 2000a, pl. 2, figs 24, 25 |
| <i>Hormosinella distans</i> | M & A, 1994, pl. 1, fig 12 |
| <i>Jadammina macrescens</i> | M & A, 1999b, fig. 2D, F-H |
| <i>Karrerulina apicularis</i> | M & A, 1994, pl. 1, fig 13 |
| <i>Lagenammina micaceus</i> | M & A, 1994, pl. 1, fig 14 |
| <i>Leptohalysis catella</i> | A & M, 1995a, pl. 1, figs 12, 13 |
| <i>Liebusella goësi</i> | M & A, 2000a, pl. 1, fig 18; M, 2003a, fig. 3.3 |
| <i>Miliammina fusca</i> | M & A, 1999b, fig. 2L |
| <i>Morulaepecta bulbosa</i> | A & M, 1995a, pl. 1, figs 14, 15; M & A, 2000a, pl. 2, figs 18-20 (as <i>Textularia</i> sp.); M, 2003a, figs 3.4, 3.5 |
| <i>Paratrochammina (Lepidoparatrochammina) haynesi</i> | M & A, 1993, fig. 1-3 |
| <i>Portatrochammina murrayi</i> | M & A, 1994, pl. 1, fig. 21?; M & A, 2000a, pl. 2, figs 1-3; M, 2003a, figs 3.6, 3.7 |
| <i>Recurvoides trochamminiforme</i> | A & M, 1995a, pl. 1, figs 16-18; M & A, 2000a, pl. 2, figs 11-13; M, 2003a, figs 3.9, 3.10 |
| <i>Reophax fusiformis</i> | A & M, 1995a, pl. 1, fig. 19; M & A, 2000a, pl. 1, figs 5 |
| <i>Reophax micaceus</i> | A & M, 1995a, pl. 1, figs 20-21 |
| <i>Reophax moniliformis</i> | M & A, 1999a, pl. 1, figs 6-14; M & A, 1999b, fig. 2U |
| <i>Reophax scorpiurus</i> | M & A, 1994, pl. 1, fig 19 |
| <i>Repmanina charoides</i> | M & A, 1994, pl. 1, fig 20 |
| <i>Saccammina</i> sp. | A & M, 1995a, pl. 1, fig. 22 |

TABLE 4 (continued).

| Species | Published illustrations - SEM |
|-----------------------------------|---|
| <i>Textularia earlandi</i> | A & M, 1995a, pl. 1, fig. 23 (as <i>T. tenuissima</i>); M & A, 2000a, pl. 2, fig 6 (as <i>T. tenuissima</i>); M, 2003a, figs 3.15, 3.16 |
| <i>Tiphotrocha comprimata</i> | M & A, 1999b, fig. 2N-P |
| <i>Tritaxis britannica</i> | M & A, 2000a, pl. 2, figs 4, 5 |
| <i>Tritaxis fusca</i> | M & A, 2000a, pl. 1, figs 3, 4 |
| <i>Trochammina inflata</i> | M & A, 1999b, fig. 2Q-S |
| <i>Trochammina</i> sp. | M & A, 1994, pl. 1, fig 23 |
| <i>Trochamminopsis quadriloba</i> | A & M, 1995a, pl. 1, figs 24, 25 (as <i>T. pusillus</i>) |

deep sea but it is impossible to determine the precise controls on species distributions. ATAs sometimes show the localised effects of transport in which case species distributions are slightly broader than for their live counterparts. For instance, transport of marsh species onto adjacent tidal flats and vice versa. However, there is no evidence of widespread transport of agglutinated tests.

Although the genus *Miliammina* is confined to marginal marine environments in the study area, it occurs on the deep shelf sea off Antarctica so it is not exclusively an index of marginal marine environments.

As experimentally induced ATAs fill the no-analogue gap for modern environments (alternative 2), there is no need to invoke different ecological preferences for fossil taxa (alternative 1).

The data on species abundance, species diversity, distribution of species and genera with respect to environment and geography, provide comparative baselines for the interpretation of fossil agglutinated assemblages.

TAXONOMIC NOTES AND COMMENTS ON SPECIES ECOLOGY

For each species the name used is followed by the original name, with notes on taxonomy where appropriate. The generic scheme of Loeblich and Tappan (1987) has been followed except for trochamminids. This list is arranged in the same order as the illustrations. Many species are illustrated in Figures 15 (mainly marginal marine taxa), 16-18 (shelf sea, shelf deep and fjord taxa) and 19 (deep sea taxa); SEM illustrations from our previous studies are listed in Table 4.

The geographical and environmental distribution of many species (marked with **) in our data set is given in Figures 7-9 so the details are not repeated here. However, for the less common species the statement concluding with * refers to the ATA distribution recorded in this study. Relative

abundance terms: rare = occasional occurrence; minor = commonly present in abundance <10%; common \geq 10%; dominant = the most abundant species in the assemblage. All other referenced ecological comments are based on live (stained) occurrences in the study area (NE Atlantic) unless otherwise specified. Where the notes on species ecology are from Murray (2006) they include references cited therein.

Mainly Brackish Marginal Marine Taxa

Ammobaculites balkwilli Haynes, 1973.
Figure 15.1**.

Restricted to Europe; mainly low intertidal to subtidal; salinity 15-29 around the Skagerrak-Kattegat (Alve and Murray 1999).

Ammoscalaria runiana (Heron-Allen and Earland) = *Haplophragmium runianum* Heron-Allen and Earland, 1916. Figure 15.2-5**.

Intertidal-subtidal; common only in fine to medium sand with <20% mud and low TOC (0.2-0.7%); salinity 16-18 (Alve and Murray 1999).

Ammotium cassis (Parker) = *Lituola cassis* Parker, 1870. Figure 15.6 (specimen metal coated)**.

Infauunal detritivore lying horizontally in the top 5 cm of sediment; in brackish marginal marine environments, in the transitional water layer and possibly indicating the halocline; always subtidal; reproduces at <8°C (Olsson, 1976; Murray 2006).

Ammotium salsum (Cushman and Brönnimann) = *Ammobaculites salsus* Cushman and Brönnimann, 1948**.

Infauunal down to 10 cm, detritivore; marshes; withstands salinities of 60 (Murray 2006).

Balticamina pseudomacrescens Brönnimann, Lutze and Whittaker, 1989**.

Epifaunal; characteristic of low-salinity, brackish high marsh closest to land (Murray 2006).

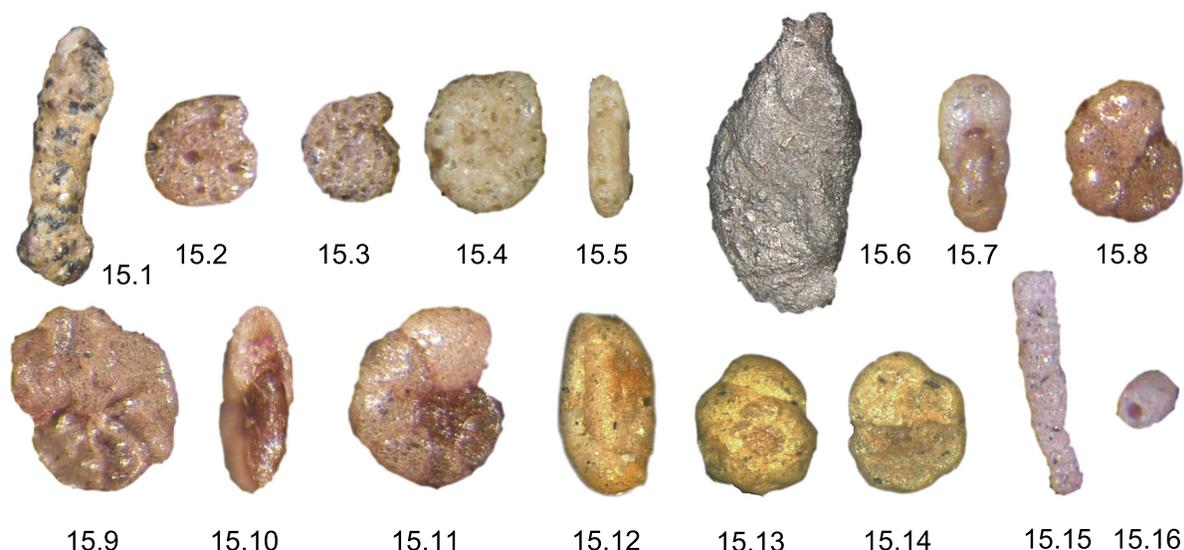


FIGURE 15. Mainly marginal marine taxa. The dimensions refer to the length or greatest diameter according to shape. # = sample number. The type specimens are housed in the Natural History Museum, London. 15.1 *Ammobaculites balkwilli* Haynes, 1973, Holotype 1970:11:26:16, 600 μm . 15.2 *Ammoscalaria runiana* (Heron-Allen and Earland) #S145, Kungsbackafjord, Sweden, 200 μm , 15.3 #P10-95, Poole Harbour, England, 200 μm , 15.4, 5 *Ammoscalaria runiana* (Heron-Allen and Earland) = *Haplophragmium runianum* Heron-Allen and Earland, 1916, Syntype 1955:19:24:25-39, 300, side and apertural views. 15.6 *Ammotium cassis* (Parker) = *Lituola cassis* Parker, 1870, Lectotype ZF4637, (metal coated) size not available as specimen was subsequently damaged. 15.7, 8 *Haplophragmoides wilberti* Andersen #S126, Kalundborg, Sweden, 255, 310 μm . 15.9-11 *Jadammina macrescens* (Brady) #S124, Kalundborg, Sweden, 420, 330, 330 μm . 15.12 *Miliammina fusca* (Brady) = *Quinqueloculina fusca* Brady, 1870 Syntype 1955:10:28:67-106, 450 μm (previously gold-coated). 15.13, 14 *Paratrochammina* (*Lepidoparatrochammina*) *haynesi* (Atkinson) = *Trochammina haynesi* Atkinson, 1969 Holotype 1968:5:16:1, 360 μm (previously gold-coated). 15.15, 16 *Reophax moniliformis* Siddall #S64, Hafstensfjord, Sweden, 15. 600 μm , apertural view 125 μm .

Haplophragmoides wilberti Anderson, 1953. Figure 15.7, 8**.

Epifaunal and infaunal down to 30 cm; marshes (Murray 2006)

Jadammina macrescens (Brady) = *Trochammina inflata* (Montagu) var. *macrescens* Brady, 1870. Figure 15.9-11**.

Epifaunal, sometimes on decaying leaves, and infaunal down to 60 cm; herbivore or detritivore; widespread on high to mid marsh (Murray 2006).

Miliammina fusca (Brady) = *Quinqueloculina fusca* Brady, 1870. Figure 15.12**.

Epifaunal or infaunal down to 50 cm in marshes; intertidal to shallow subtidal in brackish waters (Murray 2006). The last survivor in marine environments that are cut off from the sea perhaps due to being infaunal (Lloyd and Evans 2002).

Paratrochammina (*Lepidoparatrochammina*) *haynesi* (Atkinson) = *Trochammina haynesi* Atkinson, 1969. Figure 15.13, 14.

Occasionally common in subtidal marginal marine*. Attached on gravel and shells, in the protection of crevices or ribs; current-swept areas such as channels (Murray and Alve 1993; Murray 2006).

Reophax moniliformis Siddall, 1886. Figure 15.15, 16*.

Detritivore on plant debris; husband chloroplasts; intertidal to subtidal in brackish environments (Murray 2006).

Tiphrotracha comprimata (Cushman and Brönnimann) = *Trochammina comprimata* Cushman and Brönnimann, 1948**.

Epifaunal, free or clinging to algae, and infaunal down to 42 cm; herbivore or detritivore; marshes (Murray 2006).

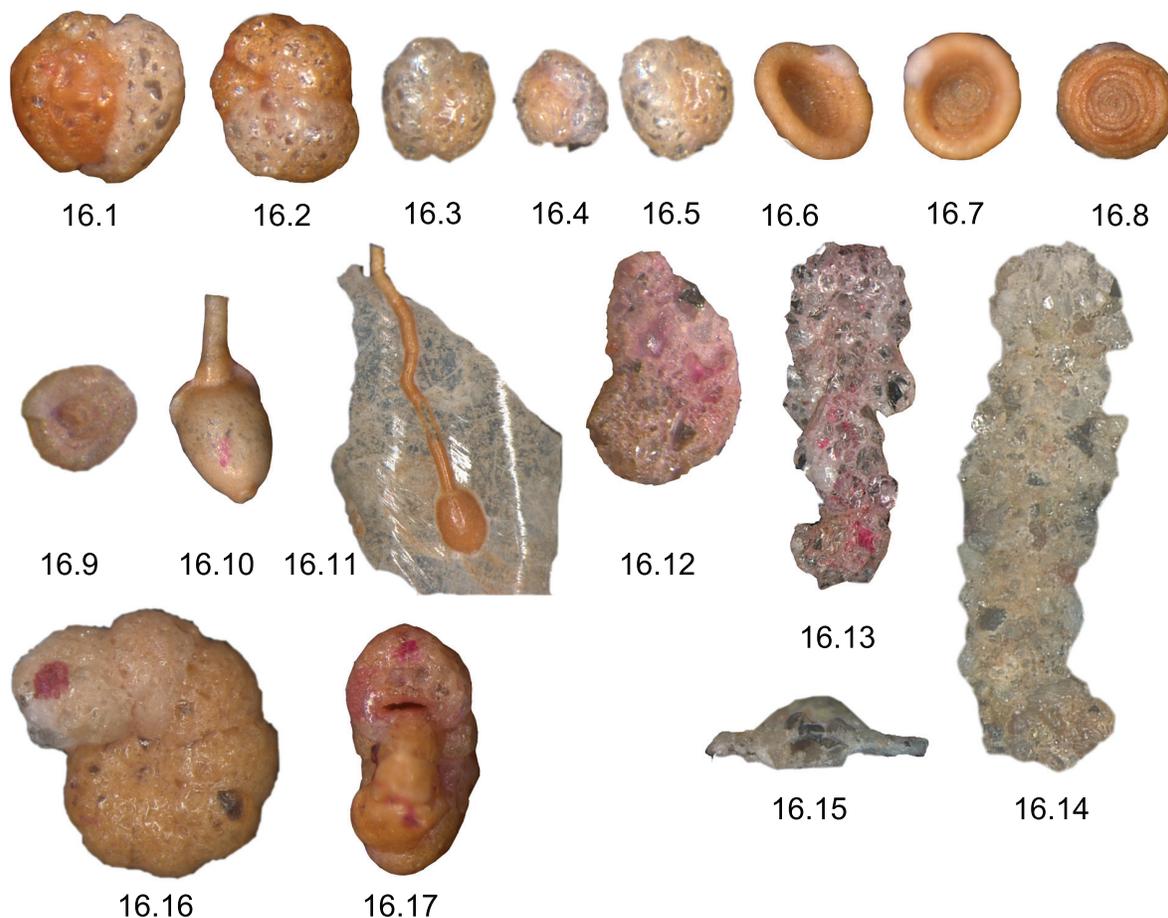


FIGURE 16. Shelf sea, shelf deep and fjord taxa. The dimensions refer to the length or greatest diameter according to shape. # = sample number. The type specimens are housed in the Natural History Museum, London. 16.1, 2 *Adercotryma glomeratum* (Brady) #69-92, Skagerrak, side view 200 μm , end view 290 μm . 16.3-5 *Adercotryma wrighti* Brönnimann and Whittaker #Md6b, Muck Deep, Scotland, 120 μm , end and side views. 16.6-8 *Ammodiscus catinus* Höglund #SK168, Skagerrak, 164, 200, 255 μm . 16.9 *Ammodiscus gullmarenensis* Höglund #3117, North Sea, 200 μm . 16.10 *Ammolagena clavata* (Jones and Parker) #SK57, Skagerrak, 475 μm . 16.11 *Ammolagena clavata* (Jones and Parker) = *Trochammina irregularis* (d'Orbigny) var. *clavata* Jones and Parker, 1860, Lectotype ZF4873, 1800 μm . 16.12 *Ammoscalaria pseudospiralis* (Williamson) #1460, English Channel, 820 μm . 16.13 *Ammoscalaria tenuimargo* (Brady) #69-92, Skagerrak, 1400 μm . 16.14, 15 *Ammoscalaria tenuimargo* (Brady) = *Haplophragmium tenuimargo* Brady, 1884, Syntype ZF1554, 2300 μm , side and apertural views. 16.16, 17 *Cribrostomoides crassimargo* Norman #69-92, Skagerrak, 820, 900 μm .

Trochammina inflata (Montagu) = *Nautilus inflatus* Montagu, 1808**.

Epifaunal and infaunal down to 60 cm; herbivore or detritivores, mid marsh (Murray 2006).

Shelf Sea, Shelf Deep and Fjord Taxa

Adercotryma glomeratum (Brady) = *Lituola glomerata* Brady, 1878. Figure 16.1-2**.

Prior to 1987 adult tests with three or four chambers in the final whorl were included in this species

but in that year Brönnimann and Whittaker erected a new species (*A. wrighti*) for those with three chambers.

Infaunal - epifaunal; a negative correlation with TOC but tolerates a wide range of temperature 1.8-16.6°C in Gulf of Guinea (Timm 1992). However, in the Arctic Ocean it favours temperatures of 1.8-3.0°C (Williamson et al. 1984). Inhabits the phyto-detritus layer and sediment (Gooday 1988). It moves up and down in sediment seasonally: phyto-

detritus feeder in spring, shallow infaunal for the remainder of the year (Kuhnt et al. 2000).

Adercotryma wrighti Brönnimann and Whittaker, 1987. Figure 16.3-5**.

Ammodiscus catinus Höglund, 1947. Figure 16.6-8.

Rare in shallow fjord, shelf, shelf deeps*.

Ammodiscus gullmarensis Höglund, 1948. Figure 16.9.

Occasionally common but mainly rare in shallow fjord, shelf, shelf deeps*. Brackish, salinity 20-32; temperature 4-14°C, on organic-rich muddy sediment, dominant in deeper water close to the permanently anoxic layer, in Norwegian fjords (Alve 1995).

Ammolagena clavata (Jones and Parker) = *Trochammina irregularis* (d'Orbigny) var. *clavata* Jones and Parker, 1860. Figure 16.10, 11.

Rare in Shelf deeps, deep sea*. Sea floor organic flux 0.8-60 g m² yr⁻¹ (Altenbach et al. 1999).

Ammoscalaria pseudospiralis (Williamson) = *Proteonina pseudospiralis* Williamson, 1858. Figure 16.12. More mature specimens have a longer uniserial part.

Rare in shallow fjord, shelf, and common in shelf deeps*. Infaunal in top 1 cm (Barmawidjaja et al. 1992). Sea floor organic flux 7->100 g m² yr⁻¹ (Altenbach et al. 1999).

Ammoscalaria tenuimargo (Brady) = *Haplophragmium tenuimargo* Brady, 1882. Figure 16.13-15.

Rare in shallow fjord and deep sea, occasionally common in shelf deeps*.

Cribrostomoides crassimargo (Norman) = *Haplophragmium crassimargo* Norman, 1826. Figure 16.16, 17**.

Cribrostomoides jeffreysii (Williamson) = *Nonionina jeffreysii* Williamson, 1858. Figure 17.1-4**.

In #2070 there are smaller tests with a shiny surface and finer texture than the typical *C. jeffreysii* yet in other respects the morphology is the same. Tests with more mica are grey, and brown with no mica. We had considered using the name *C. kostensis* but it was impossible to consistently separate the two. In Murray and Alve (2000a) we separated off *Cribrostomoides* sp. A but now that we have seen a larger data set we realise that it is not possible to consistently separate sp. A from *C. jeffreysii*.

Infaunal to epifaunal, attached mobile (Murray 2006).

Cribrostomoides nitidus (Goës) = *Haplophragmium nitidum* Goës, 1896. Figure 17.5, 6.

Rare in shelf deeps, deep fjord, deep sea*.

Cribrostomoides subglobosus (Sars) = *Lituola subglobosa* Sars, 1868. Figure 17.7, 8**.

Epifaunal – infaunal, detritivore (Murray 2006). Sea floor organic flux 0.2-90 g m² yr⁻¹ (Altenbach et al. 1999). Linke (1989) suggested that the species entered a resting phase when food was in short supply and responded quickly to phytodetritus input.

Cuneata arctica (Brady) = *Reophax arctica* Brady, 1881. Figure 17.9**.

The range of morphology of *Clavulina obscura* Chaster seems to overlap that of this species. See Alve and Goldstein (2010) for further comments on synonymy.

Deuterammina (Deuterammina) balkwilli Brönnimann and Whittaker, 1983.

Minor in deep fjord*.

Deuterammina (Deuterammina) rotaliformis (Heron-Allen and Earland) = *Trochammina rotaliformis* Heron-Allen and Earland, 1911.

Rare in shelf, shelf deeps*.

Deuterammina plymouthensis Brönnimann and Whittaker, 1990.

Minor in shelf deep*.

Deuterammina (Lepidodeuterammina) ochracea (Williamson) = *Rotalina ochracea* Williamson, 1858. Figure 17.10, 11**.

Epifaunal, attached mobile (Murray 2006).

Earlandammina bullata (Höglund) = *Trochammina bullata* Höglund, 1947. Figure 17.12, 13.

Brönnimann and Whittaker (1988) treat this as a synonym of *E. inconspicua* (Earland). However, that species is tiny and has a thin fragile wall – quite unlike our material or that of Höglund.

Occasionally common in shelf deeps, minor in deep fjord and deep sea*.

eggerella europea (Christiansen) = *Verneuilina europeum* Christiansen, 1958, new name for *Verneuilina advena* Cushman of Höglund, 1947. Figure 17.14, 15**.

#3234 has a few specimens that have a terminal biserial section.



FIGURE 17. Shelf sea, shelf deep and fjord taxa. The dimensions refer to the length or greatest diameter according to shape. # = sample number. The type specimens are housed in the Natural History Museum, London. 17.1, 2 *Cribrostomoides jeffreysii* (Williamson) #SK66, Skagerrak, 310 μm . 17.3, 4 *Cribrostomoides jeffreysii* (Williamson) = *Nonionina jeffreysii* Williamson, 1858 Syntype 96:8:13:14, 370 μm , side and apertural views. 17.5, 6 *Cribrostomoides nitidus* (Goës) #SK63, Skagerrak, 475, 290 μm . 17.7, 8 *Cribrostomoides subglobosus* (Sars) #SK68, Skagerrak, 455, 380 μm . 17.9 *Cuneata arctica* (Brady) #SK65, Skagerrak, 235 μm . 17.10, 11 *Deuterammina (Lepidodeuterammina) ochracea* (Williamson) = *Rotalina ochracea* Williamson, 1858 Lectotype ZF4837, 180 μm . 17.12, 13 *Earlandammina bullata* (Höglund) #SK57, Skagerrak, 240, 240 μm . 17.14, 15 *Eggerella europea* Christiansen #3117, North Sea, 300 μm . 17.16 *Eggerelloides medius* (Höglund) #SK68, Skagerrak, 365 μm . 17.17, 18 *Eggerelloides scaber* (Williamson) = *Bulimina scabra* Williamson, 1858 Syntype 96:8:13:30, both 650 μm . 17.19 *Gaudryina pseudoturris* (Cushman) #SK57, Skagerrak, 1055 μm . 17.20 *Glomospira gordialis* (Jones and Parker) #72-92, Skagerrak, 130 μm . 17.21 *Glomospira gordialis* (Jones and Parker) = *Trochammina squamata* var. *gordialis* Jones and Parker, 1860 Lectotype ZF4876, 300 μm . 17.22, 23 *Haplophragmoides bradyi* (Robertson) #SK67, Skagerrak, 290 μm . 17.24, 25 *Haplophragmoides bradyi* (Robertson) = *Trochammina bradyi* Robertson, 1891 Syntype 62:2:14:467-502, 230 μm . 17.26, 27 *Haplophragmoides membranaceum* (Höglund) #SK67, Skagerrak, 90 μm . 17.28, 29 *Haplophragmoides* sp. 1 #2203, Western Approaches, England, 220, 220 μm .

Eggerelloides medius (Höglund) = *Verneuilina media* Höglund, 1947. Figure 17.16**.

Infaunal, positive correlation with % TOC and to a lesser extent with % <63 µm sediment; a strong negative correlation with grain size >1000 µm (Murray 2006).

Eggerelloides scaber (Williamson) = *Bulimina scabra* Williamson, 1858. Figure 17.17, 18**.

Infaunal, detritivore, subtidal, mainly shelf but tolerates salinity >24 for most of the year and temperatures 1-20°C (Murray et al. 2003; Murray 2006).

Gaudryina pseudoturris (Cushman) = *Textularia pseudoturris* Cushman, 1922. Figure 17.19.

Rare in shelf basin and deep sea*.

Glomospira glomerata Höglund, 1947.

Minor in fjord*.

Glomospira gordialis (Jones and Parker) = *Trochammina squamata* var. *gordialis* Jones and Parker, 1860. Figure 17.20, 21**.

Shallow infaunal (Kuhnt et al. 2000). Sea floor organic flux 11-25 g m² yr⁻¹ (Altenbach et al. 1999).

Haplophragmoides bradyi (Robertson) = *Trochammina bradyi* Robertson, 1891. Figure 17.22-25**.

Shallow infaunal (Gooday 1990; Kuhnt et al. 2000).

Haplophragmoides membranaceum Höglund, 1947. Figure 17.26, 27.

Minor in shelf deeps, deep fjord, deep sea*.

Haplophragmoides sp. 1. Figure 17.28, 29.

Light brown yellowish, shiny, 4-5 chambers, flat.

Rare in shelf, deep fjord*.

Haplophragmoides sp. hetta (helmet) because of the large final chamber. Figure 18.1, 2.

We have not found a species name for this.

Rare in fjords, shelf and deep sea*.

Lagenammia tubulata (Rhumbler) = *Saccammia tubulata* Rhumbler, 1931. Figure 18.3.

Minor in shelf basin, deep fjord, deep sea*.

Leptohalysis catella (Höglund) = *Reophax catella* Höglund, 1947. Figure 18.4**.

Leptohalysis catenata (Höglund) = *Reophax catenata* Höglund, 1947.

Minor in fjord and shelf*.

Leptohalysis gracilis (Kiaer) = *Reophax gracilis* Kiaer, 1900.

Minor in fjord, shelf basin, deep fjord*.

Leptohalysis scottii (Chaster) = *Reophax scottii* Chaster, 1892. Figure 18.5.

Fjord, shelf, shelf basin, deep fjord*. Under experimental conditions, lives in the top cm of sediment, responds quickly to disturbance and is very active, thus avoiding hostile environmental conditions, and is considered to be a good competitor (Ernst et al. 2000).

Liebusella goesi Höglund, 1947. Figure 18.6**.

Sea floor organic flux 7-90 g m² yr⁻¹ (Altenbach et al. 1999).

Morulaeplecta bulbosa Höglund, 1947. Figure 18.7.

Occasionally common in shelf, rare in shelf basin*. Infaunal in top cm (Barmawidjaja et al. 1992).

Paratrochammina (*Lepidoparatrochammina*) *harti* Brönnimann and Whittaker, 1990.

Minor in shelf deeps*.

Paratrochammina (*Paratrochammina*) *wrighti* Brönnimann and Whittaker, 1983.

Minor in shelf*.

Portatrochammina murrayi Brönnimann and Zaninetti, 1984. Figure 18.8-10**.

The same as *Trochammina globigeriniformis* var. *pygmaea* of authors – including papers by Murray.

Psammosphaera bowmani Heron-Allen and Earland, 1912. Figure 18.11.

Minor in fjord and shelf*. Common just below the surface brackish layer in inner Drammensfjord, Norway (Alve 1990).

Psammosphaera fusca Schultze, 1875. Figure 18.12**.

Common in lower canyon at depths of 4810-4976 m off Portugal (Koho et al. 2007).

Recurvoides trochamminiforme Höglund, 1947. Figure 18.13, 14**.

Recurvoides turbinatus (Brady) = *Haplophragmium turbinatum* Brady, 1881.

Minor in fjord*.

Remaneica anglica Brönnimann and Whittaker, 1990.

Minor in shelf*.

Remaneica helgolandica Rhumbler, 1938.

Minor in fjord and shelf*.

Remaneica plicata (Terquem) = *Patellina plicata* Terquem, 1876.

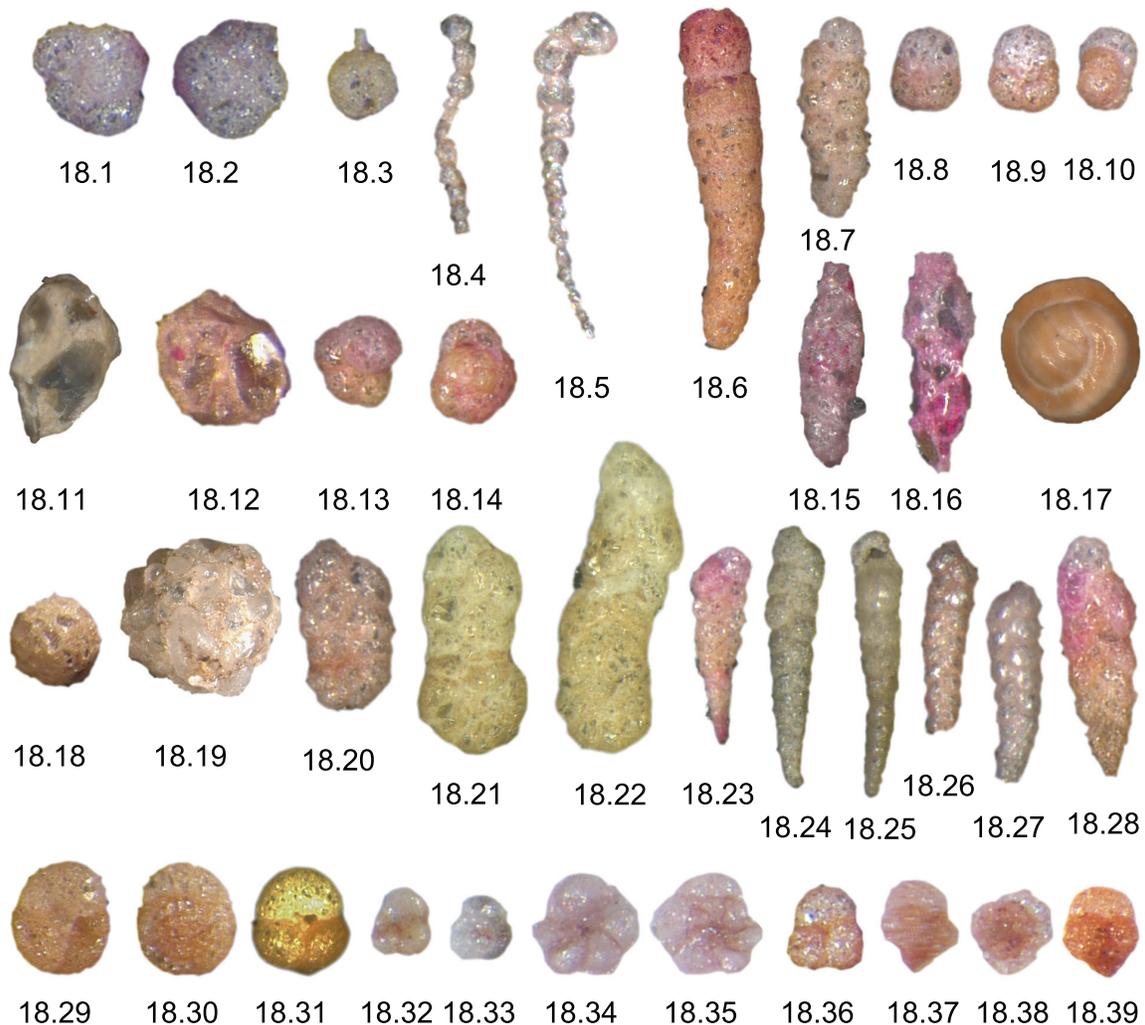


FIGURE 18. Shelf sea, shelf deep and fjord taxa. The dimensions refer to the length or greatest diameter according to shape. # = sample number. The type specimens are housed in the Natural History Museum, London. 18.1, 2 *Haplophragmoides* sp. hetta #YL12, Lyngdalsfjord, Norway, specimen lost. 18.3 *Lagenammia tubulata* (Rhumblér) #SK62, Skagerrak, 180 μm . 18.4 *Leptohalysis catella* (Höglund) #SK66, Skagerrak, 400 μm . 18.5 *Leptohalysis scottii* (Chaster) #SK65, Skagerrak, 655 μm . 18.6 *Liebusella goesi* Höglund #SK65, Skagerrak, 1910 μm . 18.7 *Morulaeplecta bulbosa* Höglund #Md6a, Muck Deep, Scotland, 400 μm . 18.8-10 *Portatrochammina murrayi* Brönnimann and Zaninetti, #Md6a, Muck Deep, Scotland, 145 μm . 18.11 *Psammosphaera bowmani* Heron-Allen and Earland, 1912 Syntype 1957:11:14:93, 620 μm . 18.12 *Psammosphaera fusca* Schultze #3453, North Sea, 240 μm . 18.13, 14 *Recurvoides trochamminiforme* Höglund #69-92, Skagerrak, 180, 165 μm . 18.15 *Reophax fusiformis* (Williamson) #SK67, Skagerrak, 600 μm . 18.16 *Reophax micaceus* (Cushman) #SK67, Skagerrak, 400 μm . 18.17 *Repmanina charoides* (Jones and Parker) #SK57, Skagerrak, 420 μm . 18.18 *Saccamina socialis* Brady #SK57, Skagerrak, 290 μm . 18.19 *Saccamina sphaerica* Sars #2894, North Sea, 1275 μm . 18.20 *Spiroplectammia biformis* (Jones and Parker) #72-92, Skagerrak, 220 μm . 18.21, 22 *Spiroplectammia biformis* (Parker and Jones) = *Textularia agglutinans* d'Orbigny var. *biformis* Jones and Parker, 1865 Lectotype ZF3639, 370 μm , Paralectotype ZF3638, 500 μm . 18.23 *Textularia earlandi* Parker SK65, Skagerrak, 345 μm . 18.24, 25 *Textularia earlandi* Parker = new name for *Textularia tenuissima* Earland, 1933 Syntype ZF3518, 400 μm , 380 μm showing aperture. 18.26, 27 *Textularia kattedgatensis* (Höglund) #72-92, Skagerrak, 310, 330 μm . 18.28 *Textularia skagerakensis* Höglund #2895, North Sea, 380 μm . 18.29, 30 *Tritaxis britannica* Brönnimann and Whittaker #2203, Western Approaches, England 280 μm . 18.31 *Tritaxis conica* (Parker and Jones) = *Valvulina triangularis* d'Orbigny var. *conica* Parker and Jones, 1865 Syntype ZF3529, 170 μm (specimen gold-coated). 18.32-35 *Trochammina* sp. skrumpa #12-96, Skagerrak, 180 μm . 18.36-39 *Trochamminopsis quadriloba* Höglund #1-96, Hardangerfjord, Norway, 36-38 150 μm , 39 165 μm , (39 Höglund material from Gullmar Fjord).

Minor in shelf*.

Remaneicella gonzalezi (Seiglie) = *Remaneica gonzalezi* Seiglie, 1964.

Minor in shelf and deep sea*.

Reophax fusiformis (Williamson) = *Proteonina fusiformis* Williamson, 1858. Figure 18.15**.

Normal marine salinity and temperature -1 to 13°C on sand and muddy sand down to >3000 m (Murray et al. 2003).

Reophax micaceus Earland, 1934. Figure 18.16**.

Reophax rostrata Höglund, 1947.

Rare fjord, shelf*.

Reophax scorpiurus Montfort, 1808.

Minor in fjord, shelf and shelf basin*. Shallow infaunal (Kuhnt et al. 2000). Epifaunal; sea floor organic flux 0.8-60 g m² yr⁻¹ (Altenbach et al. 1999).

Repmanina charoides (Jones and Parker) = *Trochammina squamata* Jones and Parker var. *charoides* Jones and Parker, 1860. Figure 18.17**.

Shallow infaunal (Gooday 1990; Kuhnt et al. 2000).

Saccammina socialis Brady, 1884. Figure 18.18**.

Common in Laptev Sea (Wollenburg and Kuhnt 2000).

Saccammina sphaerica Sars, 1872. Figure 18.19.

Rare in shelf, deep fjord, deep sea*. Common in Laptev Sea (Wollenburg and Kuhnt 2000).

Spiroplectammina biformis (Parker and Jones) = *Textularia agglutinans* d'Orbigny var. *biformis* Parker and Jones, 1865. Figure 18.20-22**.

Estuarine, fjord, shelf in northern regions; tolerates salinity down to 20; low oxygen <2 ml/l (Williamson et al. 1994; Alve 1990; Alve and Nagy 1990).

Technitella legumen Norman, 1878.

Rare in shelf deep, deep sea*. Epifaunal, attached (Castignetti and Hart 2000). The genus is considered to thrive in organic-rich sediment and an opportunistic coloniser of barren sediments following sediment disturbance (Anschutz et al. 2002; Koho et al. 2007).

Textularia contorta Höglund, 1947.

Minor in shelf and deep fjord*.

Textularia earlandi Parker = new name for *Textularia tenuissima* Earland, 1933. Figure 18.23-25**.

Shallow infaunal, tolerates dysoxia (Bernhard et al. 1997). Seems to be an omnivorous opportunist (Alve 2010).

Textularia kattedgatensis (Höglund) = *Textularia gracillima* Höglund, 1947. Figure 18.26, 27.

Minor in fjord, shelf, shelf deep*. Respiration rate 5.3 ± 1.9 nmol O₂ d⁻¹ ind⁻¹ for individuals 563-611 µm in length (Nomaki et al. 2007)

Textularia skagerakensis Höglund, 1947. Figure 18.28.

Minor in shelf, shelf deep, deep fjord, deep sea*.

Tritaxis britannica Brönnimann and Whittaker, 1990. Figure 18.29, 30.

Höglund (1947) called this *Trochammina* cf. *rotaliformis*.

Rare in fjord, shelf and deep sea*.

Tritaxis conica (Parker and Jones) = *Valvulina triangularis* d'Orbigny var. *conica* Parker and Jones, 1865. Figure 18.31.

Minor in shelf deep*.

Tritaxis fusca (Williamson) = *Rotalina fusca* Williamson, 1858.

Minor in shelf and deep fjord*.

Trochammina sp. skrumpa (shrunken chambers). Figure 18.32-35.

Distinguished by its thin test wall, almost transparent, possibly made of mica. A low trochospiral. A characteristic feature is that some chambers may collapse through shrinkage when dried. Subtriangular with 4 chambers in the final whorl, the final chamber forming at least one third of the test.

Rare in shallow fjord, deep fjord, shelf basin and deep sea*. Some chambers may collapse through shrinkage when dried.

Trochamminopsis quadriloba Höglund, 1948 = *Trochammina pusilla* Höglund, 1947. Figure 18.36-39**.

Deep Sea Taxa

Buzasina ringens (Brady) = *Trochammina ringens* Brady, 1879.

Rare in deep sea*.

Cystammina pauciloculata (Brady) = *Trochammina pauciloculata* Brady, 1884. Figure 19.1**.

Shallow infaunal (Kuhnt et al. 2000). Tolerates dysoxia (Schönfeld 1997). Sea floor organic flux 1-9 g m² yr⁻¹ (Altenbach et al. 1999).

Eratidus foliaceus (Brady) = *Lituola (Haplophragmium) foliaceum* Brady, 1881. Figure 19.2-4**.

Infaunal; correlates with higher TOC but tolerates temperature of 1.8-7.9°C in Gulf of Guinea (Timm

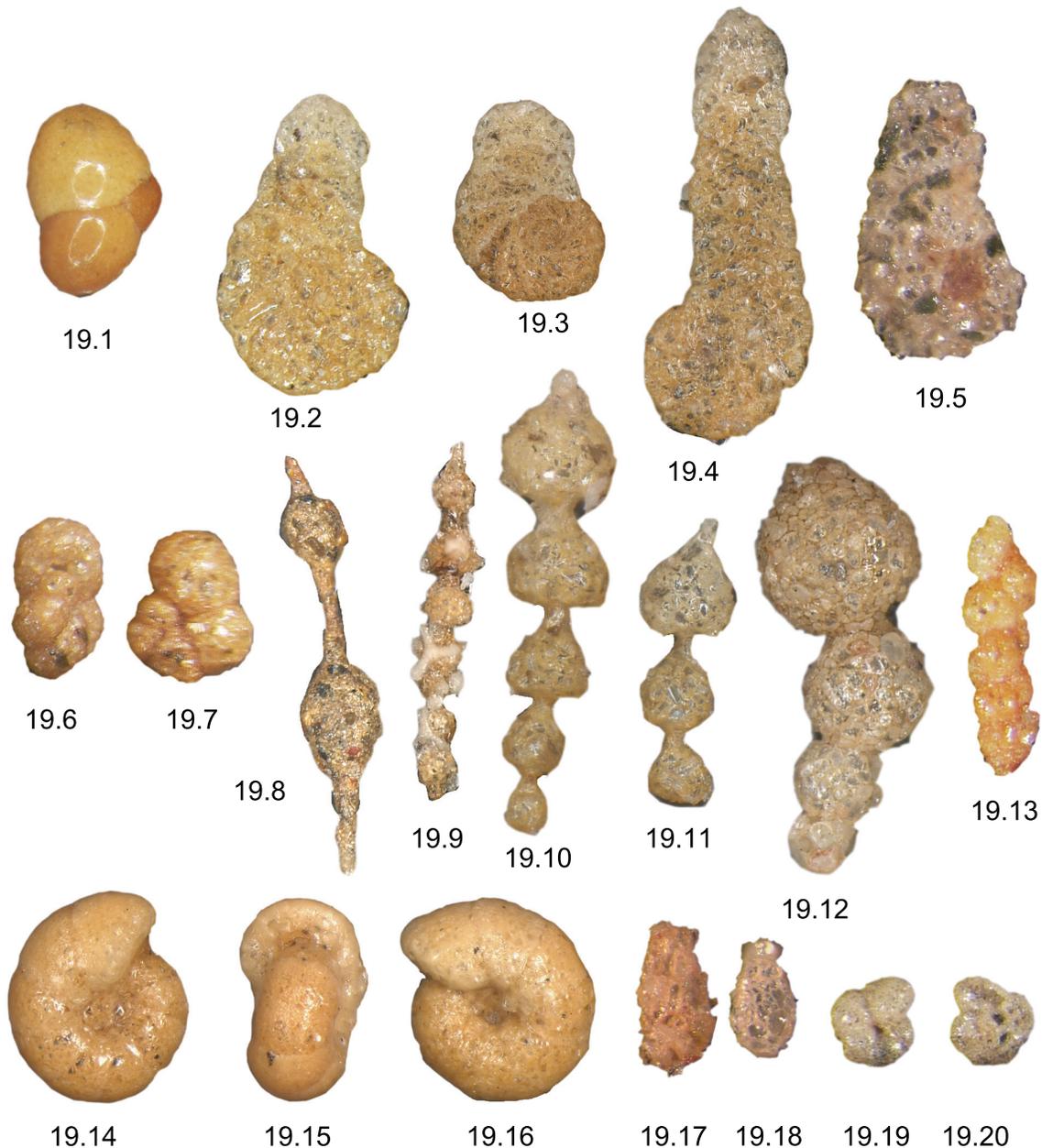


FIGURE 19. Deep sea taxa. The dimensions refer to the length or greatest diameter according to shape. # = sample number. The type specimens are housed in the Natural History Museum, London. 19.1 *Cystammina pauciloculata* (Brady) = *Trochammina pauciloculata* Brady, 1884, Lectotype ZF2508, 500 μ m. 19.2-4 *Eratidus foliaceus* (Brady) = *Lituola (Haplophragmium) foliaceum* Brady, 1881. Syntypes ZF1533, 900 μ m, 480 μ m, 1250 μ m. 19.5 *Glaphyrammina americana* (Cushman) #3235, NE Atlantic, 745 μ m. 19.6, 7 *Haplophragmoides sphaeriloculus* Cushman #3296, NE Atlantic, both 380 μ m. 19.8 *Hormosinella distans* (Brady) = *Lituola (Reophax) distans* Brady, 1881 Syntype ZF2271, 5000 μ m. 19.9-11 *Hormosinella guttifer* (Brady) = *Lituola (Reophax) guttifer* Brady, 1881 Syntypes ZF2276, 600 μ m, 810 μ m, 700 μ m. 19.12 *Reophax pilulifera* Brady, 1884 Syntype ZF2284/ZF4878-80, 2060 μ m. 19.13 *Karrerulina apicularis* (Cushman) #3236, NE Atlantic, 530 μ m. 19.14-16 *Labrospira scitula* (Brady) = *Lituola (Haplophragmium) scitulum* Brady, 1881 Syntypes ZF1551, 950 μ m, 750 μ m, 850 μ m. 19.17, 18 *Lagenammina arenulata* (Skinner) #3236, NE Atlantic, 440, 345 μ m. 19.19, 20 *Trochammina subtrbinatus* Cushman #3209, NE Atlantic, 200 μ m.

1992). Sea floor organic flux 0.2-20 g m² yr⁻¹ (Altenbach et al. 1999). Shallow infaunal (Kuhnt et al. 2000).

Glaphyramina americana (Cushman) = *Ammobaculites americanus* Cushman, 1910. Figure 19.5.

Rare in deep sea*.

Haplophragmoides sphaeriloculus Cushman, 1910. Figure 19.6, 7**.

Shallow infaunal (Gooday 1986; Kuhnt et al. 2000).

Hormosinella distans (Brady) = *Lituola (Reophax) distans* Brady, 1881. Figure 19.8.

Minor in deep sea*. Shallow infaunal (Kuhnt et al. 2000). Found in lower canyon at depths of 4810-4976 m in sediments low in phytodetritus and with refractory organic matter and subject to near-annual sediment gravity flows (off Portugal, Koho et al. 2007).

Hormosinella guttifer (Brady) = *Lituola (Reophax) guttifer* Brady, 1881. Figure 19.9-11**.

Epifaunal; may respond to sea floor organic fluxes/phytodetritus inputs (Wollenburg and Kuhnt 2000; Fontanier et al. 2003); highest total occurrences at 4°C in the Barents Sea (Hald and Steinsund 1992).

Hyperammina laevigata Wright = *Hyperammina elongata* Brady var. *laevigata* Wright, 1891.

Minor in fjord, shelf deeps, deep fjord, deep sea*.

Reophax pilulifera Brady, 1884. Figure 19.12.

Rare deep sea*.

Karrerulina apicularis (Cushman) = *Gaudryina apicularis* Cushman, 1911. Figure 19.13.

The juveniles of this species are very difficult to distinguish from *Eggerelloides medius*. In samples with only the triserial tests we call them *E. medius*.

Occasionally common in deep sea*. Deep infaunal (Kuhnt et al. 2000). Sea floor organic flux 0.8-10 g m² yr⁻¹ (Altenbach et al. 1999).

Labrospira scitula (Brady) = *Lituola (Haplophragmium) scitulum* Brady, 1881. Figure 19.14-16.

Rare in deep sea*. Sea floor organic flux 0.9-50 g m² yr⁻¹ (Altenbach et al. 1999).

Labrospira wiesneri Parr, 1950.

Rare in deep sea*. Infaunal (Gooday 1990).

Lagenammina arenulata (Skinner) = *Reophax difflugiformis arenulata* Skinner, 1961. Figure 19.17, 18**.

Nodellum membranaceum (Brady) = *Reophax membranaceum* Brady, 1879.

Minor deep sea*.

Placopsilina confusa Cushman, 1920.

Rare in deep sea*.

Portatrochammina challengerii Brönnimann and Whittaker, 1988.

Rare in deep sea*.

Reophax bilocularis Flint, 1899**.

Shallow infaunal (Kuhnt et al. 2000). Sea floor organic flux 0.1-90 g m² yr⁻¹ (Altenbach et al. 1999).

Reophax dentaliniformis Brady, 1881.

Rare in deep fjord and deep sea*. Shallow infaunal (Kuhnt et al. 2000). Sea floor organic flux 0.8-90 g m² yr⁻¹ (Altenbach et al. 1999).

Trochammina subturbinatus Cushman, 1920. Figure 19.19, 20**.

Other authors may have called this *T. inflata* in deep sea samples. The umbilical opening seems to get deeper as the individuals grow larger and the later chambers become more globular. Some have a kummerform final chamber. This form appears to be distinct from *T. pseudoinflata* Scott and Vilks, 1991 from the Arctic Ocean.

Trochamminella siphonifera Cushman, 1943

Rare in deep sea*.

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APPENDICES

Appendix 1. Data on foraminiferal abundance and environmental variables in brackish marginal marine environments presented in PDF format online).

Appendix 2. Data on foraminiferal abundance and environmental variables in fjord and normal marine environments (presented in PDF format online).