

THE LATER HOLOCENE FORAMINIFERA OF LIVERPOOL BAY (BAE LERPWL), BRITISH ISLES: MORPHOSPECIES AND COMMUNITY LEVEL PATTERNS

BRENT WILSON^{1,2,*} AND LEE-ANN C. HAYEK³

ABSTRACT

Two cores were studied from Liverpool Bay (~40 m water depth). The lowest 80 cm of ISLF13 (290 cm long) comprised clay, gypsum and pyritised foraminifera (Surface Layer 2 Member, gypsiferous lithofacies GLF) from a tidal flat dominated by *Criboelphidium excavatum*. Perturbation Detection Analysis (PDA) found two ISLF13 GLF abundance biozones (ABs) with assemblages in stasis. ISLF16 (80 cm long) and between 30–202 cm in ISLF13 were open marine, sandy with gastropods and bivalves (Surface Layer 1 Member, shelly sand lithofacies SSLF). Assemblages in the SSLF sections differed, despite their proximity. That in ISLF13 comprised dominant *C. excavatum* with lesser *Ammonia batava*, *Asterigerinata mamilla*, *Cibicides refulgens* and *Bulimina elongata*. PDA identified two ISLF13 SSLF ABs, both in growth stages. The ISLF16 assemblage was co-dominated by *C. excavatum*, *A. mamilla* and *A. batava* from a single AB in stasis. This difference might reflect sorting. *Asterigerinata murrayhaynesi* n. sp. is described.

INTRODUCTION

The neritic Liverpool Bay (Bae Lerpwl in Welsh) lays in the SE part of the eastern Irish Sea, which in turn extends from the northern coast of North Wales to the Solway Firth, and west to the Isle of Man (Aldridge & Davies, 1993). Liverpool Bay borders NW England and N Wales (Figure 1). Its seabed and shallow subsurface geology are well known (Mellett et al., 2015), with documented sediment transport pathways (Howarth, 2005; Kenyon & Cooper, 2005). The patchy distribution of the Holocene Surface Sands Formation (SSF) has been mapped (Jackson et al., 1995, figs. 69, 71), but its foraminifera have not yet been recorded.

Recent neritic foraminifera have been recorded elsewhere around the British Isles. Haynes (1973) noted that between the publication by Walker & Boys (1784) and his own monograph, >300 papers documented Recent British shelfal foraminifera. Most, however, provided lists only. Williamson's (1858) monograph, which described and illustrated 90 species, was the earliest attempt at a comprehensive account but gave only localities, not abundances. Earland (1902) and Heron-Allen & Earland (1909, 1910 1916, 1930a, 1930b) likewise provided localities only.

The rose Bengal staining technique, which distinguishes live foraminifera from dead (Walton, 1952), encouraged ecological work, but raised questions regarding the different distributions of live communities and thanatocoenoses. Haynes (1964) reported the foraminifera in surface scrapes taken between the Pleistocene glacial terminal moraines in Cardigan Bay (Bae Ceredigion, south of Bae Lerpwl). He found only dead foraminifera. He concluded that this was due to postmortem transport, although from where was unclear. Atkinson (1971) expanded on the issue of postmortem transport, comparing recent foraminifera and sedimentary facies in the turbulent zone of this Bay. He concluded that most living foraminifera are associated with dense macroalgal cover, which is limited to coarser sedimentary facies such as from the moraines. Finer sediment in bathymetric hollows yielded allochthonous foraminifera only.

While foraminifera can be transported by traction currents (see review in Saraswati, 2021), Haynes' (1964) dead assemblages might not be entirely transported from distant vegetated areas, epizoic foraminifera living on macrobenthos. Haward & Haynes (1976) found foraminifera living on the scallop *Chlamys opercularis* (Linnaeus), which in turn lives in both the Cardigan and Liverpool Bays. The valves of live *C. opercularis* are abundantly inhabited by foraminiferal morphospecies widespread in sediment taphocoenoses [e.g., *Ammonia batava* (Hofker), *Elphidium selseyense* (Heron-Allen & Earland), *Quinqueloculina seminulum* (Linnaeus)]. The valves yield few dead foraminifera, which dislodge on death. Other macrobenthos support foraminifera too. Moore (1985) reported *Lobatula lobatula* (Walker & Jacob) living on the isopod *Astacilla longicornis* (Sowerby), which occurs subtidally in both Bays (NBN Atlas Wales, 2021).

Regarding taxonomic studies, Murray (1971, 2000) published an atlas of British foraminiferal species, and illustrated the foraminiferal fauna of the Hebridean Shelf, offshore west Scotland (Murray, 2003). Gabel (1971) illustrated the foraminifera of the North Sea. Haynes (1973) described many shallow-water foraminifera from Cardigan Bay. Edwards (1982) illustrated some foraminifera in his study of neritic assemblages off NW Scotland. These monographs and papers, however, provide only brief ecological details (inshore vs. offshore, epifaunal vs. infaunal).

de Nooijer et al. (2008) provided an ecological analysis of the live (rose Bengal stained) benthic foraminifera across a front in the North Sea. Despite peak tidal currents of ~1 m s⁻¹ (Wallingford et al., 2002), which can transport dead benthic foraminifera (Snyder et al., 1990), de Nooijer et al. (2008) reported high standing stocks of especially *Criboelphidium excavatum* (Terquem). Similar fronts occur in the Irish Sea (Beardall et al., 1982; Howarth, 2005; Lee et al., 2005), with one in eastern Liverpool Bay (Figure 1).

Hofker (1977) illustrated benthic foraminifera on some Dutch tidal flats. In marked contrast to the open neritic work recorded above, he concluded that there is little foraminiferal

¹ Present Address: Cedar Lodge, Maenygroes, Ceinewydd, Ceredigion, Wales, SA45 9RL, UK

² Petroleum Geoscience Programme, Department of Chemical and Process Engineering, The University of the West Indies, St. Augustine, Trinidad and Tobago

³ Smithsonian Institution Mathematics and Statistics NMNH MRC-121, Washington D.C., United States of America

* Correspondence author. E-mail: brentforam@gmail.com

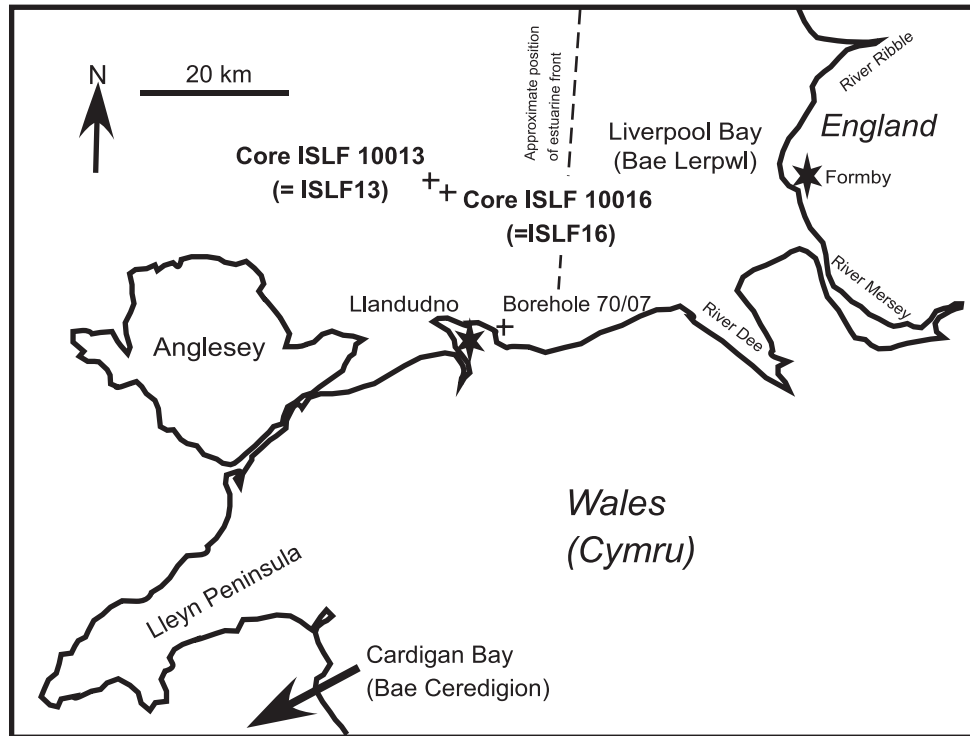


FIGURE 1. Liverpool Bay and North Wales, showing the locations of Cores ISLF13 and ISLF16, and Borehole 70/07. The approximate location of the offshore estuarine front in Liverpool Bay is also shown.

transport in the intertidal zone. Test sizes on the flats increased with increasing salinity.

In terms of stratigraphic work, the paper by Haynes et al. (1977) is geographically the closest study to Liverpool Bay of a Holocene foraminiferal succession. These authors studied the microfauna in the 3.75 m-long Hydrocore ZZ27, taken 5 km west of Aberaeron (52°15.30'N, 4°19.20'W), Cardigan Bay/Bae Ceredigion. This core reached basal till at -21.00 m OD. The uppermost 2.3 m comprised two lithologies:

- Unit 1, 0.00– 100 cmbsf, fine grained, blue-grey, muddy, shelly sands
- Unit 2, 100– 230 cmbsf, dark grey, laminated clays and silts with varying concentrations of plant material.

Haynes et al. (1977) gave only semi-quantitative details of the meiofauna in this core but recorded 100 morphospecies and varieties of foraminifera. Benthic hyaline foraminifera dominated, although some planktonic *Globigerina* spp. were recovered throughout. The fauna in the underlying Unit (2) is of upper tidal flat aspect with *Ammonia aberdoveyensis* Haynes, *Elphidium selseyense*, *Criboelphidium williamsoni* (Haynes) and *Haynesina anglica* (Murray). There was a marked faunal change between Unit (2) and Unit (1), with the entry of *Asterigerinata mamilla* (Williamson), the *Bulimina elongata* d'Orbigny group, *Ammonia batava* and abundant *L. lobatula* in Unit (1). This reflects a transition to shallow, open marine conditions. The entire section must be younger than a peat encountered at ~2.6 mbsf with a ^{14}C age of 8470 ± 110 years cal BP. This peat is widespread in eastern Cardigan Bay (Larcombe & Jago, 1994). Haynes et al. (1977) concluded that their Unit (2)

assemblages were largely allochthonous thanatacoenoses, resulting from strong tidal currents (see Evans, 1947) affecting the nearshore littoral and sublittoral. Comparable studies elsewhere around the British Isles are few, but see Konradi (2000) and Murray (2006).

Here we document the nature of washed residues and provide the first statistical examination of British Holocene neritic foraminiferal assemblages, giving both individual morphospecies and community-level evaluations. We use two cores taken within western central Liverpool Bay (hydrocore ISLF 10013 [hereafter ISLF13] and piston core ISLF 10016 [hereafter ISLF16]). Wilson & Kaminiski (2023) recorded rare benthic foraminifera from these cores that are widespread in the West Indies (*Asterigerina carinata* d'Orbigny, *Dyocibicides biserialis* Cushman & Valentine, *Elphidium discoidale* (d'Orbigny), *Nonionoides grateloupi* (d'Orbigny), *Quinqueloculina lamarckiana* d'Orbigny, *Reussella atlantica* (Cushman), *Sahulina conica* (d'Orbigny)). Those authors concluded these morphospecies to have been transported to the area as juvenile propagules by the North Atlantic Drift. We expand on that work with a quantitative evaluation of individual species-level measures and the first quantitative community level assessment of stasis. We include discussions of the issues of fronts, transport and epizoic foraminiferal inputs as evidenced in these cores.

Because indices calculated from individual samples do not account for community composition, we use the novel holistic Perturbation Detection Analysis (PDA) approach of Hayek et al. (2019). This mathematical approach uses the data's cumulative frequency function and initially determines the distribution of abundance biozones (ABs). It

is the only quantitative approach to test for both community stasis and any disruption to the contained assemblage, evidenced as deviation from the steady state of stasis. This methodology can detect positive growth or negative decline in the taphocoensis or recent assemblages. Using PDA we document change in the assemblage throughout the identified ABs and as part of this evaluation apply the sample-wise assemblage turnover index (ATI_s) of Hayek & Wilson (2013).

STUDY AREA

Liverpool Bay/Bae Lerpwl (2,528 km²) ranges in depth from mean low water to ~66 m. Much of the bay is comparatively new, a sea-level lowstand of -28 m OD having occurred in the North Welsh region at 12,300 years cal BP (Roberts et al., 2011). The rate of sea-level rise diminished around North Wales starting at ~9,000 years cal BP, water depths increasing by only 2 m since ~6,000 years cal BP (Roberts et al., 2011, fig. 12).

The bay is macrotidal (Plater & Grenville, 2010). Ramster & Hill (1969) found within it a strong residual current to the SSE augmented during north-westerly gales. Thus, there is net eastward, shoreward sediment transport. Polton et al. (2011) found maximum current velocity in Liverpool Bay to be 50–75 cm s⁻¹. Although only 60–80% of this current velocity reaches the seabed (Polton et al., 2011, fig. 2b), it exceeds the traction current velocities of 13 cm s⁻¹ needed to transport benthic foraminiferal tests (see Snyder et al., 1990).

The cores used in this study were taken from an area of large sand waves, formed where seafloor currents peak at ≥ 65 cm s⁻¹ (Kenyon & Cooper, 2005, fig. 25). These may be static features or move at mean rates of up to 0.6 m a⁻¹ (Mellett et al., 2015), but the surface sand may be far from static. Radioactive tracer studies in a comparable sand wave field in the English Channel showed that sand can travel up to 2 km in 75 days, despite little migration of the large sand waves (Beck et al., 1991).

An offshore front extending N-S across the bay's centre separates eastern lower salinity surface water from western higher salinity water (Greenwood et al., 2011) at >20 km from the mouth of the River Mersey (Bowden & Sharaf El Din, 1966). We have not found any records of microalgae, which would provide habitats for foraminifera, on the Liverpool Bay seafloor. Rocky areas as natural attachment sites for macroalgae are limited to a small area near the mouth of the River Dee (Mills, 1998) and the Welsh coastline, including around Anglesey.

Deposits of the SSF are in Liverpool Bay generally <2 m thick, but locally it can be > 40 m thick in sandbanks (Jackson et al., 1995). The formation overlays an erosional surface dated at 10,200 years cal BP, developed shortly after the start of post-glacial rapid sea-level rise in the North Wales region, which commenced 11,000 years cal BP (Roberts et al., 2011, fig. 11). The SSF comprises three members (Jackson et al., 1995). The Seabed Depression Member (SDM) occupies depressions cut into the underlying Western Irish Sea Formation A (Weichselian to earliest Holocene). Other, more extensive but generally thinner parts of the SSF are divided into the lower Surface Layer 2 (SL2) and upper Surface Layer 1 (SL1) Members. Off Llandudno (Borehole 70/07,

see Figure 1), the SL2 Member consists of peaty silt from reed swamps older than 9,200 years cal BP. On Kish Bank, 11 km east of Dublin, Ireland, the SL2 Member is of intertidal aspect. The SL1 Member either disconformably overlies an erosion surface across the SL2 Member or rests on older strata. It consists of tabular-stratified sediments but passes up into present-day mobile sediments (Layer A of Pantin & Evans, 1984), which can be up to 0.3 m thick (Jackson et al., 1995). Crickmore and Kiff (1985), however, did not find man-made metals in Liverpool Bay >0.1 m below the sediment surface, perhaps indicating the more typical depth of bioturbation or sand transport.

MATERIALS AND METHODS

Two cores were taken from central Liverpool Bay (water depth ~40 m, see fig. 1 in Polton et al., 2011). Core ISLF13 (53.517°N, 3.807°W) was a 290 cm-long vibrocore. Core ISLF16 (53.509°N, 3.785°W), taken to the ESE of ISLF13, was a ~80 cm long piston core. Both cores lay west of but close to the front illustrated by Greenwood et al. (2011), ISLF16 being closer to the front.

The seafloor at the cored sites, though locally with gravelly sand (Holmes & Tappin, 2005, fig. 7), is mostly clayey sand with sand grains ~0.5 mm in diameter (Luo et al., 2013, fig. 6A). ISLF16 penetrated only dark grey-brown clayey sand with some marine gastropods (principally *Turritella communis* up to 2.5 cm long, identified from Hayward & Ryland, 1990, p. 524) and broken bivalves. This shelly material and abundant sand was recovered from the upper 202 cm of ISLF13, but not from that core's lowest 80 cm, which comprised dark brown, structureless clay that those taking the core thought had possibly been deposited on a tidal flat (Martin Bates, pers. comm).

We had intended to sample the cores at 10 cm intervals in 2 cm slices, commencing at the core tops. This was possible throughout ISLF16 (7 samples). However, the uppermost 25 cm of ISLF13 was too sludgy and deformed for accurate sampling, this probably being Layer A. So, we commenced sampling of this core at 30 cmbsf, giving 26 samples.

One hundred grams of sediment from each sample was soaked in water until disaggregated, and then washed over a 63 μm mesh. The residue was oven dried at 90°C and the mass of dried material recorded. For each sample the >63 μm residue was split with a microsampler to give aliquot of >250 specimens. To ensure that no foraminifera were missed, each aliquot was sieved over 106, 125, 150 and 425 μm meshes and the resulting five fractions were picked clean of specimens. Planktonic foraminifera were picked but not identified further and for statistical purposes treated as forming a single taxon. We refer to the picked foraminifera as forming assemblages, but note that these are taphonomic assemblages that were subject to postmortem alteration, such as transport, rather than the community that lived at the core sites. The assemblage slides are housed at the European Micropaleontological Reference Centre, Kraków, Poland (reference number 19/1).

The numbers of specimens in each taxon were for each sample recorded on a spreadsheet for analysis. Storms around the British Isles transport in suspension many dead but few live benthic foraminifera (Murray et al.,

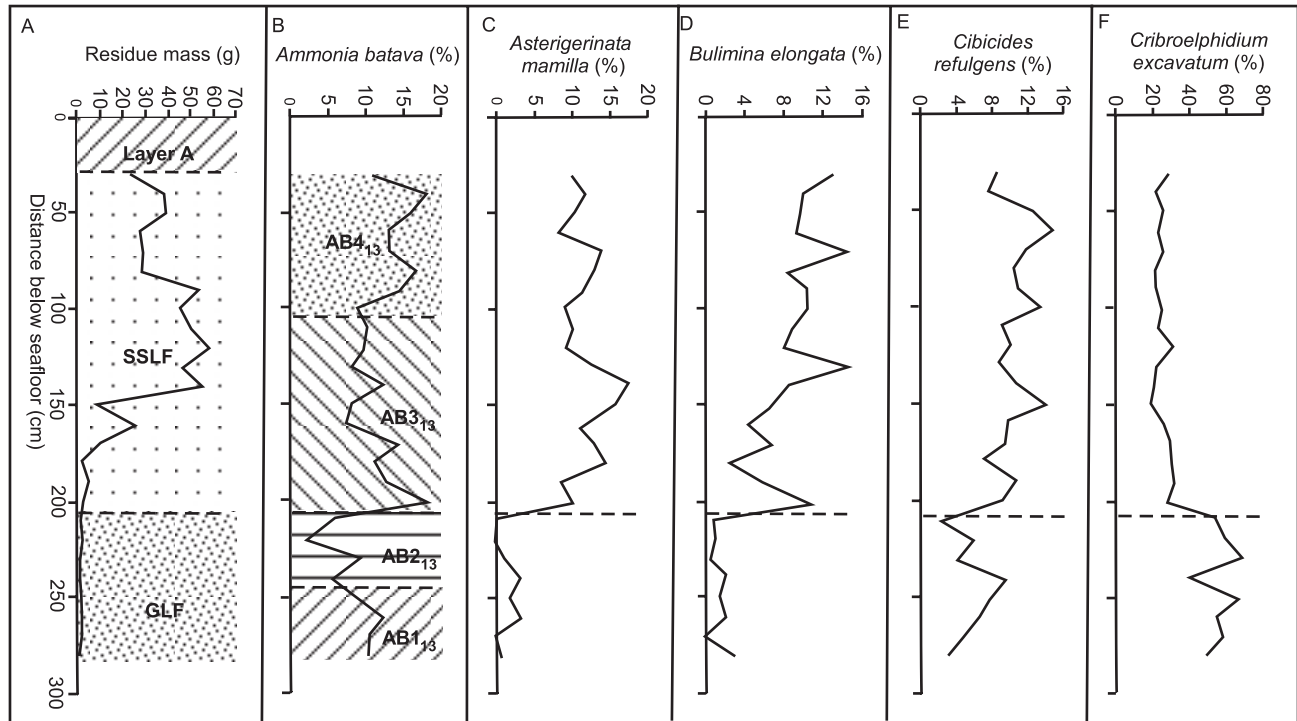


FIGURE 2. Residue masses and the proportional abundances of selected morphospecies in Core ISLF 13. A. Residue masses in grams, showing also the distributions of the gypsiferous lithofacies (GLF) and the shelly sand lithofacies (SSLF). B. *Ammonia batava*, showing also the distributions of the four abundance biozones (ABs) in this core. C. *Asterigerinata mamilla*. D. *Bulimina elongata*. E. *Cibicides refulgens*. F. *Criboelphidium excavatum*. The dashed line in C–F is the boundary between the GLF and SSLF and between AB2₁₃/AB3₁₃.

1982). With this observation in mind, the number of taxa (morphospecies, morphospecies in open nomenclature) recorded and treated as richness S included a group labelled ‘planktonic foraminifera’.

The PAST palaeontological freeware of Hammer & Harper (2005, version 4.08) was used to calculate measures at the morphospecies level. Because the numbers of foraminifera picked from the residues varied widely, and S increases with the number of specimens N picked (Hayek & Buzas, 2010), rarefied S was estimated using rarefaction to the smallest sample size for each core. Diversity was measured using the Shannon Function H [$= -\sum p_i \cdot \ln(p_i)$, in which p_i is the proportional abundance of the i th species], evenness using the Equitability Index E ($= e^H/S$), and dominance using the Berger-Parker Index $\max(p_i)$. For further details on the use of these indices, see Hayek & Buzas (2013). Means of rarefied S , and of H , E and $\max(p_i)$, transformed as appropriate to meet assumptions, were tested using Student’s t -test. Proportional abundances were for comparisons transformed using $\ln(p_i + 1)$. Probabilistic measures were accepted as significant at $p \leq 0.5$.

In addition, we calculated a version of the *Ammonia-Elphidium* (A-E) Index of Sen Gupta et al. (1996). This measure, as originally developed in surface sediments offshore Louisiana, Gulf of Mexico, was stated to be calculated from

$$\text{A-E Index} = [N_A / (N_A + N_E)] * 100,$$

where N_A and N_E were the numbers of *Ammonia* and *Elphidium*, respectively, in a sample. This index has been applied widely and rather indiscriminately to studies of marginal

marine environments (Eichler & Barker, 2020), with little regard to the identity of the species encountered. We recorded elphidiids with both rounded (*C. excavatum*) and acute (*Criboelphidium gerthi*) to carinate (*Elphidium crispum*) peripheries, each of which have quite different ecologies (Langer, 1993). Our *Criboelphidium excavatum* has been found both in the Gulf of Mexico (Buzas-Stephens et al., 2002) and around NW Europe (Darling et al., 2016). Sen Gupta et al. (1996) developed their A-E Index using *C. excavatum* (given as *Elphidium excavatum* sensu Sen Gupta et al., 1996) and *Ammonia parkinsonia* (d’Orbigny). Rather than using all our specimens of *Ammonia* spp., *Elphidium* spp. and *Criboelphidium* spp. in our assessment, we calculated our version the A-E Index using *C. excavatum*, which was our most abundant morphospecies of elphidiid, and our most abundant morphospecies of *Ammonia* ($= A. batava$). We thus term this derivative index the A-C Index. Both of these morphospecies are infaunal.

The only statistical holistic approach for examining the community-level patterns to be found in our foraminiferal data is PDA (Hayek et al., 2019), which uses the cumulative frequency function (CFF) methodology and considers samples as replicates over time so as to facilitate the identification of community-level patterns. To prepare for CFF (Hayek et al., 2019), we identified ABs by proceeding from the bottom upwards in both cores (see Wilson, 2008). The ABs are numbered from the bottom up, those in ISLF13 being differentiated using subscript 13, and that in ISLF16 using subscript 16. PDA tests the null hypothesis using stepwise the values for additional new morphospecies detected

and added to the CFF, then calculating the related diversity indices. Following Hayek et al. (2007), we draw a distinction between the terms ‘assemblage’ and ‘community’. An assemblage is any and all groupings of species, while if PDA finds an AB, then that AB is taken to be a coherent entity containing a community. As Hayek et al. (2019) noted, the composition of the assemblages cannot be expected to remain constant. Both the morphospecies themselves and their relative abundances are subject to change since both rare and even common ones will vary across time. PDA shows that stasis is the desired or expected state of an assemblage with both richness and evenness balanced (balance of nature), yet relatively minor alterations in assemblage composition and abundance can be sufficient to perturb this state of equilibrium and lead to either increased growth or decline. This information has been shown to be unobtainable with only the individual sample level measures (Hayek et al., 2019). Fitting a least squares regression to H and lnN calculated on such samples provides the basis for a quantitative mathematical examination. The slope of the diversity regression model yields the quantitative definition of stasis, or the ecological balance of the assemblage or community. Thus, stasis is defined as the steady state, with positive and negative deviations from this state being easily seen as disruptions with either community growth or decline.

With the slope coefficient used as the detection measure for the test of hypotheses and detection of balance or perturbations, both the assemblage turnover index (ATI) and conditioned on boundary index (CoBI) of Hayek & Wilson (2013) complete the PDA procedure. To assess which morphospecies contributed most to the ATI across selected AB boundaries, the CoBI provides the proportion that each morphospecies within an assemblage contributes to the change or turnover specifically across that boundary. For each morphospecies at any boundary $\text{CoBI} = |p_{i2} - p_{i1}| / \text{ATI}$, where p_{ij} , $j = 1, 2$ are the i th species’ proportions on either side of the selected boundary of interest and at which the ATI is calculated. Both ATI and CoBI can be computed with differing subsets of the data (Hayek & Buzas, 2013). Here we used the partial conditioned-on-boundary index, CoBI_t , of Hayek & Wilson (2013), in which the assemblage turnover index $\text{ATI} (= \text{ATI}_p)$ was calculated between the entire set of samples below the selected AB boundary and the first sample above it. The value of ATI_p was substituted into the CoBI equation, using p_{i1} and p_{i2} as the proportional abundances of the i th species. The proportional contribution of each morphospecies to ATI_p was assessed from the vector of CoBI_p .

The values of between sample $\text{ATI} (= \text{ATI}_s)$ were determined using pairs of adjacent samples. The depths for the ATI_s values were interpolated between those samples so that they lay at 5, 15, 25... 275 cmbsf.

RESULTS

CORE ISLF13

Sample Masses

This core’s residue masses ranged from 0.4–57.8 g (Figure 2A), reflecting the samples’ mostly muddy nature. Large, euhedral, tabular gypsum crystals were recovered

from residues between 282–210 cmbsf, these forming a gypsiferous lithofacies (GLF). The euhedral gypsum crystals, typically from the >425 μm fraction, appeared fresh overall, but those from 250–252 cmbsf were chalky and corroded.

Shelly material and quantities of fine sand were recovered from a shelly-sandy lithofacies (SSLF) between 202–30 cmbsf. A few gypsum crystals recovered from 180–182 cmbsf within the SSLF we consider to be reworked. The mean mass of sample residues from the GLF ($\bar{x} = 1.06$ g) was less than that of samples from the SSLF ($\bar{x} = 30.47$ g). The residues in the samples from the GLF were mostly <150 μm , while those from the SSLF comprised mostly 150–425 μm fine sand grade material. However, no distinct break in masses occurred that would distinguish members in the SSF.

Foraminiferal Assemblages

A total of 10,214 foraminiferal tests were recovered from this core ($\bar{x} = 393$ per sample), including 62 tests grouped as planktonic foraminifera (Appendix 1). These foraminiferal tests were placed in 125 taxa, of which 31 (24.8% of identified morphospecies and taxa in open nomenclature) were singletons. As expected (see Hayek & Buzas 2010), most taxa were rare, 59 (47.2%) being represented by ≤ 4 specimens. Total recovery was dominated by *C. excavatum* (36.1%), with lesser *A. batava* (11.0%), *Cibicides refulgens* (9.0%), *A. mamilla* (8.5%), and *B. elongata* (6.8%). The five most common morphospecies thus comprised 71.4% of the total recovery.

A total of 3,052 foraminifera were recovered from the GLF, including 21 grouped as planktonic foraminifera. The most abundant morphospecies were *C. excavatum* (58.7%), *A. batava* (8.1%) and *C. refulgens* (5.3%), together forming 72.1% of GLF recovery. A few *A. mamilla* (1.1%) and *B. elongata* (1.2%) were recovered. Many *C. excavatum* had been either partially or wholly filled with pyrite or were preserved as easily identifiable pyrite casts. They were recovered almost exclusively from the 106–150 μm fraction. Not all hyaline foraminifera had been pyritised, however. At 230–232 cmbsf well preserved *A. batavus* were abundant in the 150–425 μm fraction.

The foraminiferal assemblage composition of the SSLF differed in terms of percentage abundances from that in the GLF, and in lacking pyritisation. Five morphospecies each formed > 5% of the total recovery of 7,165 specimens, which included 41 specimens grouped as planktonic foraminifera and treated as a single morphospecies. In rank order these morphospecies were: *C. excavatum* (26.4%), *A. batava* (12.2%), *A. mamilla* (11.6%), *C. refulgens* (10.6%) and *B. elongata* (9.1%), these together forming 69.9% of the total recovery (Figures 2B–F). *Ammonia batava*, *A. mamilla*, *B. elongata* and *C. refulgens* were proportionally more abundant in the SSLF, in which some tests were worn and broken. In contrast, the percentage abundance of *C. excavatum* was markedly greater in the GLF (GLF, $\bar{x} = 57.2\%$, s.d. = 9.2%, 8 samples; SSLF, $\bar{x} = 26.1\%$, s.d. = 3.5%, 18 samples). Also recovered from this SSLF section were rare (0.17%) specimens of *Asterigerintata murrayhynesii* n. sp.

Individual Diversity Measures

Richness S in ISLF13 was rarefied to the smallest residue (N = 258) and ranged from 20.5–38.1 ($\bar{x} = 30.8$, s.d. = 4.0).

TABLE 1. Correlations and their probabilities between single sample residue masses (g), Shannon Function H, Equitability Index E and Berger-Parker Index $\max(p_i)$.

Measure	Mass	H	E	$\max(p_i)$
Mass	-	<.001	<.001	<.001
H	0.61	-	<.000001	<.000001
E	0.63	0.89	-	<.000001
$\max(p_i)$	-0.68	-0.94	-0.94	-

The mean rarefied S for the GLF ($\bar{x} = 28.9$, s.d. = 4.7) was equivalent to that from the SSLF ($\bar{x} = 32.3$, s.d. = 4.3; $t_{24} = 1.63$, $p = .056$).

Shannon's H, Equitability Index and Berger-Parker Index (Figures 3A–C) were all significantly correlated with residue masses (Table 1), either positively (H, E) or negatively ($\max(p_i)$). Only $\max(p_i)$ showed a visibly clear pattern related to the residue nature, being lower in the SSLF than in the GLF (Figure 3C), reflecting the greater proportional abundances of *C. excavatum* in the GLF. The GLF mean values of $\max(p_i)$ were larger than those for the SSLF (GLF, 282–210 cmbsf, $\bar{x} = 0.57$, s.d. = 0.09, 8 samples; SSLF, 202–30 cmbsf, $\bar{x} = 0.26$, s.d. = 0.04, 18 samples). Though not so apparent from Figure 3A, the mean values of H for the lithofacies also differed significantly (GLF, $\bar{x} = 1.87$, s.d. = 0.34, 8 samples; SSLF, $\bar{x} = 2.56$, s.d. = 0.13, 18 samples; $t_{24} = -7.70$, $p < .00001$), being greater in the SSLF.

The ISLF13 A-C Index ranged from 3.69–42.96 (Figure 3D), being low in the GLF (range 3.69–18.72, $\bar{x} = 12.53$, s.d. = 4.78), with a marked step between 210–202 cmbsf. We may not have enough data from the lower GLF section to conclude with certainty, but there may be a trend whereby A-C Index decreases up-section through the GLF, with the lowest A-C in the GLF occurring near the top at ~210cmbsf ($r = 0.801$, $p = .015$), suggesting a decrease over time. The SSLF A-C Index ranged from 21.87–42.96 ($\bar{x} = 31.89$, s.d. = 6.35) and fluctuated around the mean with no significant trend with depth ($r = -0.364$, $p = .137$) and was not correlated with residue mass ($r = 0.28$, $p = .24$).

Perturbation Detection Analysis

Abundance biozones (ABs) were identified in ISLF13 from 282–250 cmbsf (AB1₁₃, 4 samples), 242–210 cmbsf (AB2₁₃, 4 samples), 202–120 cmbsf (AB3₁₃, 9 samples) and 112–30 cmbsf (AB4₁₃, 9 samples). Thus, there were two GLF ABs and two SSLF ABs. The PDA methodology showed that the assemblages in AB1₁₃ and AB2₁₃ were in stasis. In contrast, AB3₁₃ and AB4₁₃ contained assemblages with a positive coefficient indicative of a growth state.

The mean value of ATI_s throughout ISLF13 was 0.434 (s.d. = 0.153, range 0.285–1.023), indicating a mean turnover of ~43% between adjacent samples. Values of ATI_s were calculated within the ABs. One way ANOVA showed that at least two of the within-AB means for ATI_s differed significantly ($F_{3,18} = 3.69$, $p = .031$), while the Scheffé test found a significant difference between the means of AB2₁₃ ($\bar{x} = 0.51$) and AB4₁₃ ($\bar{x} = 0.36$). Mean ATI_s was high towards the GLF top (Figure 4).

We examined $CoBI_p$ between the GLF and SSLF (i.e., across the AB2₁₃/AB3₁₃ boundary). The value of $ATI_p =$

0.864, and so exceeded greatly the mean value of ATI_s in the entire core. Eight morphospecies presented a $CoBI_p > 0.02$ (i.e., contributed >2.0% to assemblage turnover). Of these, six had a positive value of $p_{i2} - p_{i1}$, indicating a greater proportional abundance above the GLF/SSLF boundary: *A. batava* ($CoBI_p = 0.12$), *A. mamilla* (0.11), *B. elongata* (0.11), *C. refulgens* (0.05), *Q. seminula* (0.04) and *Haynesina depressula* (0.03). Two morphospecies had a negative $p_{i2} - p_{i1}$, reflecting a greater proportional abundance within the GLF: *C. excavatum* ($CoBI_p = 0.35$) and *B. frigida* (0.02). The biggest contributors to $CoBI_p$ were thus the two morphospecies used in calculating the A-C Index.

CORE ISLF16

Sample Masses

The residues from the seven ISLF16 samples comprised mostly fine sand 150–425 μm with shelly material (Figure 5A) and were thus comparable with the ISLF13 SSLF. The ISLF16 residue masses ranged from 14.7–93 g ($\bar{x} = 48.9$ g, s.d. = 27.2 g) and the residues did not contain gypsum.

Foraminifera

A total of 3,236 foraminifera were recovered from ISLF16 ($\bar{x} = 462$ per sample), in 78 taxa or morphospecies (Appendix 1). This recovery included seven planktonic foraminifera, which were grouped as a single taxon. The low richness in this core compared to ISLF13 is due to the smaller number of samples and specimens taken from ISLF16. Recovery from this core was co-dominated by *C. excavatum* (21.2%), *A. mamilla* (19.0%) and *A. batava* (18.2%), with lesser *C. refulgens* (9.5%), *B. elongata* (7.1%), and *Q. seminula* (5.6%) (Figure 5). Also recovered were rare *Asterigerinata murrayhaynesi* n. sp. (0.22% of total recovery).

Richness for this core was rarefied to the smallest number of specimens picked ($N = 369$). It ranged from 27.1–39.6 ($\bar{x} = 34.0$, s.d. = 4.4).

In ISLF16, H ranged from 2.25–2.60 ($\bar{x} = 2.43$, s.d. = 0.125; Figure 5G), and was significantly negatively correlated with the residue masses ($r = -0.923$, $p = .003$, $N = 7$ samples). In contrast E (range = 0.289–0.338, $\bar{x} = 0.310$, s.d. = 0.017; Figure 5H) was not correlated with residue masses. The Berger-Parker Index ranged from 0.211–0.256 ($\bar{x} = 0.228$, s.d. = 0.015; Figure 5I). The A-C Index ranged from 39.3–52.9 ($\bar{x} = 46.8$, s.d. = 4.6; Figure 5J) and did not show any significant trend through the core.

ISLF16 comprised a single AB (AB1₁₆) whose assemblage was probabilistically constant, or in stasis over the depths/time sampled. We note, however, that with only 7 samples this conclusion cannot be generalised for any further sediments from an SSLF below the maximum depth sampled. The sample-wise ATI_s in Core ISLF16 ranged from 0.229–0.372 ($\bar{x} = 0.302$, s.d. = 0.052).

COMPARISON BETWEEN THE SSLF IN CORES ISLF13 AND ISLF16

Both the uppermost 202 cm in ISLF13 and the 80 cm sampled in ISLF16 contained the shelly material and fine sand

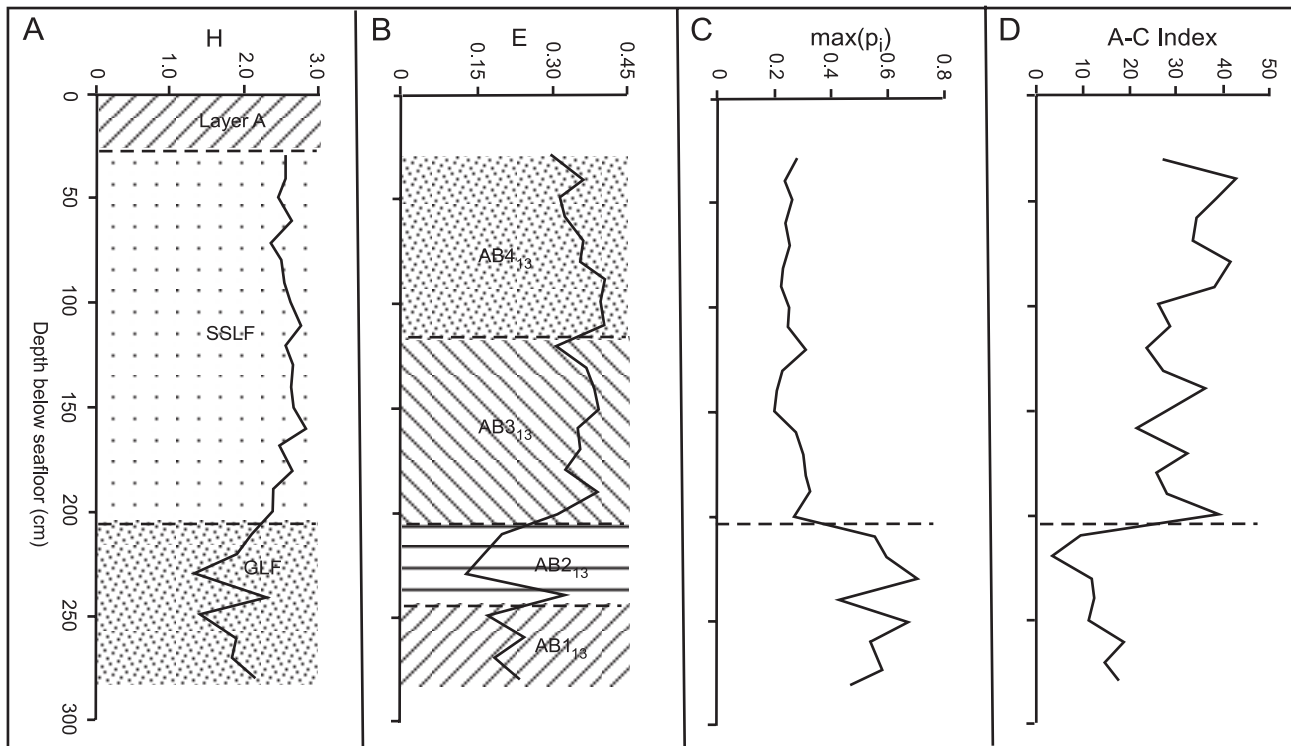


FIGURE 3. Single sample statistical measures in Core ISLF13. A. The Shannon Function, H , showing also the distributions of the gypsiferous lithofacies (GLF) and the shelly sand lithofacies (SSLF). B. The Equitability Index, E , showing also the distributions of the four abundance biozones (ABs) in this core. C. The Berger-Parker Index, $\max(p_i)$. D. The *Ammonia-Cribroelphidium* (A-C) Index. The dashed line in c and d is the boundary between the GLF and SSLF, and between AB₂₁₃/AB₃₁₃.

> 150 μm of the SSLF. The residue masses in the lower part of ISLF13 (202–150 cmbsf) were small (3–25 g) when compared to the upper part (142–30 cmbsf, 23.7–57.8 g). Those in ISLF16 ranged from 14.7–93 g, and so were comparable to the residue masses in the upper part of ISLF13.

Assemblage Level Evaluation

PDA found a single AB (AB₁₆) in ISLF16 composed of community in stasis, diversity not changing significantly over the time period. This differed from the uppermost SSLF abundance biozone (AB₄₁₃) in ISLF13, in which the community was in an expansive, growth state with diversity increasing throughout.

Given the difference detected with PDA of stasis vs. expansion/assemblage growth between AB₄₁₃ and AB₁₆, we compared these further. Community structure in the two ABs differed, though in the percentage abundances of the common (>5%) species, not their identities. The AB₄₁₃ assemblage was dominated by *C. excavatum* (25.4%) with lesser *A. batava* (13.0%), *C. refulgens* (11.1%), *B. elongata* (10.7%), and *A. mamilla* (10.8%), but the AB₁₆ assemblage was co-dominated by *C. excavatum* (21.2%), *A. mamilla* (19.0%) and *A. batava* (18.2%). However, mean rarefied S did not differ significantly between the cores.

As anticipated from differences in the common species' abundances, the sample level statistical measures employed here differed for the SSLF between the two cores. Mean H for AB₄₁₃ ($\bar{x} = 2.55$) exceeded that for AB₁₆ ($\bar{x} = 2.43$;

$t = 2.02$, $p = .031$, $df = 14$), The means of the transformed $\max(p_i)$ differed significantly ($t = 2.83$, $p = .007$, $df = 14$), the original values in AB₄₁₃ ($\bar{x} = 0.25$) exceeding those in AB₁₆ ($\bar{x} = 0.23$). Despite the geographical proximity of the two cores, the A-C Index also differed between AB₄₁₃ ($\bar{x} = 34.6$) and AB₁₆ ($\bar{x} = 46.8$).

DISCUSSION

Of the two geographically close cores examined, the residues from the shorter ISLF16 all came from a shelly, sandy lithofacies (SSLF). Those from the longer ISLF13 came from two lithofacies, a lower one of small residues with tabular gypsum (gypsiferous lithofacies = GLF), and a younger SSLF. PDA showed the foraminiferal assemblages' structure in ISLF13 GLF comprised two abundance zones (AB₁₁₃, AB₂₁₃) both in stasis. That core's SSLF contained two ABs (AB₃₁₃, AB₄₁₃) with expanding assemblages. Sample-wise assemblage turnover was in this core at its highest in AB₂₁₃, and lowest in AB₄₁₃. The samples in ISLF16 SSLF came from a single AB (= AB₁₆) in which the assemblages were in stasis.

Two comparisons can thus be made: (1) between the GLF (AB₁₁₃ + AB₂₁₃) and SSLF (AB₃₁₃ + AB₄₁₃) in ISLF13 only, and (2) between the SSLF (AB₄₁₃ vs. AB₁₆) in the two cores. While the uppermost 25 cm of ISLF13 was soupy and could not be sampled accurately, and is ascribed to the active Layer A of Pantin & Evans (1984), this layer was not found

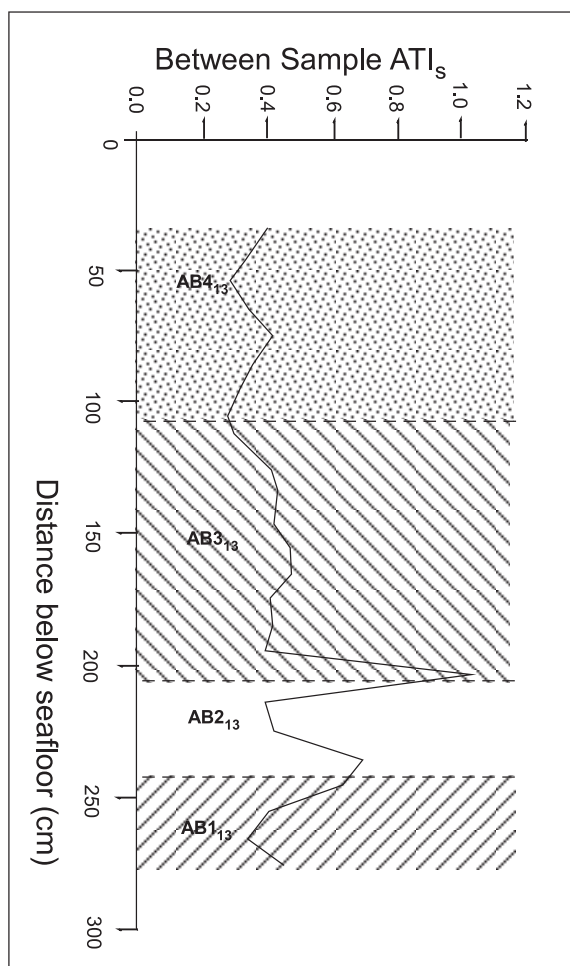


FIGURE 4. The between-sample assemblage turnover index (ATI_s) in Core ISLF13, overlain by the assemblage biozones $AB1_{13}$ – $AB4_{13}$.

at the top of ISLF16. The reason for its absence there is unclear, but it might reflect local scouring. If so, then the top of ISLF16 cannot be presumed to be of present day age, even though it coincides with the seafloor. Alternatively, the loss of Layer A in ISLF16 might reflect the difference in coring methods employed. Negative pressure inside the core barrel during piston coring, as used to take ISLF16, might have caused the disappearance of the surface sediment.

No shallow-penetration geophysical data were available for the two cores. On the basis of post-glacial stratigraphic position, lithofacies and benthic foraminiferal content, we assign them to the Surface Sands Formation (SSF). The low abundance of planktonic foraminifera in both cores reflects the nearshore to shallow-water origin of the SSF. The GLF of ISLF13 we suggest to come from the intertidal to marine SL2 Member of the SSF, while the SSLF belongs to the younger, open marine SL1 Member (cf. Mellett et al., 2015). We thus interpret the GLF as having been deposited between 10,200 – 9,200 years cal BP (ages from Jackson et al., 1995), while the SSLF is younger. We note, however, that the onset the GLF depositional lithofacies would vary based on location and elevation and may not represent either a chronologically synchronous event or necessarily the same genera-

tion of tidal flat. We cannot exclude the possibility that the SSLF is from the marine, sandy to muddy Sea Bed Depression (SBD) Member but note that Jackson et al. (1995) do not show any instances of the SBD Member overlaying the SL2 Member, as would have had to be the case in ISLF13.

Lithologically the SSLF is comparable to the open marine Unit (1) in the Cardigan Bay Core ZZ27 (Aberaeron) of Haynes et al. (1977), which comprised fine grained, blue-grey, muddy, shelly sands. However, the GLF is not comparable lithologically with Unit (2) in Core ZZ27, which contained varying concentrations of plant material but lacked gypsum. Both the GLF and the Unit (2) are, however, ascribed to tidal flats.

That the residue masses from the GLF were very small indicates the loss of large quantities of mud during sample preparation. Muddy tidal flats are extremely tide dominated (Daidu et al., 2013), waves becoming greatly damped as they travel over the fluid mud (Fan, 2012). Such muddy tidal flats occur between mean high water neap tide levels and mean high water spring tide levels (Daidu et al., 2013; Langer et al., 1989). They lack vegetation but transition landward to vegetated salt marshes that support primarily agglutinated foraminiferal assemblages (Horton & Edwards, 2006). Organisms living on muddy tidal flats are subject to high physiological stress but low ecological stress (expressed as competition for space and resources) (Paterson et al., 2019). These stresses may explain the low diversity and high dominance of the assemblage in the GLF. We note, however, that the GLF assemblage does not reflect precisely the original community that lived there, some of the specimens being allochthonous and thus affecting both S and p_i .

The intertidal origin of the GLF is nevertheless supported by the dominance of *C. excavatum* (cf. Alve & Murray, 2001), which is an infaunal species that can live on tidal flats (Langer et al., 1989) as long as salinities are sufficiently high (Hofker, 1977). Its presence might reflect a high labile organic matter flux (de Nooijer et al., 2008). It is possible, however, that the abundant *C. excavatum* also reflect freshwater influence (see Konradi, 2000; Korsun et al., 2014) during GLF times, such as from the rivers Ribble, Mersey and Dee. The presence of the gypsum must be interpreted against the backdrop of such riverine influence.

Most authors discussing gypsum's origin have historically invoked an arid to semiarid climate and high evaporation rates (Watson, 1985). They presume that intertidal gypsum is formed by the evaporation of brine in extremely shallow water on extensive tidal flats (Boggs, 2006). At least from mid Holocene times onwards, however, the British Isles have been subject to moderate to high precipitation rates (Charman, 2010), with no evidence in support of aridity in the earlier Holocene (see Plater & Grenville, 2010).

Bain (1990) reported diagenetic, tabular gypsum crystals in some Pleistocene glaciolacustrine prodeltaic deposits. He ascribed their euhedral form to the displacement of soft, water-rich, pliable muds during crystal growth. He stated that the calcium was derived from calcite in glacial deposits, and sulphate from pyrite in grey prodelta muds. The calcium in ISLF13 GLF may have been derived from the calcareous foraminiferal tests, which were often filled with or entirely replaced by pyrite. In addition to the input of allochthonous specimens and species, the dissolution might have changed

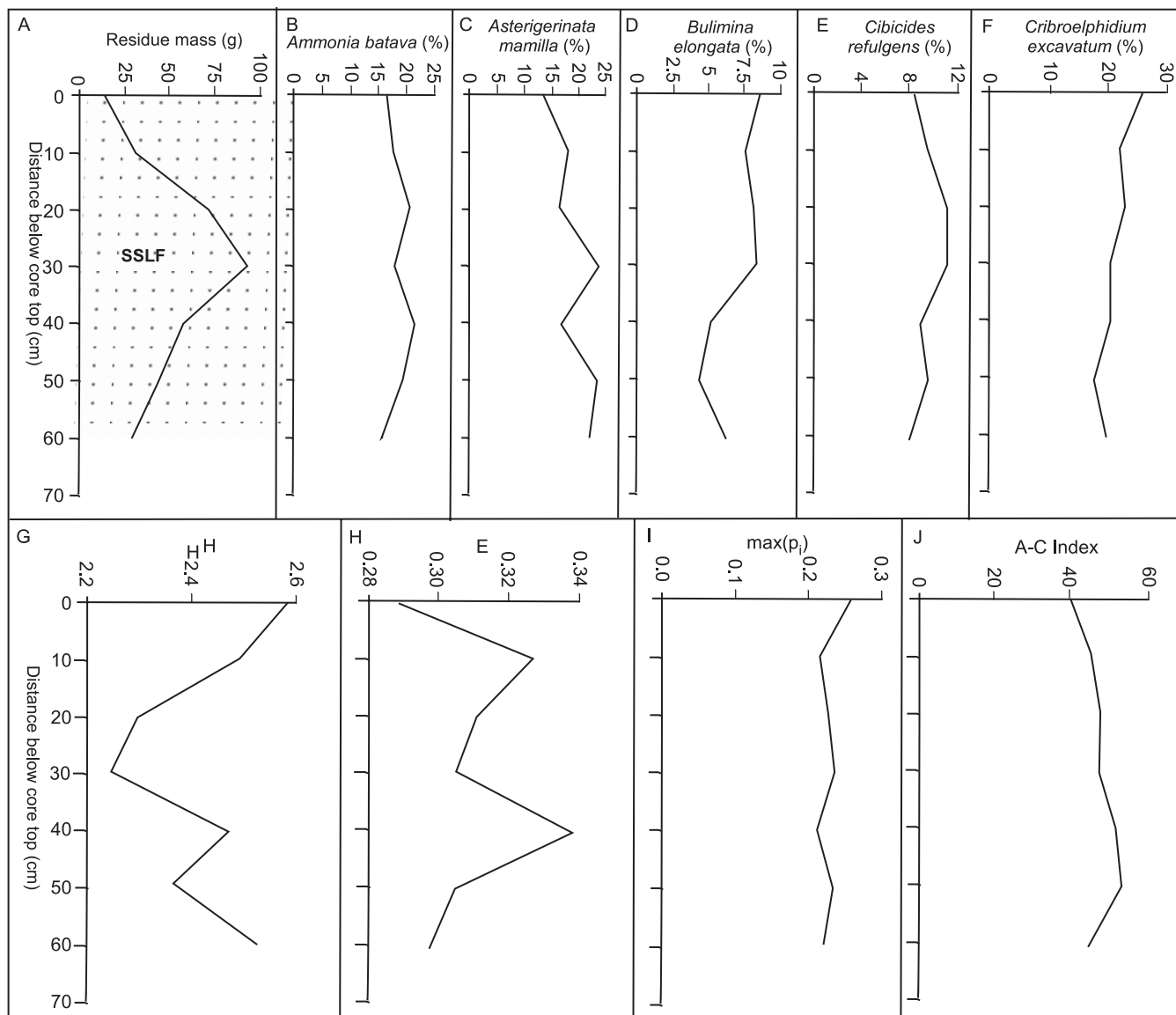


FIGURE 5. Residue masses, proportional abundances of selected morphospecies and single sample statistical measures in Core ISLF16. A. Residue masses in grams. B. *Ammonia batava*. C. *Asterigerinata mamilla*. D. *Bulimina elongata*. E. *Cibicides refulgens*. F. *Cribroelphidium excavatum*. G. The Shannon Function, H. H. The Equitability Index, E. I. The Berger-Parker Index, $\max(p_i)$. J. The *Ammonia-Cribroelphidium* (A-C) Index.

the structure of the assemblage, some species being more susceptible to dissolution than others (see Nguyen et al., 2009; Schnitker et al., 1980). The carbonate dissolution may have been associated with high acidity of pore water on the muddy tidal flat, which would also promote the formation of pyrite (Pons et al., 1982). The gypsum in the SSLF sample 180–182 cmbsf is taken to reflect reworking of the GLF during early SSLF times.

Stratification in ISLF13 GLF of the sediment and foraminiferal assemblages, with corroded gypsum at 250–252 cmbsf and abundant, large and well-preserved *A. batava* at 230–232 cmbsf, suggests that any transport and reworking of sediment and foraminifera by currents on the GLF tidal flats did not penetrate deeply. The *A. batava* are likely to be allochthonous, this species not living on the muddy portion

of tidal flats (Langer et al., 1989, fig. 5). Species indicative of open marine environments (*A. mamilla*, *B. elongata*), though recovered more abundantly from the SSLF, were also recovered from the GLF. We suggest that these specimens were washed onto the GLF tidal flat during storms (see Collins et al., 1999; Hippensteel et al., 2005; Scott et al., 2005), such as can inundate the supratidal zone under extreme conditions (Gao, 2019). That these open marine foraminifera were found throughout the GLF shows that such shoreward transport was frequent, the abundant *A. batava* at 230–232 cmbsf possibly indicating a particularly strong storm. They may have been derived from an adjacent sandy tidal flat, although this species has also been found living in deeper neritic water in the Celtic Sea (Scott et al., 2003). The reason for the decrease of the A-C Index through the GLF is un-

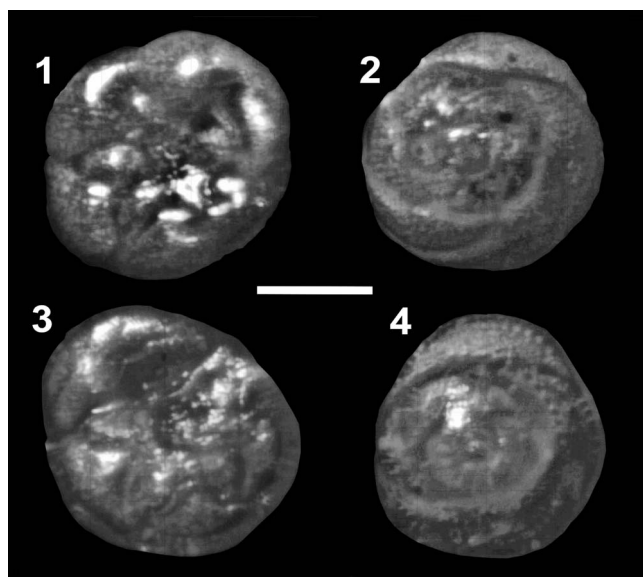


FIGURE 6. *Asterigerinata murraynhaynesi* n. sp. and *A. mamilla* (Williamson). 1 *Asterigerinata murraynhaynesi* holotype, ventral view, showing rounded periphery. 2 *Asterigerinata murraynhaynesi* holotype, dorsal view, showing absence of carina and associated pores throughout ontogeny. 3 *Asterigerinata mamilla*, ventral view, showing angular periphery. 4 *Asterigerinata mamilla*, dorsal view, showing carina and associated pores, present throughout ontogeny.

clear. It is not related to the abundance of sand, the substrate preferred by *A. batava*. It might instead suggest a decrease in the severity of storm-induced transport through GLF times, decreasing the input of *A. batava* tests.

The allochthonous specimens on the GLF tidal flat would augment the largely autochthonous assemblage, disrupting the in situ richness signal by increasing overall richness. As a result of this transport, rarefied S in Core ISLF 10013 did not differ significantly between the GLF and the SSLF.

Most specimens recovered in this study belong to free species that are either infaunal (*A. batava*, *B. elongata*, *C. excavatum*) or epifaunal (*A. mamilla*) (de Nooijer et al., 2008; Murray, 2006). Some common morphospecies in the SSLF in both cores (*C. refulgens*, *L. lobatula*), however, have flattened dorsal surfaces indicative of an attached habit (Dubicka et al., 2015). In the absence of widespread macroflora in Liverpool Bay, these attached morphospecies might in the open marine environment have lived on either the scallop *Chlamys opicularis* or the isopod *Astacilla longicornis*. The tests of such morphospecies on death become detached and act as sediment particles subject to transport (Coulbourn & Resig, 1975; Debenay, 1988; Li et al., 1997; Wilson, 2006). We did not, however, find abundant juvenile *C. opicularis* in our residues. The common presence of attached morphospecies might instead reflect the strength of the tidal bottom currents, which may have transported them from shallow, rocky areas that would support macroalgae, such as around Anglesey to the west. Such a provenance is in accord with the general eastward transport of sediment within Liverpool Bay. With the exception of some worn *A. batava* and *C. refulgens*, the fresh preservation of the majority of our benthic foraminifera in the SSLF in both cores suggests, however, that they underwent limited abrasive transport prior

to being absorbed into the taphocoenosis, despite the strong currents (Plater and Grenville, 2010), low sedimentation rate (Kershaw et al., 1988) and generally deep reworked surficial Layer A (Jackson et al., 1995; Pantin & Evans, 1984) throughout the bay.

The ISLF13 SSLF contained broken and whole bivalves, and gastropods (*Turritella communis*) that were generally pristine. These macrofauna reflect a high organic matter concentration (Younge, 1946) that is indicated also by the high proportional abundance of *C. excavatum*. The penetration depth of *T. communis* is in accordance with the depth of mixing of man-made metals (Crickmore and Kiff, 1985), but we did not note any impact, such as deformed tests, from such metals. This may be because we did not sample Layer A in ISLF13, and that ISLF16 did not extend upwards to modern times.

Having concluded that the foraminiferal assemblage in the SSLF in both cores contained many allochthonous specimens, we can draw only the broadest of palaeoenvironmental inferences. These will be general comparisons between the GLF and SSLF, with few site-specific conclusions.

The A-C Index might in ISLF13 indicate a change in the flux of organic matter between the two lithofacies (cf. Sen Gupta et al. 1996), it being markedly higher in the SSLF (abundance biozones AB₃₁₃, AB₄₁₃) than in the GLF (AB₁₁₃, AB₂₁₃). It might also indicate that the SSLF was subject to hypoxia, although the common molluscs dispute this. It is more likely that it reflects *A. batava*'s preference for the sandier deposits of the SSLF and suggests that care must be taken when interpreting the A-C Index and the A-E one too, attention being paid to the sedimentological setting also.

The increase in the proportional abundance of epifaunal *A. mamilla* and infaunal *B. elongata*, detected by CoBI at the AB₂₁₃/AB₃₁₃ boundary, reflects the change to the more open marine aspect of the ISLF 13 SSLF. Mendes et al. (2004) found *B. elongata* to live mostly between 12–40 m and suggested *A. mamilla* to live in shallower water, down to 12 m depth, though Frezza et al. (2011) found this morphospecies to 13.5m. We conclude the *A. mamilla* were transported to ISLF13 site (~40 m water depth). This contrasts the shoreward, eastward transport of sediment in the bay. It might reflect seaward transport during storms. Evidence for long-distance transport of the *A. mamilla* is limited, however, specimens of this and other foraminiferal morphospecies in ISLF13 SSLF showing few signs of abrasion that would be expected from long-distance transport (see Franceschini & Compton, 2007).

In ISLF13 diversity was greater, and species' abundances more equitably distributed, in the open marine SSLF compared to the tidal flat GLF. In contrast, dominance was less in the SSLF than in the GLF. On the basis of the size fraction from which specimens were recovered, we found that the specimens of *C. excavatum* were smaller in the GLF than in the SSLF. We take this to reflect higher salinities in the SSLF, though an impact of a higher organic matter flux on test size or of hydrodynamic sorting in the SSLF cannot be ruled out.

Despite the geographical proximity of the cores, morphospecies abundances differed in AB₄₁₃ (the youngest in ISLF13) and AB₁₁₆. It is possible that the greater proportional abundance of *A. batava* in AB₁₁₆ reflects the closer

proximity of this core to the nutrient-rich N-S front within the bay (cf. Greenwood et al., 2011). However, given the allochthonous nature of the SSLF assemblages, this appears unlikely. Instead, the difference in the assemblages might be related to differences in hydrodynamic sorting due to different positions of the two cores relative to the large sand waves at the core sites.

FORAMINIFERAL TAXONOMY

Superfamily ASTERIGERINOIDEA d'Orbigny, 1839

Family ASTERIGERINATIDAE Reiss, 1963

Genus *Asterigerinata* Bermúdez, 1949

Type species: *Asterigerinata dominicana* Bermúdez, 1949

Asterigerinata murrayhaynesi n. sp.

Figures 6.1, 6.2

1973 *Asterigerinata mamilla* Haynes (pars) p. 164–167; pl. 18, figs. 1, 4 (not Williamson).

Derivation of name: After Professors John Murray and John Roland Haynes for their contributions to British micropalaeontology.

Type Specimens: Deposited in the European Micropaleontological Reference Centre, Kraków Poland, and catalogued as number 7/27c (holotype [cell 1] and two unfigured paratypes [cell 2]).

Description: test plano-convex, low to medium trochospiral, three to four whorls visible on the rounded, evolute dorsal side; ventral side involute; periphery rounded, entire, becoming slightly lobate; maximum 12 crescentic chambers visible on dorsal side, increasing in breadth so final chamber occupies about a quarter of the final whorl; dorsal sutures limbate, flush, strongly backward curved; 4.5 chambers visible on ventral side, alternating towards umbilicus with subrhomboidal supplementary chamberlets, giving a stellate appearance; ventral sutures irregularly curved, depressed between chamberlets; wall thick and glassy; aperture a high, umbilical arch at the base of the final chamber, with a narrow lip.

Material: 19 specimens, all from the Holocene SL1 Member of the Surface Sands Formation, Liverpool Bay; 12 specimens from Core ISLF13, 7 specimens from Core ISLF16.

Estimated age: Holocene

Holotype: from Core ISLF13, 160–160 cmbsf.

Dimensions: diameter, 250 µm, height, 150 µm.

Paratypes: three specimens from core ISLF13, 140–142 cmbsf.

Remarks: Haynes (1973, pl. 18, fig. 4) presented an oblique ventral view of a specimen that he called *Asterigerinata mamilla* and termed a 'juvenile with a rounded periphery'. His pl. 18, fig. 1 is also of a peripherally rounded specimen, although he does not state this to be a juvenile. The holotype illustration of *A. mamilla* by Williamson (1858, figs. 109–111) in contrast shows a decidedly conical specimen with a distinct carina marked by what he termed a 'marginal row of elongated white foramina' (ibid., p. 55). Our specimens of *Asterigerinata murrayhaynesi* n. sp. (Figures 6.1, 6.2) have a rounded periphery, are gently domed dorsally and lack both a marginal carina and the row of pores that would throughout the test mark the inner edge of that carina (see Haynes, 1973 pl. 19, fig. 9; Murray, 1971, pl. 59.1). We did not in

our 1,480 specimens of *A. mamilla* find any that showed a transition from a rounded to a sharp periphery. Our specimens of *A. murrayhaynesi* n. sp. were not smaller than our *A. mamilla* (illustrated for comparison, Figures 6.3, 6.4). We are therefore confident that our specimens are from a previously unnamed species.

CONCLUSIONS

The Holocene succession in central Liverpool Bay includes an older lithofacies (the GLF) with much mud and some gypsum indicative of a muddy tidal flat. This we ascribed to the SL2 Member. The foraminiferal assemblage there showed high dominance by infaunal *Criboelphidium excavatum*, which are presumed to be largely in situ, wave action being strongly damped on such flats. However, an allochthonous component of sandy tidal flat (*Ammonia batava*) and marine (*Asterigerinata mamilla*, *Bulimina elongata*) morphospecies in this facies is indicative of shoreward transport of offshore material onto the tidal flat, possibly during storms. The gypsum was diagenetic, the calcium perhaps being derived from foraminiferal tests and the sulphate from pyrites, which commonly either filled or completely replaced the *C. excavatum* tests. Perturbation detection analysis (PDA) detected two abundance biozones (ABs) in the tidal flat succession and showed that the community structure of the contained assemblages was in stasis in both. The AB boundary may be related to the high level of assemblage turnover, as quantified using the between-sample assemblage turnover index (ATI_s), coupled with a decrease in the *Ammonia-Criboelphidium* index through the younger of the ABs in the muddy tidal flat lithofacies.

The muddy tidal flat was succeeded by a marine shelly sand (the SSLF lithofacies) with large gastropods. This we ascribed to the SL1 Member. The absence of an intervening sandy tidal flat deposit reflects the erosive nature of the surface separating the two lithofacies (members).

The foraminiferal assemblages in this shelly sand contained abundant inner neritic (*A. mamilla*) and middle neritic (*B. elongata*) species, and are concluded to comprise almost entirely allochthonous material, much being derived from epiphytal communities. This is supported by the strong tidal currents in this area, the velocity of which exceed the traction currents needed to transport benthic foraminifera and which generally transport the bedload shorewards. Only the broadest of palaeoenvironmental interpretations can be made using these allochthonous assemblages.

Assemblage turnover was lower in the ISLF13 SSLF than in the GLF. The higher *Ammonia-Criboelphidium* Index in the SSLF might reflect the preference of *A. batava* for sandy deposits, while the low values for this index in the GLF might reflect the small allochthonous input of *A. batava* compared to the indigenous *C. excavatum*. This index cannot, therefore, be taken as unequivocally indicating that the organic matter flux was higher in the sandy, marine lithofacies than in the muddy GLF.

The total assemblages from the two sections from the SSLF differed in their species' proportional abundances. Given the proximity of the cores, this difference is thought to reflect the cores' positions relative to the large sand waves between which they were collected. This might have resulted in

differences in hydrodynamic sorting of the foraminiferal assemblages. This difference is reflected also in the PDA, which showed the SSLF assemblages in one core to be in stasis, and in the other to be growing.

As a result of this work, we recommend using not only individual sample indices when working on a successions of samples from cores, but also Perturbation Detection Analysis (PDA), which will identify community-level patterns of stasis, growth or decline within them. Using this range of analyses will reveal differences between the foraminiferal successions and within the assemblages that are of previously-undetected palaeoenvironmental importance.

ACKNOWLEDGMENTS

Thanks are due to Martin Bates, University of Wales, Trinity St. David, Lampeter, who provided the samples from these cores and for insightful discussions. Thanks are also due to the staff at the Cardigan Bay Marine Wildlife Centre (Sarah Perry, Laura Evans, Gemma Woodford) for taking time to discuss matters in this paper. Copies of much of the older foraminiferal literature cited here were provided by the late John Murray. We are grateful for this opportunity to expand on the quantitative techniques developed by Marty Buzas and his colleagues, including the junior author. Marty provided much encouragement to the senior author throughout his career.

REFERENCES

- Aldridge, J. N., and Davies, A. M., 1993, A High-Resolution Three-Dimensional Hydrodynamic Tidal Model of the Eastern Irish Sea: *Journal of Physical Oceanography*, v. 23, p. 207–224.
- Alve, E., and Murray, J. W., 2001, Temporal variability in vertical distributions of live (stained) intertidal foraminifera, southern England: *Journal of Foraminiferal Research*, v. 31, p. 12–24.
- Atkinson, K., 1971, The relationship of Recent foraminifera to the sedimentary facies in the turbulent zone, Cardigan Bay: *Journal of Natural History*, v. 5, p. 385–439.
- Bain, R. J., 1990, Diagenetic, nonevaporative origin for gypsum: *Geology*, v. 18, p. 447–450.
- Beardall, J., Foster, P., Voltolina, D., and Savidge, G., 1982, Observations on the surface water characteristics in the western Irish Sea: July 1977: *Estuarine, Coastal and Shelf Science*, v. 14, p. 589–598.
- Beck, C., Clabaut, P., Dewez, S. O. V., Chamley, H., Augris, C., Hoslin, R., and Caillot, A., 1991, Sand bodies and sand transport paths at the English Channel-North Sea border: Morphology, hydrodynamics and radioactive tracing: *Oceanologica Acta*, Special issue v. 11, p. 111–121.
- Bermúdez, P. J., 1949, Tertiary smaller foraminifera of the Dominican Republic. Cushman Laboratory for Foraminiferal Research, Special Publication 25, 322 p.
- Boggs Jr, S., 2006, *Principles of Sedimentology and Stratigraphy*. Pearson Education, New Jersey, USA, 688 p.
- Bowden, K. F., and Sharaf El Din, S. H., 1966, Circulation and mixing processes in the Liverpool Bay area of the Irish Sea: *Geophysical Journal International* v. 11, p. 279–292.
- Buzas-Stephens, P., Pessagno, Jr., E. A., and Bowen C. J., 2002, A review of species names for *Ammonia* and *Elphidium*, common foraminifera along the Texas Gulf Coast: *The Texas Journal of Science* v. 54, p. 3–16.
- Charman, D. J., 2010, Centennial climate variability in the British Isles during the mid-late Holocene: *Quaternary Science Reviews*, v. 29, p. 1539–1554.
- Collins, E. S., Scott, D. B., and Gayes, P. T., 1999, Hurricane records on the South Carolina coast: Can they be detected in the sediment record?: *Quaternary International*, v. 56, p. 15–26.
- Coulbourn, W. T., and Resig, J. M., 1975, On the use of benthic foraminifera as sediment tracers in a Hawaiian bay: *Pacific Science*, v. 29, p. 99–115.
- Crickmore, M. J. and Kiff, P. R., 1985, Vertical profiles of heavy metals and organic carbon in sediments of eastern Liverpool Bay. Hydraulics Research Limited Wallingford, Oxfordshire, UK, 13 p.
- Daidu, F., Yuan, W., and Min, L., 2013, Classifications, sedimentary features and facies associations of tidal flats: *Journal of Palaeogeography*, v. 2, p. 66–80.
- Darling, K. F., Schweizer, M., Knudsen, K. L., Evans, K. M., Bird, C., Roberts, A., Filipsson, H. L., Kim, J.-H., Gudmundsson, C., Wade, C. M., Sayer, M. D. J. and Austin, W. E. N., 2016, The genetic diversity, phylogeography and morphology of Elphidiidae (Foraminifera) in the Northeast Atlantic: *Marine Micropaleontology*, v. 129, p. 1–23.
- de Nooijer, L. J., Duijnste, I. A. P., Bergman, M. J. N. and van der Zwaan, G. J., 2008, The ecology of benthic foraminifera across the Frisian Front, southern North Sea: *Estuarine, Coastal and Shelf Science*, v. 78, p. 715–726.
- Debenay, J.-P., 1988, Recent foraminifera tracers of oceanic water movements in the southwestern lagoon of New Caledonia: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 65, p. 59–72.
- d'Orbigny, A. D., 1839, Foraminifères, in Sagra, R. de la., *Histoire physique, politique et naturelle de l'île de Cuba*: A. Bertrand, Paris, France, 224 p.
- Dubicka, Z., Zlotnik, M., and Borszcz, T., 2015, Test morphology as a function of behavioral strategies — Inferences from benthic foraminifera: *Marine Micropaleontology*, v. 116, p. 38–49.
- Earland, A., 1902, A plea for a new 'Williamson': *Journal of the Quekett Microscopical Club*, Ser. 2, v. 8, p. 268–270.
- Edwards, P. G., 1982, Ecology and distribution of selected foraminiferal species in the North Minch Channel, northwestern Scotland, in F. T. Banner and A. R. Lord (eds.), *Aspects of Micropalaeontology*: Springer Netherlands, Dordrecht: p. 111–141.
- Eichler, P. P. B., and Barker, C. P. 2020, *Benthic Foraminiferal Ecology: Indicators of Environmental Impacts*: Springer Nature, Switzerland, 226 p.
- Evans, R. G., 1947, The intertidal ecology of Cardigan Bay: *Journal of Ecology*, v. 34, p. 273–309.
- Fan, D., 2012, Open-Coast Tidal Flats, in R. Davis, Jr. (ed.), *Principles of Tidal Sedimentology*: Springer, Dordrecht, Germany, p. 187–229.
- Franceschini, G., and Compton, J. S., 2007, Abrasion of foraminifera tests along an active dune cordon, Western Cape, South Africa: *Palaos*, v. 22, p. 686–690.
- Frezza, V., Mateu-Vicens, G., Gaglianone, G., Baldassarre, A., and Brandano, M., 2011, Mixed carbonate-siliclastic sediments and benthic foraminiferal assemblages from *Posidonia oceanica* seagrass meadows of the central Tyrrhenian continental shelf (Latium, Italy): *Italian Journal of Geosciences*, v. 130, p. 352–369.
- Gabel, B., 1971, Die Foraminiferen der Nordsee: *Heligoland Marine Research*, v. 1971, p. 1–65.
- Gao, S., 2019, Geomorphology and Sedimentology of Tidal Flats, in G. M. E. Perillo, et al. (eds.), *Coastal Wetlands (Second Edition)*: Elsevier, Amsterdam, Netherlands, p. 359–381.
- Greenwood, N., Hydes, D., Mahaffey, C., Wither, A., Barry, J., Sivyer, C., Pearce, D., Hartman, S., Andres, O., and Lees, H., 2011, Spatial and temporal variability in nutrient concentrations in Liverpool Bay, a temperate latitude region of freshwater influence: *Ocean Dynamics*, v. 61, p. 2181–2199.
- Hammer, Ø. and Harper, D. A. T., 2005, *Paleontological Data Analysis*: Wiley-Blackwell, Oxford, UK, 368 p.
- Haward, N. J. B., and Haynes, J. R., 1976, *Chlamys opercularis* (Linnaeus) as a mobile substrate for foraminifera: *Journal of Foraminiferal Research*, v. 6, p. 30–38.
- Hayek, L. C., and Buzas, M. A., 2010, *Surveying Natural Populations: Quantitative Tools for Assessing Biodiversity*: Columbia University Press, New York, USA, 590 p.
- Hayek, L. C., and Buzas, M. A., 2013, On the proper and efficient use of diversity measures for individual field samples: *Journal of Foraminiferal Research*, v. 43, p. 305–313.
- Hayek, L. C., and Buzas, M. A., and Osterman, L. E., 2007, Community structure of foraminiferal communities within temporal

- biozones from the western Arctic Ocean: *Journal of Foraminiferal Research*, v. 37, p. 33–40.
- Hayek, L. C., and Buzas, M. A., and Thomas, E., 2019, Identifying disruptions to the ecological balance of nature: a foraminiferal example across the initiation of the Paleocene–Eocene thermal maximum: *Paleobiology*, v. 45, p. 98–113.
- Hayek, L. C., and Wilson, B., 2013, Quantifying assemblage turnover and species contributions at ecologic boundaries: *PLoS ONE*, v. 8, p. e74999.
- Haynes, J. R., 1964, Live and dead foraminifera between the Sarns, Cardigan Bay: *Nature*, v. 204, p. 774.
- Haynes, J. R., 1973, Cardigan Bay Recent foraminifera (Cruises of the R. V. Antur, 1962–1964): *Bulletin of the British Museum (Natural History)*, Supplement 4, p. 1–245.
- Haynes, J. R., .. Kiteley, R. J., Whatley, R. C., and Wilks, P. J., 1977, Microfaunas, microfloras and the environmental stratigraphy of the Late Glacial and Holocene in Cardigan Bay: *Geological Journal*, v. 12, p. 129–158.
- Hayward, B. W., and Ryland, J. S., 1990, *Handbook of the Marine Fauna of North-West Europe*: Oxford University Press, England, 860 p.
- Heron-Allen, E., and Earland, A., 1909, On the recent and fossil foraminifera of the shore-sands of Selsey Bill, Sussex – IV: *Journal of the Royal Microscopical Society*, v. 1909, p. 677–698.
- Heron-Allen, E., and Earland, A., 1910, On the recent and fossil foraminifera of the shore-sands of Selsey Bill, Sussex. – VI. A Contribution towards the aetiology of *Massilina secans* (d'Orbigny sp.): *Journal of the Royal Microscopical Society*, v. 30, p. 693–695.
- Heron-Allen, E., and Earland, A., 1916, XIII. The foraminifera of the west of Scotland. Collected by Prof. W. A. Herdman, on the cruise of the S. Y. 'Runa,' July–Sept. 1913. Being a contribution to 'Spolia Runiuna': *Transactions of the Linnean Society of London*, v. 11, p. 197–300.
- Heron-Allen, E., and Earland, A., 1930a, The foraminifera of the Plymouth District, I: *Journal of the Royal Microscopical Society*, v. 50, p. 46–84.
- Heron-Allen, E., and Earland, A., 1930b, The foraminifera of the Plymouth District, II: *Journal of the Royal Microscopical Society*, v. 50, p. 161–199.
- Hippensteel, S. P., Martin, R. E., and Harris M. S., 2005, Records of prehistoric hurricanes on the South Carolina coast based on micropaleontological and sedimentological evidence, with comparison to other Atlantic Coast records: *Discussion: Geological Society of America Bulletin*, v. 117, p. 250–253.
- Hofker, J., 1977, The foraminifera of Dutch tidal flats and salt marshes: *Netherlands Journal of Sea Research*, v. 11, p. 223–296.
- Holmes, R., and Tappin, D. R., 2005, DTI strategic environmental assessment area 6, Irish Sea, seabed and surficial geology and processes: *British Geological Survey Commissioned Report CR/05/057*, 72 p.
- Horton, B. P., and Edwards, J. C., 2006, Quantifying Holocene sea-level change using intertidal foraminifera: Lessons from the British Isles: *Cushman Foundation for Foraminiferal Research, Special Publication 40*, 97 p.
- Howarth, M. J., 2005, Hydrography of the Irish Sea: SEA6 Technical Report, POL Internal Document 174, UK Department of Trade and Industry, 30 p.
- Jackson, D. I., Jackson, A. A., Evans, D., Wingfield, R. T. R., Barnes, R. P., and Arthur, M. J., 1995, *United Kingdom Offshore Regional Report: The Geology of the Irish Sea: Her Majesty's Stationary Office, London, for the British Geological Survey*, 123 p.
- Kenyon, N. H., and Cooper, B., 2005, Sand Banks, Sand Transport and Offshore Wind Farms: *Kenyon Marine Geo and ABP Marine Environmental Research Ltd.*, 106 p.
- Kershaw, P. J., Swift, D. J., and Denoon, D. C., 1988, Evidence of recent sedimentation in the eastern Irish Sea: *Marine Geology*, v. 85, p. 1–14.
- Konradi, P. B., 2000, Biostratigraphy and environment of the Holocene marine transgression in the Heligoland Channel, North Sea: *Bulletin of the Geological Society of Denmark*, v. 47, p. 71–79.
- Korsun, S., Hald, M., Golikova, E., Yudina, A., Kuznetsov, I., Mikhailov, D., and Knyazeva, O., 2014, Intertidal foraminiferal fauna and the distribution of Elphidiidae at Chupa Inlet, western White Sea: *Marine Biology Research*, v. 10, p. 153–166.
- Langer, M., 1993, Epiphytic foraminifera: *Marine Micropaleontology*, v. 20, p. 235–265.
- Langer, M., Hottinger, L., and Huber, B., 1989, Functional morphology in low-diverse benthic foraminiferal assemblages from tidal flats of the North Sea: *Senckenbergiana Maritima*, v. 20, p. 81–89.
- Larcombe, P., and Jago, C. F., 1994, The late Devensian and Holocene evolution of Barmouth Bay, Wales: *Sedimentary Geology*, v. 89, p. 163–180.
- Lee, O., Nash, R. D. M., and Danilowicz, B. S., 2005, Small-scale spatio-temporal variability in ichthyoplankton and zooplankton distribution in relation to a tidal-mixing front in the Irish Sea: *ICES Journal of Marine Science*, v. 62, p. 1021–1036.
- Li, C., Jones, B., and Blanchon, P., 1997, Lagoon-shelf sediment exchange by storms: Evidence from foraminiferal assemblages, east coast of Grand Cayman, British West Indies: *Journal of Sedimentary Research*, v. 67, p. 17–25.
- Luo, J., Li, M., Sun, Z., and O'Connor, B. A., 2013, Numerical modelling of hydrodynamics and sand transport in the tide-dominated coastal-to-estuarine region: *Marine Geology*, v. 342, p. 14–27.
- Mellett, C. L., Long, D., and Carter, G., 2015, *Geology of the seabed and shallow subsurface: The Irish Sea: British Geological Survey Commissioned Report*, v. CR/15/057, 52 p.
- Mendes, I., Gonzalez, R., Dias, J. M. A., Lobo, F., and Martins, V., 2004, Factors influencing recent benthic foraminifera distribution on the Guadiana shelf (Southwestern Iberia): *Marine Micropaleontology*, v. 51, p. 171–192.
- Mills, D. J. L., 1998, Liverpool Bay to the Solway (Rhos-on-Sea to the Mull of Galloway) (MNCR Sector 11), in K. Hiscock (ed.), *Marine Nature Conservation Review, Benthic Marine Ecosystems of Great Britain and the Northeast Atlantic Ocean*, Joint Nature Conservation Committee (Coasts and seas of the United Kingdom. MNCR series) Peterborough, U. K., p. 315–338.
- Moore, P. G., 1985, *Cibicides lobatulus* (Protozoa: Foraminifera) epizoic on *Astacilla longicornis* (Crustacea: Isopoda) in the North Sea: *Journal of Natural History*, v. 19, p. 129–133.
- Murray, J. W., 1971, *Atlas of British Recent Foraminiferids*. American Elsevier Publishing Company Inc., New York, USA, 244 p.
- Murray, J. W., 2000, Revised taxonomy, An Atlas of British Recent Foraminiferids: *Journal of Micropaleontology*, v. 19, p. 44.
- Murray, J. W., 2003, An illustrated guide to the benthic foraminifera of the Hebridean shelf, west of Scotland, with notes on their mode of life: *Palaeontologia Electronica*, v. 5, 31 p.
- Murray, J. W., 2006, *Ecology and Applications of Benthic Foraminifera*: Cambridge University Press, U. K., 438 p.
- Murray, J. W., Sturrock, S., and Weston, J., 1982, Suspended load transport of foraminiferal tests in a tide- and wave-swept sea: *Journal of Foraminiferal Research*, v. 12, p. 51–65.
- NBN Atlas Wales, 2021, *Astacilla longicornis* (Sowerby, 1806). Volume 2022, NBN Atlas Partnership. <https://wales-species-inns.nbnatlas.org/species/NBNSYS0000173993>. Accessed 25/02/2022.
- Nguyen, T. M. P., Petrizzo, M. R., and Speijer, R. P., 2009, Experimental dissolution of a fossil foraminiferal assemblage (Paleocene–Eocene Thermal Maximum, Dababiya, Egypt): Implications for paleoenvironmental reconstructions: *Marine Micropaleontology*, v. 73, p. 241–258.
- Pantin, H. M., and Evans, C. D. R., 1984, The Quaternary history of the central and southwestern Celtic Sea: *Marine Geology*, v. 57, p. 259–293.
- Paterson, D. M., Fortune, I., Aspden, R. J., and Black, K. S., 2019., Intertidal Flats: Form and Function: in G. M. E. Perillo et al. (eds.), *Coastal Wetlands (Second Edition)*, Elsevier, p. 383–406.
- Plater, A. J., and Grenville, J., 2010, Liverpool bay: Linking the eastern Irish Sea to the Sefton coast: in A. T. Worsley et al. (eds.), *Sefton's Dynamic Coast: Coastal Defence, Sefton MBC Technical Services Department, Ainsdale-on-Sea, Southport, U. K.*, p. 28–54.
- Polton, J. A., Palmer, M. R., and Howarth, M. J., 2011, Physical and dynamical oceanography of Liverpool Bay: *Ocean Dynamics*, v. 61, p. 1421–1439.
- Pons, L. J., Van Breemen, N., and Driessen, P. M., 1982, Physiography of coastal sediments and development of potential soil acidity, in J. Kittrick et al. (eds.), *Acid Sulfate Weathering: Soil Science Society of America, Inc.*, p. 1–18.
- Ramster, J. W., and Hill, H. W., 1969, Current system in the northern Irish Sea: *Nature*, v. 224, p. 59–61.

- Reiss, Z., 1963, Reclassification of perforate foraminifera: Bulletin of the Geological Survey of Israel, v. 35, p. 1–111.
- Roberts, M. J., Scourse, J. D., Bennell, J. D., Huws, D. G., Jago, C. F., and Long, B. T., 2011, Late Devensian and Holocene relative sea-level change in North Wales, UK: Journal of Quaternary Science, v. 26, p. 141–155.
- Saraswati, P. K., 2021, Foraminiferal Micropaleontology for Understanding Earth's History: Elsevier, Amsterdam, Netherlands, 329 p.
- Schnitker, D., Mayer, L. M., and Norton, S., 1980, Loss of calcareous microfossils from sediments through gypsum formation: Marine Geology, v. 36, pt. 3, M35–M44.
- Scott, D. B., Collins, E. S., Gayes, P. T., and Wright, E., 2005, Reply: Geological Society of America Bulletin, v. 117, p. 254–256.
- Scott, G. A., Scourse, J. D., and Austin, W. E. N., 2003, The distribution of benthic foraminifera in the Celtic Sea: The significance of seasonal stratification: Journal of Foraminiferal Research, v. 33, p. 32–61.
- Sen Gupta, B. K., and Platon, E., 2006, Tracking past sedimentary records of oxygen depletion in coastal waters: Use of the *Ammonia-Elphidium* Foraminiferal Index: Journal of Coastal Research, v. 39, p. 1351–1355.
- Sen Gupta, B. K., Turner, R. E., and Rabalais, N. N., 1996, Seasonal oxygen depletion in continental-shelf waters of Louisiana: Historical record of benthic foraminifers: Geology, v. 24, p. 227–230.
- Snyder, S. W., Hale, W. R., and Kontrovitz, M., 1990, Assessment of post mortem transportation of modern benthic foraminifera of the Washington continental shelf: Micropaleontology, v. 36, p. 259–282.
- Walker, G., and Boys, W., 1784, *Testacea Minuta Rariora Nuperrime Detecta in Arena Littoris Sandvicensis (A Collection of the Minute and Rare Shells Recently Discovered in the Sand of the Sea Shore Near Sandwich)*, J. March, London, U. K., 25 p.
- Wallingford, H., Haskoning, P., and d'Olier, B., 2002, *Southern North Sea Sediment Transport Study, Phase 2*, H. R. Wallingford, Wallingford, Oxford, U. K., 94 p.
- Walton, W. R., 1952, Techniques for recognition of living foraminifera: Contributions from the Cushman Foundation for Foraminiferal Research, v. 3, p. 56–60.
- Watson, A., 1985, Structure, chemistry and origins of gypsum crusts in southern Tunisia and the central Namib Desert: Sedimentology, v. 32, p. 855–875.
- Williamson, W. C., 1858, On the Recent Foraminifera of Great Britain: Ray Society, London, UK, 107 p.
- Wilson, B., 2006, The environmental significance of some microscopic organisms around Nevis, West Indies: West Indian Journal of Engineering, v. 28, p. 53–64.
- Wilson, B., 2008, Using SHEBI (She Analysis for Biozone Identification): To proceed from the top down or the bottom up? A discussion using two Miocene foraminiferal successions from Trinidad, West Indies: Palaios, v. 23, p. 637–645.
- Wilson, B., and Kaminski, M., 2023, Rare species of West Indian aspect in the Holocene of Liverpool Bay and their biogeographic and environmental significance: Micropaleontology, v. 69, p. 103–112.
- Younge, C. M., 1946, On the habits of *Turritella communis* Risso: Journal of the Marine Biological Association of the United Kingdom, v. 26, p. 377–380.

Received 27 January 2023
Accepted 14 April 2023

