SEASONAL DISTRIBUTIONS OF FORAMINIFERA AND THEIR IMPLICATIONS FOR SEA-LEVEL STUDIES, COWPEN MARSH, U.K.

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ABSTRACT: Analyses of total abundance of dead foraminifera from a twelve-month study of surface samples (0–1 cm) from Cowpen Marsh shows no definite seasonal pattern, but significant seasonal variations are evident in the relative abundance of agglutinated and calcareous taxa. Agglutinated species are most dominant in the winter months whilst calcareous foraminifera reach their peak relative abundances during the summer. We identify three cluster zones: a high-marsh and middle-marsh zone of *Jadammina macrescens* and *Trochammina inflata*; a low-marsh zone of *Miliammina fusca* and *Jadammina macrescens*; and a mudflat zone of calcareous foraminiferal species, notably *Elphidium williamsoni*, *Haynesina germanica*, and *Quinqueloculina* spp. The variations of contemporary foraminiferal distribution across the intertidal zone during an annual cycle modify the elevation of the zonal boundaries by as much as 0.9 m. Consequently, a contemporary sample taken in one month can significantly underestimate (0.35 m) or overestimate (0.48 m) the elevation range of a zone. Hence, the value of cluster zones as indicators of former sea levels can be assessed only following a consideration of the elevation errors induced by the seasonal variability in saltmarsh foraminiferal distributions.

We developed monthly and annual foraminifera-based transfer functions using weighted averaging regression and calibration. Results suggest that precise reconstructions of former sea levels are possible ($r^2 \geq 0.82$) but that the accuracy of these reconstructions varies during the course of the year. Greatest precision is achieved using samples collected in the winter months (± 0.29 m) and weakest during the summer (± 0.35 m) because the foraminiferal assemblages are dominated by agglutinated and calcareous species, respectively. We conclude that an investigation of contemporary saltmarsh foraminifera that recovers a complete set of samples in the winter, spring, summer, and autumn will provide the best-quality data for use in sea-level investigations (error = ± 0.21 m). If only one set of measurements can be obtained, sampling in the winter months may represent the most reliable alternative.

INTRODUCTION

Reconstruction of former sea levels on the basis of identification and interpretation of fossil foraminiferal assemblages requires an understanding of contemporary vertical distributions. Contemporary investigations carried out on the Atlantic and the Pacific Coasts of North America and the Atlantic seaboard of Europe demonstrate that saltmarsh foraminifera are vertically zoned in a way similar to that of floral assemblages but that these zonations are more tightly constrained. In particular, high-marsh faunas show little variation between intertidal environments, and the pronounced decline in foraminiferal abundance towards the upper limit of marine influence offers the potential to locate highest high water with a maximum precision of ± 5 cm (Scott and Medioli, 1978, 1986). On this basis, Scott and Medioli (1978, 1986) suggested that assemblages of agglutinated saltmarsh foraminifera are the most accurate sea-level indicators on temperate coastlines and exhibit a strong correlation with elevation above mean tidal level (MTL).

As a result various authors have since used foraminifera as precise sea-level indicators, often using samples collected only at one time of the year (Lutze, 1965, 1980; Scott and Medioli, 1978, 1986; Petrucci et al., 1983; Patterson, 1990; Jennings and Nelson, 1992; Jennings et al., 1995). However, seasonal variation in foraminiferal assemblages have been documented in many studies (Buzas, 1965; Jones and Ross, 1979; Scott and Medioli 1980b; Alve and Murray, 1995, 1999; Murray and Alve, 1999; Murray, 2000). Indeed Buzas (1968) concluded that the examination of a foraminiferal assemblage at any one time is analogous to observing "a single frame of a motion picture". Therefore, a contemporary assemblage sampled at any one occasion may or may not be in equilibrium with the environment or be typical of assemblages over a longer time period, which would undermine reconstructions of former sea levels.

To rectify the above, the aims of the study at Cowpen Marsh are: (i) to identify any seasonal patterns in the contemporary distribution of dead foraminifera across the intertidal zone during a single annual cycle; and (ii) to determine the implications of seasonality for future contemporary sampling strategies associated with studies of Holocene sea-level change.

STUDY AREA

The Tees estuary is located on the northeast coast of England and forms a large proportion of the Tees lowlands (Fig. 1). It has a mesotidal range (6.0 m) and a salinity of 5–35‰ (Table 1). The study site of Cowpen Marsh lies on the west side of the Tees estuary between Greatham Creek and the A178 road and is a remnant of a once extensive area of tidal flat, much of which has been reclaimed for agricultural use.

We divide Cowpen Marsh into high, middle, and low marsh on the basis of the vascular flora (Table 2). Approximately 90% of the marsh area is designated as high and middle marsh. The high marsh has the greatest number of floral species and is dominated by *Elymus pycnanthus*, *Festuca ovina*, *Limonium vulgare*, *Orache* spp., *Plantago maritime*, and *Sueada maritima*. The middle marsh is dominated by *Aster tripolium*, *Festuca ovina*, *Salicornia europaea*, and *Sueada maritima*. The transition to the low marsh is marked by a decrease in floral diversity with only *Festuca ovina* and *Salicornia europaea* present.

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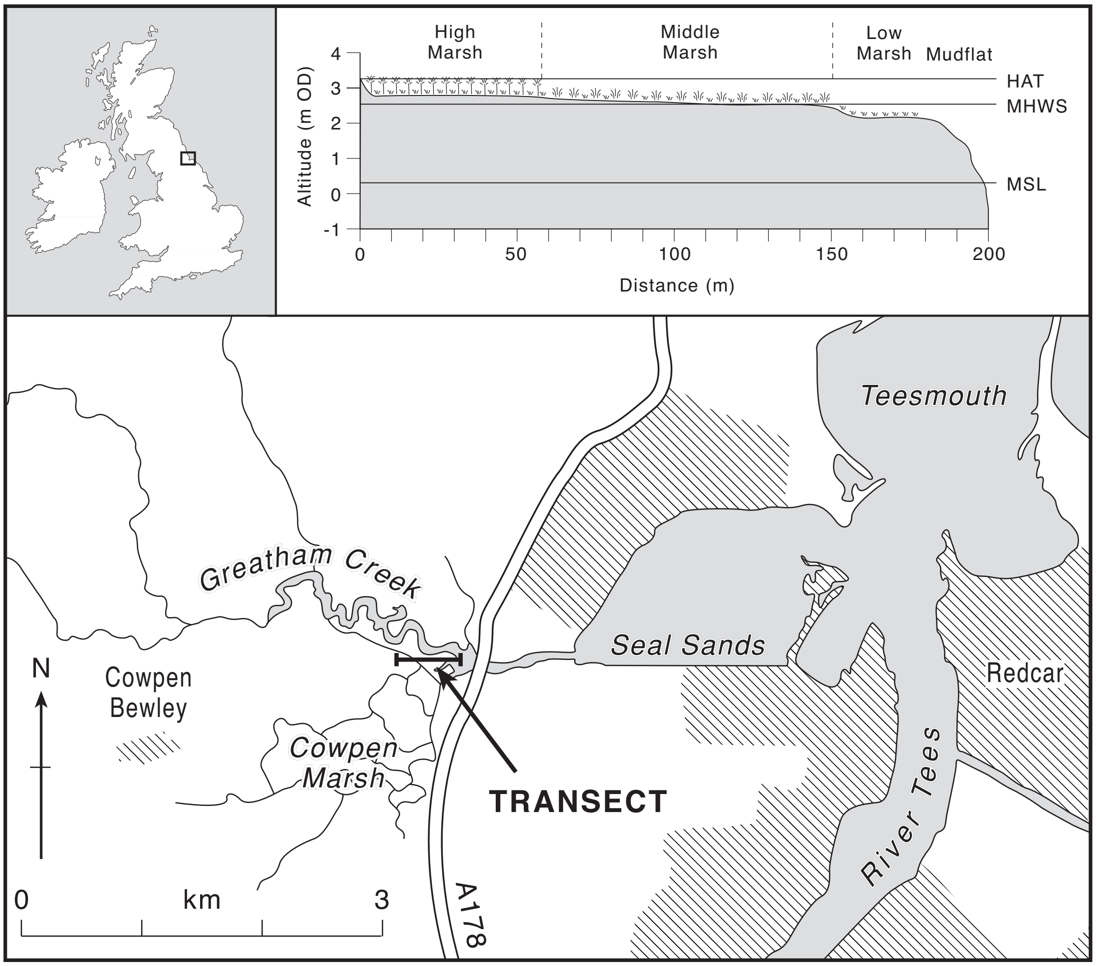

FIG. 1.—Location map of Cowpen Marsh with an insert of the transect.

MATERIALS AND METHODS

We established 32 sample stations with regular vertical sampling intervals along a transect from high marsh to mudflat, covering the intertidal zone from highest astronomical tide (HAT) to below MTL. Stations were leveled relative to Ordnance Datum (OD; Mean Sea Level Newlyn—the UK national leveling datum). We collected 10 cm^3 samples (10 cm^2 surface sample by 1 cm thick) at monthly intervals for a twelve-month period between 1994 and 1995 with each sampling date coinciding with a spring tide. In contrast to the work of Goldstein (1988) and Goldstein and Harben (1993), we assumed that infaunal foraminifera did not significantly hinder paleoenvironmental interpretations based upon a 1-cm surface slice. Analyses by Horton (1997) and Horton et al. (1999b) have shown that the intertidal foraminifera of Cowpen Marsh live primarily in epifaunal habitats (over 95% of total live population). The silt substrate of this marsh prevents significant penetration of the subsurface by the fauna and is not conducive to supporting deep infaunal foraminifera (Horton, 1997; Horton et al. 1999b).

Analysis of Foraminifera

Foraminiferal samples were stored in buffered ethanol using the protein stain rose Bengal to identify organisms living at the time of collection. Rose Bengal is routinely used to differentiate

TABLE 1.—Tidal range and tide levels of Cowpen Marsh.

Tidal range (m)	HAT (m OD)	MHWST (m OD)	MHWNT (m OD)	MSL (m OD)	MLWNT (m OD)	MLWST (m OD)	LAT (m OD)
Meso (6.0)	3.15	2.65	1.45	0.32	-0.85	-1.95	-2.85

HAT = highest astronomical tide; MHWST = mean high water spring tide; MHWNT = mean high water neap tide; MSL = mean sea level; MLWNT = mean low water neap tide; MLWST = mean low water spring tide; LAT = lowest astronomical tide (Source: Admiralty Tide Tables, 1997).

TABLE 2.—Vegetational zones of Cowpen Marsh.

High Marsh	Middle Marsh	Low Marsh
Elytrigia atheria	*Festuca ovina*	*Salicornia europaea*
Atriplex	*Plantago maritima*	*Festuca ovina*
	Suaeda maritima	*Plantago maritima*
	Limonium vulgare	*Aster tripolium*

living from dead foraminifera (Walton, 1952; Scott and Medioli, 1980b; Murray, 1991; Murray and Browser, 2000). Protoplasm is stained bright red whereas test walls and organic lining are either unstained or lightly stained. We assumed that tests containing protoplasm within the last few chambers were living at the time of collection (following Murray and Alve, 1999; Horton et al., 1999a, 1999b). Whilst there is some debate regarding which assemblage constituents should be analyzed in population studies of modern foraminifera (Scott and Medioli, 1980b; Murray, 1991; Murray and Alve, 1999), here we consider only dead individuals. Horton (1997, 1999) indicates that the modern death assemblages provide the best analogues for the subsurface assemblages employed in sea-level reconstruction. Foraminiferal preservation was generally high, and we counted a minimum of 300 tests for most samples (following Patterson and Fishbein, 1989) from the > 63 μm size fraction. Sample preparation follows that of Scott and Medioli (1980a), de Rijk (1995), and Horton (1997). The taxonomy follows Murray (1973, 1979) with three exceptions: *Haynesina germanica* in this study is equivalent to *Protelphidium germanicum* (Murray, 1973); the species *Haplophragmoides manilaensis* and *Haplophragmoides wilberti* are difficult to differentiate and are grouped as *Haplophragmoides* spp; similarly, the various *Quinqueloculina* species are grouped as *Quinqueloculina* spp.

Data Analysis

We used unconstrained incremental sum-of-squares cluster analysis based on unweighted Euclidean distance to analyze each monthly contemporary foraminiferal distribution (no transformation or standardization of the data). The elevation of each station within the cluster zones was analyzed to determine the vertical zonation of the intertidal environment for each month during a single annual cycle. It must be noted, however, that the landward and seaward limits of the vertical zonation are not based on the cluster zonation but on the elevation range of the transect.

Cluster analysis was based on computations made with the TILIA release 2.0 b.0.5 (Grimm, 1991–1993) program. We included only samples with counts greater than 40 individuals and species that contributed greater than 5% of the death foraminiferal assemblage to reduce the effect of allochthonous species (following Gehrels, 1994a; Shennan et al., 2000). Figure 2 shows an example of unconstrained cluster analysis based on unweighted Euclidean distance of foraminiferal death assemblages for the month of January 1996. Other monthly cluster analysis diagrams are available from the authors.

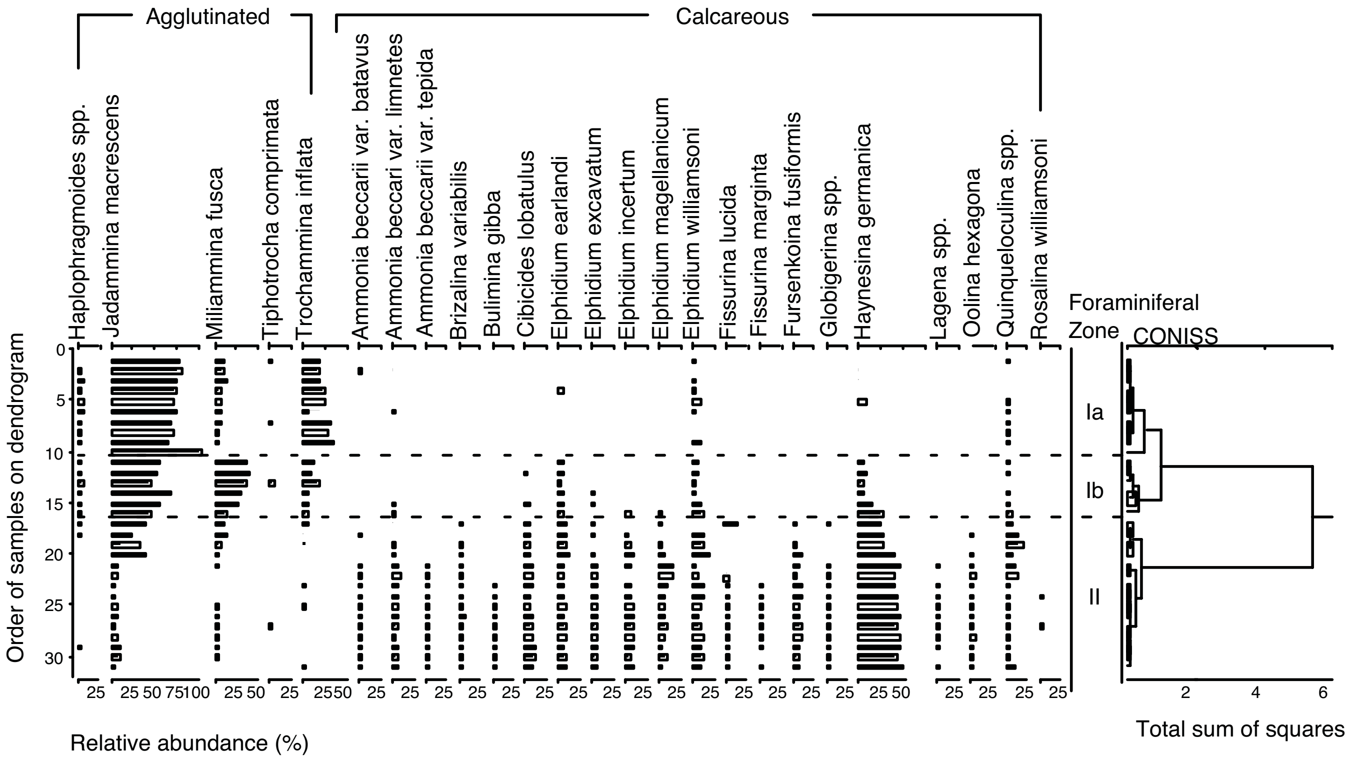

FIG. 2.—Unconstrained cluster analysis based on unweighted Euclidean distance of foraminiferal death assemblages from January 1996 from Cowpen Marsh. Only samples with counts greater than 40 individuals and species that reach 5% of the total sum are included.

TABLE 3.—The dominant foraminiferal taxa of Cowpen Marsh

High/Middle marshes	Low Marsh	Tidal flat
Jadammina macrescens	*Miliammina fusca*	*Elphidium williamsoni*
Trochammina inflata	*Jadammina macrescens*	*Haynesina germanica*
		Quinqueloculina spp.

RESULTS

Foraminiferal Assemblages

We identified 53 dead foraminiferal species during the twelve-month study of surface distributions. The maximum number of species recorded in a single sample is 24. The mean sample foraminiferal abundance is 412, with a maximum of 2304 individuals per 10 cm^3 sample. Three agglutinated species (*Jadammina macrescens*, *Miliammina fusca,* and *Trochammina inflata*) and three calcareous species (*Elphidium williamsoni*, *Haynesina germanica,* and *Quinqueloculina* spp.) dominate the foraminiferal death assemblages throughout the twelve-month period, accounting for at least 75% of the death assemblage per month. The agglutinated species *J. macrescens* and *T. inflata* dominate the high and middle marsh, with a monospecific *J. macrescens* assemblage often present at the upper limit of the high marsh (Table 3). The transition between the middle and low marsh corresponds to a decrease in the relative abundance of *J. macrescens* and *T. inflata* and an increase in *M. fusca*. The relative abundance of all three agglutinated species decreases rapidly at the transition from low marsh to mudflat. Here the agglutinated species are replaced by a more diverse assemblage dominated by calcareous taxa and characterized by the presence of *H. germanica* with lesser numbers of other species such as *E. williamsoni* and *Quinqueloculina* spp.

Seasonal Variations

The death foraminiferal assemblage of Cowpen Marsh varied from 6708 individuals in May 1995 to 9168 individuals in March 1996 with a standard deviation of 862 (Fig. 3). The species diversity also varies during the 12-month period. Both the Shannon–Weiner (*H*(*S*)) (Shannon, 1948) and Fisher alpha indices of diversity reach a maximum during the summer and a minimum during with winter (Fig. 3). This pattern is related to variations in the number of calcareous species present. Many species, such as *Bolivinellina pseudopuncta*, *Lagena laevis,* and *Patellina corrugata,* are found at Cowpen Marsh only in the summer season.

FIG. 3.—Seasonal variations of total foraminifera death population and the Shannon–Weiner (H(S)) and Fisher alpha indices of species diversity from all stations over a twelve-month study period from Cowpen Marsh.

Analysis of the relative abundance of the six most important foraminiferal species (Fig. 4A–F) shows distinct differences between the calcareous and agglutinated taxa. During the summer months the calcareous species reach their peak relative abundance. For example, the maximum relative abundances of the calcareous species *E. williamsoni* (9%), *H. germanica* (24%), and *Quinqueloculina* spp. (6%) occur in July 1995, June 1995, and July 1995, respectively. In the winter months the decline in calcareous species means that the agglutinated taxa reach their peak relative abundances. For example, the maximum relative abundances of the agglutinated species *J. macrescens* (50%), *M. fusca* (9%), and *T. inflata* (15%) are reached in November 1995, November 1995, and March 1996, respectively. The contribution of calcareous species to the whole death assemblage shows a larger degree of variation throughout the year than is evident in the agglutinated component. For example, the relative abundance of the dominant calcareous taxon, *H. germanica*, varied from 24% in June 1995 to 12% in October 1995 with a coefficient of variance (V_c) of 0.22, whereas the most important agglutinated species, *J. macrescens*, fluctuated between 50% in October 1995 to 32% in May 1996 with a V_c of 0.14.

Cluster Analysis

Cluster analysis of each monthly foraminiferal death assemblage distinguishes three cluster zones (Ia, Ib, and II), which possess similar species and sample composition (Figs. 2, 5). Zone Ia is dominated by varying abundances of *J. macrescens* and *T. inflata*. It is distinct from other zones in having the highest percentages of both species recorded in the intertidal zone. The zone has a relatively large elevation range (maximum of 1.5 m in February 1996) compared to Zone Ib because of the incorporation of samples at the upper boundary of the high marsh that have a monospecific *J. macrescens* assemblage (see Fig. 2). Zone Ib is also dominated by agglutinated species, notably *J. macrescens* and *M. fusca*, but also possesses low frequencies of calcareous species such as *E. earlandi, E. williamsoni,* and *H. germanica*. It is distinct from other zones in having the highest percentage frequencies of *M. fusca* and exhibits a relatively small elevation range (minimum of 0.10 m in November 1995). Zone II has the highest species diversity and is dominated by calcareous species such as *H. germanica, E. williamsoni*, and *Quinqueloculina* spp. It has the largest elevation range of the three cluster zones (maximum of 2.77 m in June 1995).

The vertical zonation of Cowpen Marsh varies during the year in response to the seasonality of foraminiferal distributions described above (Table 4, Fig. 5). The lower boundary of Zone Ia reaches a maximum elevation of 2.57 m OD in the late spring to early summer months (May and June 1995) and a minimum elevation of 1.74 m OD in the winter (February 1996). Similarly, the elevation of the upper boundary of Zone II ranges from a summer maximum of 2.42 m OD in June 1995 to a winter minimum of 1.52 m OD in February 1996.

DISCUSSION

The number of individuals constituting the foraminiferal death assemblage of Cowpen Marsh remains relatively stable during the twelve-month period and exhibits no definite seasonal pattern. The death assemblage reaches a minimum of 6708 individuals in May 1995 and a maximum of 9168 individuals in March 1996. However, seasonal variations are evident in analyses of species diversity and in the relative abundance of individual species. For example, the relative abundances of the three principal calcareous taxa, *E. williamsoni*, *H. germanica,* and

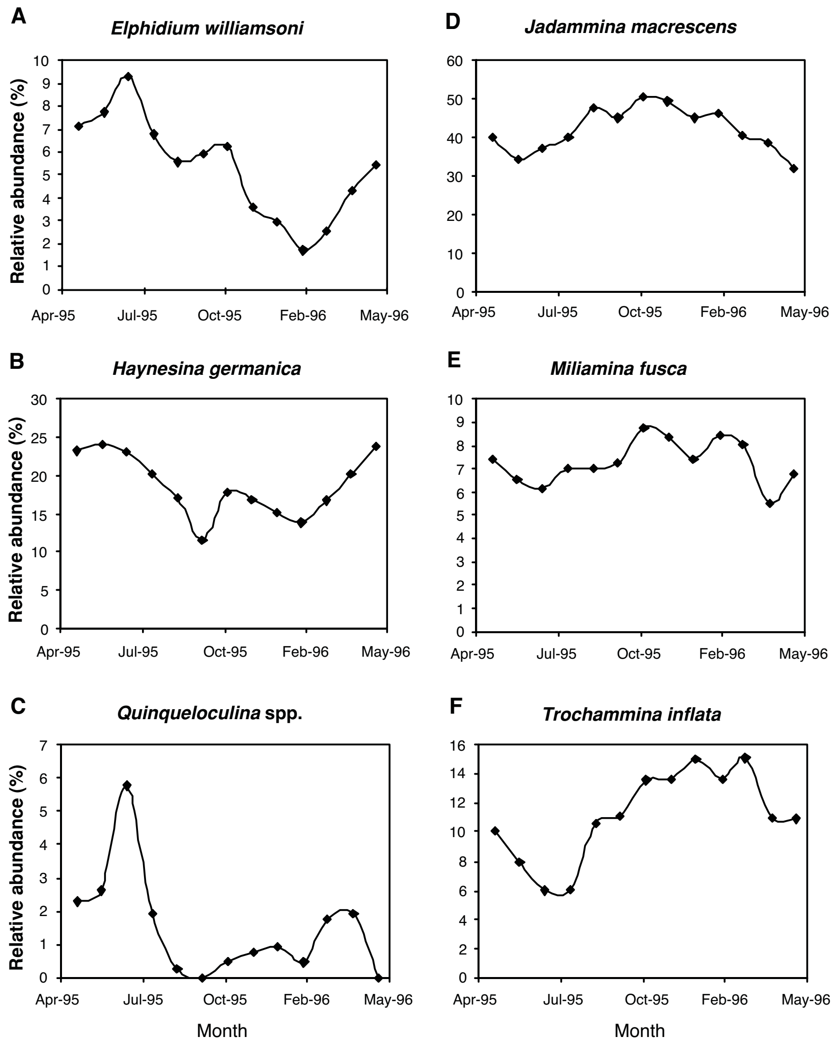

FIG. 4.—Seasonal variations of **A)** *Elphidium williamsoni,* **B)** *Haynesina germanica,* **C)** *Quinqueloculina* spp., **D)** *Jadammina macrescens,* **E)** *Miliammina fusca,* and **F***)* *Trochammina inflata* from all stations over a twelve-month study period from Cowpen Marsh.

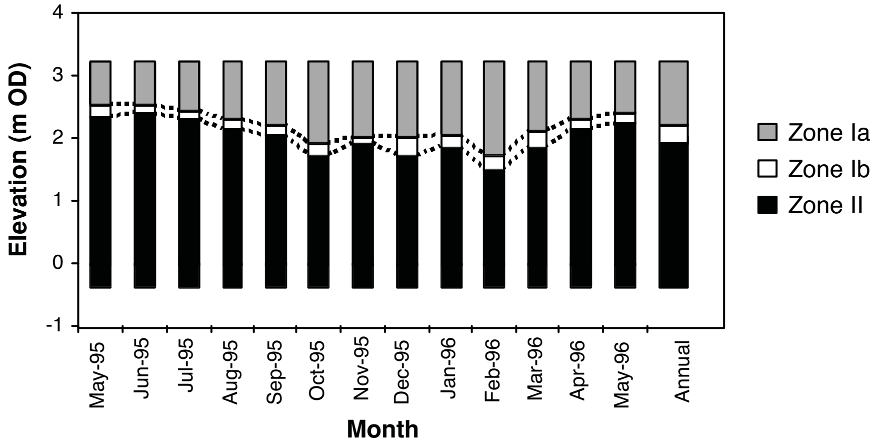

FIG. 5.—Seasonal variations of elevation ranges of monthly cluster zones. The unconstrained cluster analysis was based on unweighted Euclidean of monthly foraminiferal death assemblages from samples collected over a twelve-month period from Cowpen Marsh. Only samples with counts greater than 40 individuals and species that reach 5% of the total sum are included (Annual Cluster zone is from Horton, 1999).

TABLE 4.—Elevation ranges of monthly foraminiferal cluster zones of Cowpen Marsh. The elevation range of the annual cluster zones is based on annual average of foraminiferal distributions (see Horton et al., 1999a).

Month	Zone Ia (m OD)[1]	Zone Ib (m OD)	Zone II (m OD)[2]
May 1995	3.24 to 2.57 (0.67)	2.57 to 2.38 (0.19)	2.38 to -0.35 (2.73)
June 1995	3.24 to 2.57 (0.67)	2.57 to 2.42 (0.15)	2.42 to -0.35 (2.77)
July 1995	3.24 to 2.47 (0.77)	2.47 to 2.33 (0.14)	2.33 to -0.35 (2.68)
August 1995	3.24 to 2.33 (0.91)	2.33 to 2.18 (0.15)	2.18 to -0.35 (2.53)
September 1995	3.24 to 2.22 (1.02)	2.22 to 2.09 (0.13)	2.09 to -0.35 (2.44)
October 1995	3.24 to 1.94 (1.30)	1.94to 1.74 (0.20)	1.74 to -0.35 (2.09)
November 1995	3.24 to 2.04 (1.20)	2.04 to 1.94 (0.10)	1.94 to -0.35 (2.29)
December 1995	3.24 to 2.04 (1.20)	2.04 to 1.74 (0.30)	1.74 to -0.35 (2.09)
January 1996	3.24 to 2.09 (1.15)	2.09 to 1.88 (0.21)	1.88 to -0.35 (2.12)
February 1996	3.24 to 1.74 (1.50)	1.74 to 1.52 (0.22)	1.52 to -0.35 (1.87)
March 1996	3.24 to 2.14 (1.10)	2.14 to 1.88 (0.26)	1.88 to -0.35 (2.12)
April 1996	3.24 to 2.33 (0.91)	2.33 to 2.17 (0.16)	2.17 to -0.35 (2.52)
May 1996	3.24 to 2.42 (0.82)	2.42 to 2.27 (0.15)	2.27 to -0.35 (2.62)
Annual	3.24 to 2.22 (1.02)	2.22 to 2.04 (0.18)	2.04 to -0.35 (2.39)

[1, 2] The upper boundary of Zone Ia and lower boundary of Zone II are based on the elevation range of the transect.

Quinqueloculina spp., reach a maximum in the summer months but are at a minimum during the winter. In a study of the seasonal distribution and abundance of foraminifera in Long Island Sound, Buzas (1965) observed that the total number of living individuals was at its greatest in the summer, and that this correlated with maximum temperature and abundance of zooplankton and phytoplankton. Similar results have been produced in other studies of foraminiferal assemblages (Jones and Ross, 1979; Scott and Medioli 1980b; Alve and Murray, 1995, 1999; Murray and Alve, 1999). It is possible, therefore, that the summer rise in the calcareous component of the death assemblage reflects the increase in productivity of the saltmarsh at this time. If this is correct it implies that protoplasm degrades rapidly upon death and that variations in the life assemblage are quickly transmitted to the death assemblage (Murray and Bowser, 2000). Destruction of the calcareous tests of saltmarsh foraminifera by dissolution is widely recognized (Scott and Medioli, 1980a; Jonasson and Patterson, 1992; Murray and Alve, 1999). The absence of a post–summer bloom peak in dead calcareous foraminifera suggests that this test destruction occurs rapidly in the marsh environment. This could indicate that any dead calcareous specimens recovered on the marsh have either only recently died or are freshly transported onto its surface. Alternatively, the surface conditions of the saltmarsh during the summer months may be more conducive to test dissolution. Indeed the problem of dissolution of calcareous foraminifera in certain sedimentary settings has led Edwards and Horton (2000) to develop a transfer function with the entire calcareous dataset deleted.

The variations in seasonal death foraminiferal assemblages modify the pattern of cluster zonation across the intertidal zone during the twelve-month study period. These variations are reflected in the changing elevations of the three cluster zones and their zonal boundaries. For example, the upper boundary of Zone II varies between 2.42 m OD in June 1995 to 1.52 m OD in February 1996 (0.9 m). Consequently, a contemporary sample taken in one month can significantly underestimate or overestimate the elevation range of an annual zone. For example, a contemporary sample taken in one month can underestimate or overestimate the elevation range of annual Zone Ia (Horton et al., 1999a) by as much as 0.35 m and 0.48 m, respectively (Table 5). Hence, the reliability of cluster zones as indicators of former sea levels can be assessed only following a consideration of the seasonal errors affecting the elevations of their upper and lower boundaries. The maximum and minimum values can be used to produce monthly error bars for the upper and lower boundaries of each zone (Table 5).

Implications for Studies of Holocene Sea-Level Changes

Horton et al. (1999b) have recently developed a transfer function or biotic index to reconstruct former sea levels on the basis of the statistically significant relationship between foraminiferal assemblages and elevation with respect to the tidal frame. Foraminiferal and elevation data were collected from ten contemporary UK intertidal environments and a predictive foraminifera-based transfer function (FBTF) was developed using weighted averaging (WA) regression and calibration (Birks, 1995; Jones and Juggins, 1995; Gasse et al., 1997; Juggins and ter Braak, 1997; Horton et al., 2000). However, no account was made of seasonal variations. We have, therefore, used the same statistical methodology on the foraminiferal data collected from Cowpen Marsh over the twelve-month study period to assess the implications of seasonal changes for studies of Holocene sea-level change.

TABLE 5.—The errors of the upper and lower boundaries of monthly cluster zones, and maximum underestimation and overestimation of monthly cluster zones when compared to the equivalent annual zones (following Horton et al., 1999a) of Cowpen Marsh.

Zone	Upper boundary (m OD)	Lower boundary (m OD)	Maximum under-estimation	Maximum over-estimation
Ia	3.24*	2.22 ± 0. 25	0.35 m	0.48 m
Ib	2.22 ± 0. 25	2.04 ± 0.28	0.08 m	0.08 m
II	2.04 ± 0.28	-0.35*	0.52 m	0.38 m

*The upper boundary of Zone Ia and lower boundary of Zone II are based on the elevational range of the transect.

The scatter graphs of monthly FBTFs and an annual average FBTF (Fig. 6) show a strong linear relationship between observed and foraminifera-predicted elevations ($r^2 \geq 0.82$), supporting the conclusions of Horton et al. (1999b, 2000) that precise reconstructions of former sea levels are possible.

The accuracy of the monthly FBTFs, however, varies during the course of the year. The highest r^2 occurs in the winter months ($r^2 = 0.93$, February 1996) and the lowest in the summer ($r^2 = 0.82$, May 1995). This seasonal effect is due to variations in the reconstructed elevation optima and tolerances of individual foraminiferal species along the Cowpen Marsh transect (Table 6). The optimum and tolerance of a species are its weighted average and standard deviation, respectively. Therefore, at a site with a particular elevation, species with their optima for elevation close to the site tend to be the most abundant present. The elevation tolerances of the principal calcareous species commonly found within the tidal flat (e.g., *H. germanica*, *E. williamsoni*, and *Quinqueloculina* spp.) are greater than 0.32 m. The agglutinated species that dominate saltmarsh environments (e.g., *J. macrescens*, *M. fusca*, and *T. inflata*) have relatively small elevation ranges with tolerances below 0.29 m. Therefore, the transfer function is most precise in the winter months, when the influence of agglutinated taxa is at its greatest.

The seasonal variations of FBTFs have important implications for future contemporary sampling strategies. We have investigated the relationship between elevation errors (observed versus foraminifera-predicted) and the number of measurements per year and the timing of sampling by averaging the monthly foraminiferal data. Figure 7 shows that the magnitude of the errors is greatest when measurements are taken once a year in the summer (± 0.35 m). The most accurate sampling season is the winter (± 0.29 m). There is also a noticeable reduction in the error (± 0.21 m) for four measurements per year (winter, spring, summer, and autumn). Further sampling is time consuming and does not appreciably decrease the error (minimum error of ± 0.18 m for 12 measurements per year). Therefore, an investigation of contemporary saltmarsh foraminifera that recovers a complete set of samples in each season will provide the best-quality data for the construction of FBTFs to reconstruct sea-level change.

CONCLUSIONS

1. We identified fifty-three dead foraminifera species from a twelve-month study of surface samples from Cowpen Marsh. The death foraminiferal assemblage varies from 6708 in May

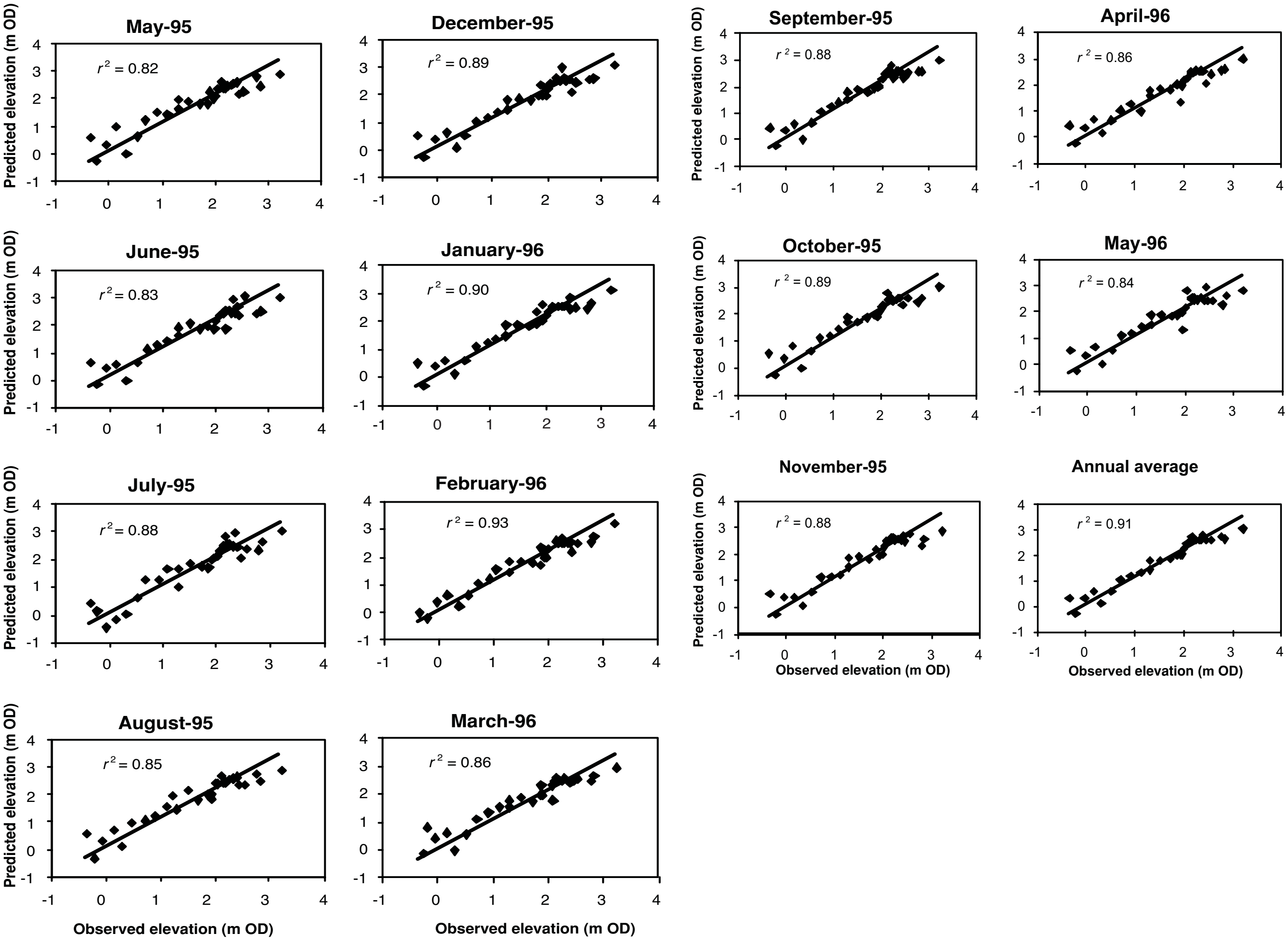

FIG. 6.—Scatter plots showing the relationship of the observed versus foraminifera-predicted elevation for monthly and annual average weighted average transfer functions.

TABLE 6.—Foraminiferal species optima (weighted average) and tolerances (weighted standard deviation) for elevation (m OD) showing all taxa present in the foraminiferal dataset. The only species included are those that reach 5% dead foraminifera and that have passed the screening procedure (see Gasse et al., 1997).

Species	Optima (m OD)	Tolerance (m)
Buliminella elegantissima	1.75	0.45
Elphidium incertum	1.80	0.31
Elphidium excavatum	1.81	0.32
Cibicides lobatulus	1.81	0.33
Fursenkoina fusiformis	1.85	0.42
Elphidium margeritaceum	1.93	0.60
Lagena spp.	1.94	0.54
Elphidium earlandi	1.96	0.32
Ammonia beccarii	1.98	0.44
Haynesina germanica	2.04	0.32
Bulimina marginata	2.06	0.61
Elphidium williamsoni	2.13	0.41
Rosalina williamsoni	2.15	0.32
Brizalina spp.	2.15	0.50
Elphidium magellanicum	2.17	0.41
Globigerina spp.	2.18	0.46
Quinqueloculina spp.	2.31	0.33
Miliammina fusca	2.42	0.22
Jadammina macrescens	2.52	0.29
Trochammina inflata	2.53	0.29
Trochammina comprimata	2.60	0.38
Haplophragmoides spp.	2.78	0.36

1995 to 9168 individuals in March 1996 (standard deviation of 862), showing no obvious seasonal pattern in absolute abundance. However, significant seasonal differences are observed in the relative abundances of individual agglutinated and calcareous species. Analyses of the most numerically important species revealed that the calcareous taxa reach their peak abundances in the summer whilst the agglutinated species are most dominant in the winter months. Furthermore, the seasonality in relative abundance of the calcareous species is more pronounced than their agglutinated counterparts.

2. Cluster analysis of monthly foraminiferal assemblages of Cowpen Marsh identifies three reliable cluster zones: a high-marsh and middle-marsh zone of *J. macrescens* and *T. inflata*; a low-marsh zone of *J. macrescens* and *M. fusca*; and a mudflat zone of calcareous foraminiferal species, notably *E. williamsoni*, *H. germanica*, and *Quinqueloculina* spp. This zonation is identical to those of Horton et al. (1999a), which were based on annual average assemblages from Cowpen Marsh. Furthermore, these assemblage zones are similar to those in other mid-latitude, cool temperate intertidal environments identified from the Atlantic (Scott and Medioli, 1978, 1980a; Scott and Leckie, 1990; Gehrels, 1994a, 1994b) and the Pacific (Williams, 1989, 1999; Patterson, 1990; Jennings and Nelson, 1992; Jennings et al., 1995) coasts of North America , and the Atlantic seaboard of Europe (le Campion, 1970; Pujos, 1976; Coles and Funnell, 1981; Murray, 1991; Horton, 1997, 1999; Edwards, 1998, Horton et al., 1999a).

3. The seasonal variations of contemporary foraminiferal distribution across the intertidal zone during an annual cycle modify the elevations of the three cluster zones. The elevation range of Zone Ia is largest in winter (1.5 m, February 1996) whereas the largest elevation range of Zone II is in summer (2.77 m, June 1995), which coincides with the maximum abundances of the major agglutinated and calcareous species, respectively. The elevation range of Zone Ib remains relatively constant through the year (0.18 ± 0.06 m) though it transgresses the intertidal zone, reaching its highest elevation

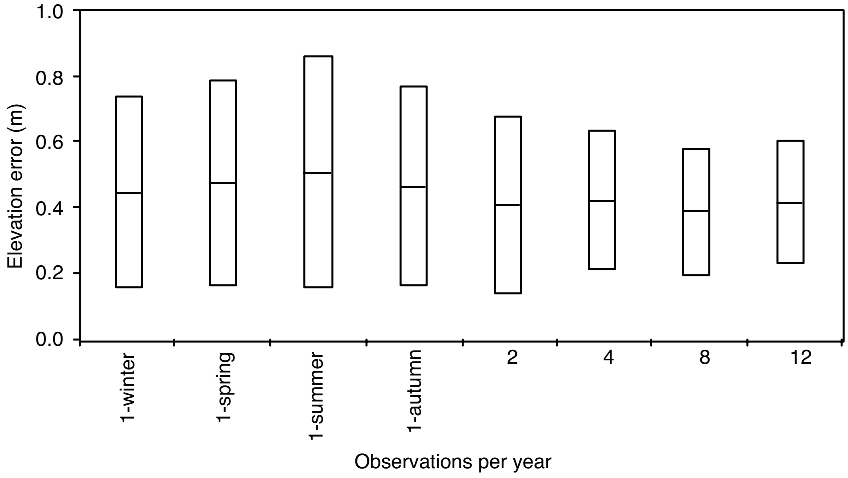

FIG. 7.—Bar chart showing the relationship between elevation errors (mean and standard deviation) for the Cowpen Marsh transect (observed versus foraminifera-predicted) and the number of measurements per year. Elevations are calculated using a weighted average transfer function. Sampling abbreviations:1-winter = sampled once in winter; 1-spring = sampled once in spring; 1-summer = sampled once in summer; 1-autumn = sampled once in autumn; 2 = sampled once in winter and summer; 4 = sampled once in winter, spring, summer, and autumn; 8 = sampled twice in winter, spring, summer, and autumn; 12 = sampled every month of the year.

in the summer (2.57 m OD, May and June 1995). Consequently, a contemporary sample taken in one month can significantly underestimate or overestimate the elevation range of a zone. Hence, the reliability of cluster zones as indicators of former sea levels can be assessed only following a consideration of the seasonal errors affecting the elevations of their upper and lower boundaries.

4. Seasonal foraminiferal variations have important implications for the studies of former sea level and future contemporary sampling strategies. We have developed monthly and annual foraminifera-based transfer functions using weighted averaging regression and calibration. Results show a strong linear relationship between observed and foraminifera-predicted elevations, suggesting that precise reconstructions of former sea levels are possible ($r^2 \geq 0.82$). However, the accuracy of the monthly transfer function varies during the course of the year, with the greatest precision obtained in the winter months, when agglutinated species dominate the assemblages. The error between predicted and observed elevations is ± 0.29 m when sampled in winter compared to ± 0.35 m in summer. This seasonality means that a contemporary assemblage sampled at any one occasion may or may not be in equilibrium with its environment or be typical of assemblages over a longer time period. For this reason, we conclude that an investigation of contemporary saltmarsh foraminifera that recovers a complete set of samples in the winter, spring, summer, and autumn (i.e., four samples per year), will provide the best-quality data for use in sea-level investigations (error = ± 0.21 m). If only one set of measurements can be obtained, sampling in the winter months may represents the most reliable alternative.

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REFERENCES

ALVE, E., AND MURRAY, J.W., 1995, Experiments to determine the origin and palaeoenvironmental significance of agglutinated foraminiferal assemblages, *in* Kaminski, M.A., Geroch, S., and Gasinski, M.A., eds., Fourth International Workshop on Agglutinated Foraminifera, Krakow Poland, September 12–19, 1993: Grzybowski Foundation, Proceedings, Special Publication no. 3, p. 1–11.

ALVE, E., AND MURRAY, J.W., 1999, Marginal marine environments of the Skagerrak and Kattegat: a baseline study of living (stained) benthic foraminiferal ecology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 146, p. 171–193.

BIRKS, H.J.B., 1995, Quantitative palaeoenvironmental reconstructions, *in* Maddy, D., and Brew, J.S., eds., Statistical Modelling of Quaternary Science Data: Cambridge, U.K., Quaternary Research Association, Technical Guide no. 5, p. 161–236.

BUZAS, M.A., 1965, The distribution and abundance of foraminifera in Long Island Sound: Smithsonian Miscellaneous Collections, no. 149, p. 1–89.

BUZAS, M.A., 1968, On spatial distribution of foraminifera: Cushman Foundation for Foraminiferal Research, Contributions, v. 19, p. 1–11

COLES, B.P.L., AND FUNNELL, B.M., 1981, Holocene palaeoenvironments of Broadland, England, *in* Nio, S-D., Shuttenhelm, R.T.E., and Van Weering, T.C.E., eds., Holocene Marine Sedimentation in the North Sea Basin: International Association of Sedimentologists, Special Publication 5, p. 123–131.

EDWARDS, R.J., 1998, Late Holocene relative sea-level change and climate in southern Britain: unpublished Ph.D. thesis, University of Durham, 317 p.

EDWARDS, R.J., AND HORTON, B.P., 2000, High resolution records of relative sea-level change from U.K. salt-marsh foraminifera: Marine Geology, v. 169, p. 41–56.

GASSE, F., BARKER, P., GELL, P.A., FRITZ, S.C., AND CHALIE, F., 1997, Diatom-inferred salinity in palaeolakes: An indirect tracer of climate change: Quaternary Science Reviews, v. 16, p. 547–563.

GEHRELS, W.R., 1994a, Determining relative sea-level change from saltmarsh foraminifera and plant zones on the coast of Maine, USA: Journal of Coastal Research, v. 10, p. 990–1009.

GEHRELS, W.R., 1994b, Holocene sea-level changes in the northern Gulf of Maine: regional trends and local fluctuations determined from foraminiferal analyses and paleotidal modelling: unpublished Ph.D. thesis, University of Maine, Orono, 337 p.

GOLDSTEIN, S.T., 1988, Foraminifera of relict saltmarsh deposits, St. Catherines Island, Georgia: Taphonomic implications: Palaios, v. 3, p. 327–334.

GOLDSTEIN, S.T., AND HARBEN, E.B., 1993, Taphofacies implications of infaunal foraminiferal assemblages in a Georgia saltmarsh, Sapelo Island: Micropaleontology, v. 39, p. 55–62.

GRIMM, E., 1991–1993, Tilia: Illinois State Museum, Springfield, Illinois, U.S.A.

HORTON, B.P., 1997, Quantification of the indicative meaning of a range of Holocene sea-level index points from the western North Sea: unpublished Ph.D. thesis, University of Durham, 194 p.

HORTON, B.P., 1999, The contemporary distribution of intertidal foraminifera of Cowpen Marsh, Tees Estuary, U.K.: implications for studies of Holocene sea-level changes: Palaeogeography, Palaeoclimatology, Palaeoecology, Special Issue, v. 149, p. 127–149.

HORTON, B.P., EDWARDS, R.J., AND LLOYD, J. M., 1999a, Reconstruction of former sea-levels using a foraminiferal-based transfer function: Journal of Foraminiferal Research, v. 29, p. 117–129.

HORTON, B.P., EDWARDS, R.J., AND LLOYD, J.M., 1999B, U.K. intertidal foraminiferal distributions: implications for sea-level studies: Marine Micropaleonotology, v. 36, p. 205–223.

HORTON, B.P., EDWARDS, R.J., AND LLOYD, J.M., 2000, Implications of a microfossil transfer function in Holocene sea-level studies, *in* Shennan, I., and Andrews, J.E., eds., Holocene Land–Ocean Interaction and Environmental Change around the Western North Sea: Geological Society of London, Special Publication 166, p. 41–54.

JENNINGS, A.E., AND NELSON, A.R., 1992, Foraminiferal assemblage zones in Oregon tidal marshes—relation to marsh floral zones and sea level: Journal of Foraminiferal Research, v. 22, p. 13–29.

JENNINGS, A.E., NELSON, A.R., SCOTT, D.B., AND AREVENA, J.C., 1995, Marsh foraminifera assemblages in the Valdiva estuary, south-central Chile, relative to vascular plants and sea level: Journal of Coastal Research, v. 11, p. 107–123.

JONASSON, K.E., AND PATTERSON, R.T., 1992, Preservation potential of salt marsh foraminifera from the Fraser River Delta, British Columbia: Micropaleontology, v. 38, p. 289–301.

JONES, V.J., AND JUGGINS, S., 1995, The construction of a diatom-based chlorophyll transfer function and its application at three lakes on Signy Island (maritime Antarctic) subject to differing degrees of nutrient enrichment: Freshwater Biology, v. 34, p. 433–445.

JONES, J.R., AND ROSS, CA., 1979, Seasonal distribution of foraminifera in Samish Bay, Washington: Journal of Paleontology, v. 53, p. 245–257.

JUGGINS, S., and TER BRAAK, C.J.F., 1997, CALIBRATE: Department of Geography, University of Newcastle.

LE CAMPION, J., 1970, Contribution à l' études des foraminifères du Bassin d' Arcachon et du proche ocean: Institut de Géologie du Bassin d' Aquitaine, Bulletin, v. 8, p. 3–98.

LUTZE, G.F., 1965, Zur Foraminiferen-Fauna der Ostsee: Meyniana, v. 15, p. 75–142.

LUTZE, G.F., 1980, Depth distribution of benthic foraminifera on the continental margin off NW Africa: 'Meteor' Forschungs-Ergebnisse, v. C32, p. 31–80.

MURRAY, J.W., 1973, An Atlas of British Recent Foraminiferids: London, Heinemann Educational Books, 244 p.

MURRAY, J.W., 1979, British Nearshore Foraminiferids: London, Academic Press, 68 p.

MURRAY, J.W., 1991, Ecology and Palaeoecology of Benthic Foraminifera: Harlow, England, Longman Scientific and Technical, 397 p.

MURRAY, J.W., and Alve, E., 1999, Natural dissolution of modern shallow water benthic foraminifera: taphonomic effects on the palaeoecological record: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 146, p. 195–209.

MURRAY, J.W., 2000, Major aspects of foraminiferal variability (standing crop and biomass) on a monthly scale in an intertidal zone: Journal of Foraminiferal Research, v. 30, p. 177–191.

MURRAY, J.W., AND BOWSER, S.S., 2000, Mortality protoplasm decay rate, and reliability of staining techniques to recognise 'living' foraminifera: a review: Journal of Foraminiferal Research, v. 30, p. 66–70.

PATTERSON, R.T., 1990, Intertidal benthic foraminifera biofacies on the Fraser River Delta, British Columbia: Micropaleontology, v. 36, p. 229–244.

PATTERSON, R.T., and FISHBEIN, E., 1989, Re-examination of the statistical methods used to determine the number of point counts needed for micropaleontological quantitative research: Journal of Paleontology, v. 63, p. 245–248.

PETRUCCI, F., MEDIOLI, F.S., SCOTT, D.B., PIANETTI, F.A., and CAVAZZINI, R., 1983, Evaluation of the usefulness of foraminifera as sea-level indicators in the Venice lagoon (N. Italy): Ateneo Parmense, Acta Naturalia, v. 19, p. 63–77.

PUJOS, M., 1976, Ecologie des foraminifères benthiques et des thécamoebiens de la Gironde et au plateau continental Sud-Gascogne. Application à la connaissaance du Quaternaire terminal de la région Ouest-Gironde: Institut de Géologie du Bassin d' Aquitaine, Memoires, v. 8, 274 p.

DE RIJK, S., 1995, Salinity control on the distribution of salt marsh Foraminifera (Great Marshes, Massachusetts): Journal of Foraminiferal Research, v. 25, p. 156–166.

SCOTT, D.B., and MEDIOLI, F.S., 1978, Vertical zonation of marsh foraminifera as accurate indicators of former sea levels: Nature, v. 272, p. 528–531.

SCOTT, D.B., and MEDIOLI, F.S., 1980a, Quantitative studies of marsh foraminifera distribution in Nova Scotia: implications for sea-level studies: Journal of Foraminiferal Research, Special Publication 17, 58 p.

SCOTT, D.B., and MEDIOLI, F.S., 1980b, Living vs. total foraminifera populations: their relative usefulness in palaeoecology: Journal of Paleontology, v. 54, p. 814–831.

SCOTT, D.B., and MEDIOLI, F.S., 1986, Foraminifera as sea-level indicators, *in* van de Plassche, O., ed., Sea-Level Research: A Manual for the Collection and Evaluation of Data: Norwich, U.K., Geobooks, p. 435–456.

SCOTT, D.K., and LECKIE, R.M., 1990, Foraminiferal zonation of Great Sippwissett Salt Marsh (Falmouth, Massachusetts): Journal of Foraminiferal Research, v. 20, p. 248–266.

SHENNAN, I., HORTON, B.P., INNES, J.B., LLOYD, J.L., MCARTHUR, J.J., and RUTHERFORD, M.M., 2000, Holocene crustal movements and relative sea-level changes on the east coast of England, *in* Shennan, I., and Andrews, J.E., eds., Holocene Land–Ocean Interaction and Environmental Change around the Western North Sea: Geological Society of London, Special Publication 166, p. 275–299.

SHANNON, C.E., 1948, A mathematical theory of communication: Bell System Technical Journal, v. 27(1/2), p. 379–423; v. 17(3), p. 623–656.

WALTON, W.R., 1952, Techniques for recognition of living foraminifera: Cushman Foundation for Foraminiferal Research, Contributions, v. 3, p. 56–60.

WILLIAMS, H.F.L., 1989, Foraminiferal zonations on the Fraser River Delta and their application to paleoenvironmental interpretations: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 73, p. 39–50.

A data repository of all foraminiferal and environmental data can be found on the following website: http://www.geography.dur.ac.uk/information/official_sites/bph.html