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Quantifying Holocene Sea Level Change Using Intertidal Foraminifera: Lessons from the British Isles

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Abstract

Salt-marsh foraminifera have been used to reconstruct Holocene sea-level changes from coastlines around the world. In this work, we compile the results of surface foraminiferal surveys from fifteen study sites located on the east, south and west coasts of Great Britain, and the west coast of Ireland. These data, which comprise 236 samples and 84 species, are used to summarize the contemporary distributions of intertidal foraminifera around the British Isles, and to examine the environmental controls governing them.

Seasonal and sub-surface foraminiferal data suggest that foraminiferal dead assemblages provide the most appropriate dataset for studying patterns of foraminiferal distributions in the context of sea-level reconstruction. In contrast to live populations or total assemblages, the dead assemblages are less affected by seasonal fluctuations and post-depositional modifications. Sub-surface foraminiferal data also indicate that foraminifera at the study sites live primarily in epifaunal habitats. Consequently, foraminiferal samples comprising the upper centimeter of sediment are appropriate analogues for the study of past sea-level change employing fossil assemblages contained within intertidal deposits.

Surface dead assemblages from the fifteen study sites indicate a vertical zonation of foraminifera within British and Irish salt-marshes that is similar to those in other mid-latitude, cool temperate intertidal environments. Whilst the composition and vertical ranges of assemblage zones vary between sites, two general sub-divisions can be made: an agglutinated assemblage restricted to the vegetated marsh; and a high diversity calcareous assemblage that occupies the mudflats and sandflats of the intertidal zone. Three of the fifteen study sites permit further subdivision of the agglutinated assemblage into a high and middle marsh zone (Ia) dominated by *Jadammina macrescens* with differing abundances of *Trochammina inflate* and *Miliammina fusca*, and a low marsh zone (Ib) dominated by *M. fusca*. The calcareous assemblage is commonly comprised of *Ammonia* spp., *Elphidium williamsoni* and *Haynesina germanica*, in association with a wide range of minor taxa.

The vertical zonations of the study areas suggest that the distribution of foraminifera in the intertidal zone is usually a direct function of elevation relative to the tidal frame, with the duration and frequency of intertidal exposure as the most important controlling factors. This relationship is supported by canonical correspondence analyses of the foraminiferal data and a series of environmental variables (elevation, pH, salinity, substrate and vegetation cover).

These modern foraminiferal data are used to develop predictive transfer functions capable of inferring the past elevation of a sediment sample relative to the tidal frame from its fossil foraminiferal content. The results indicate that transfer functions perform most reliably when they are based on modern data collected from a wide range of intertidal environments. The careful combination of foraminiferal estimates of paleomarshsurface elevation with detailed lithostratigraphy and chronostratigraphy can produce high-resolution records of relative sea-level change with sufficient resolution to detect low-magnitude variability but long enough duration to reliably establish climate-ocean relationships and secular trends. Thus, the transfer function approach has the potential to link short-term instrumental and satellite records with established longer-term geologically based reconstructions of relative sea level.

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QUANTIFYING HOLOCENE SEA-LEVEL CHANGE USING INTERTIDAL FORAMINIFERA: LESSONS FROM THE BRITISH ISLES

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Salt-marsh foraminifera have been used to reconstruct Holocene sea-level changes from coastlines around the world. In this work, we compile the results of surface foraminiferal surveys from fifteen study sites located on the east, south and west coasts of Great Britain, and the west coast of Ireland. These data, which comprise 236 samples and 84 species, are used to summarize the contemporary distributions of intertidal foraminifera around the British Isles, and to examine the environmental controls governing them.

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1. INTRODUCTION

Salt-marsh foraminifera are widely acknowledged as useful tools for reconstructing Holocene sea-level change (e.g. Scott, 1976; Scott and Medioli, 1978, 1980a; Patterson, 1990; Gehrels, 1994, 2000, 2002; Varekamp and others, 1992, 1999; Guilbault and others, 1996; Saffert and Thomas, 1998; Varekamp and Thomas, 1998; Hayward and others, 1999, 2004a; Horton, 1999; Horton and others, 1999a, b, 2000, 2003, 2005b; Patterson and others, 1999, 2000, 2004, 2005; Edwards and Horton, 2000; Hippensteel and others, 2000; Gehrels and others, 2000, 2001, 2004, 2005; Horton and Edwards, 2001, 2005; Martin and others, 2003; Edwards and others, 2004a, b; Gehrels and Newman, 2004; Duchemin and others, 2005; Tobin and others, 2005; Boomer and Horton, 2006; Horton and Culver, in press). Their utility as sea-level indicators is underpinned by the concept that characteristic foraminiferal assemblages are vertically zoned with respect to the tidal frame, that these modern relationships can be quantified, and that they are representative of past conditions encountered in Holocene salt-marsh sedimentary sequences. In this way, the foraminifera contained within a preserved salt-marsh deposit can be used to fix its former elevation relative to the tidal frame at its time of formation (termed the indicative meaning). This measure of paleomarsh-surface elevation, when combined with other lithostratigraphic data, can be used to infer the past position of local relative sea-level (RSL).

Scott and Medioli (1980a) demonstrated that salt-marsh foraminifera are vertically zoned with respect to tide level. Most notably, a near ubiquitous, monospecific assemblage of *Trochammina macrescens* was recorded just below the level of higher high water (HHW), above which all foraminifera rapidly disappeared. Scott and Medioli (1978, 1980a) suggested that this assemblage zone could be used to relocate former HHW with a maximum precision of ± 5 cm. Other vertical assemblage zones were also recorded across a range of study marshes (e.g. Gehrels, 1994; Horton, 1999; Horton and Edwards, 2001, 2003, 2005), although variations in salinity and tidal regime influenced their precise composition and elevation (de Rijk, 1995a, b; de Rijk and Troelstra 1997). Consequently, the precision with which former relative sea-level can be reconstructed using an assemblage zone approach varies within and between sites (Edwards and others, 2004a). This variability necessitates the collection and interpolation of site-specific data and complicates inter-site comparison of records. Hence, whilst the vertical zonation concept remains powerful twenty-five years after its exposition, the drive to interrogate the sedimentary record with increasing levels of accuracy and precision requires a more flexible method of application.

One such method of application, the use of foraminiferal transfer functions for tide level, is the subject of this paper. It is principally concerned with the development and application of foraminiferal transfer functions from the minerogenic salt-marshes of the British Isles. However, much of the discussion is applicable to a wide range of marshes in both hemispheres from arid to tropical environments. For readers unfamiliar with British and Irish salt-marsh environments, we first outline their principal characteristics and the controls responsible for their formation and evolution. We then examine the modern distributions of British and Irish intertidal foraminifera and the factors that are responsible for them. Once these modern patterns and controls have been described, we outline the methodology employed to develop and apply foraminiferal transfer functions for tide level. We assess the relative strengths and weaknesses of the approach, our current level of understanding, and conclude with recommendations for future research.

1.1 TERMINOLOGY

Sea-level research crosses disciplinary boundaries and draws together groups of scientists with contrasting backgrounds including archeology, botany, engineering, geography, geology, geophysics and oceanography. It is therefore useful at the outset to clarify some of the general terminology we will employ.

The relative significance of processes and variables is strongly dependent upon the temporal and spatial scales at which they are considered. For convenience, we distinguish change over very short (days to years), short (decades), medium (centuries) and long (millennia) timescales. Similarly, we consider local-scale variability as it is expressed at a single site or location, and regional-scale variability that is evident from a number of sites. We do not consider global-scale changes since sea level is spatially variable and cannot be reduced to a single curve over Holocene timescales due to gravitational effects (Mörner, 1976; Mitrovica and Peltier, 1991; Milne, 2002).

For convenience, we also employ a simple distinction between 'modern' (surface), and 'fossil' (sub-surface) foraminiferal assemblages. Modern assemblages are considered to comprise very short timescale

accumulations in the upper centimeter of sediment that reflect modern salt-marsh conditions. In contrast, fossil foraminiferal assemblages are considered to comprise dead assemblages that have accumulated over short to long timescales and reflect former marsh surface conditions. Infaunal foraminifera complicate this general distinction, and special reference is made to this in Section 2.4.

We refer to relative sea-level changes, which are a compound of vertical movements in ocean level and vertical movements in the land surface due to isostatic or tectonic processes (e.g. Suess, 1885; Daley, 1934; Godwin and others, 1958; Fairbridge, 1961, 1992; Jelgersma, 1961; Bloom and Stuiver, 1963; Shephard, 1963; Mörner, 1969; Kidson and Heyworth, 1973, 1978; Tooley, 1974, 1978, 1982; Chappell, 1974; Kidson, 1977; Clark and others, 1978; Preuss, 1979; Peltier, 1980; van de Plassche, 1982, 1986; Shennan, 1982; Shennan and others, 1983; 2000a, 2000b, 2002; Long and Shennan, 1993; Lambeck, 1995; Pirazzoli, 1996; Törnqvist and others, 1998, 2004; Peltier and others, 2002; Shennan and Horton 2002; Donnelly and others, 2004; Gehrels and others, 2004; Horton and others, 2004, in press). Vertical changes in RSL are expressed in terms of their altitude relative to a geodetic datum (see Glossary), which in the case of Great Britain is Ordnance Datum, Newlyn (m OD), and in Ireland is Ordnance Datum, Malin Head (m OD). In contrast, we use the term elevation to describe height relative to the local, contemporaneous tidal frame. As a consequence, changes in marsh surface altitude are not synonymous with changes in marsh surface elevation. The conversion of elevation to altitude, and the implications surrounding this, are examined in detail in Section 4.2.1. An increase in marsh surface elevation reflects a reduction in marine influence and is termed a negative sea-level tendency. A decrease in marsh surface elevation equates to an increase in marine influence and is termed a positive sea-level tendency (Shennan and others, 1983). Since changes in marsh surface elevation reflect shifts in the balance between marsh accumulation and RSL change, switches in sea-level tendency do not require changes in the altitude of RSL.

1.2 THE SALT-MARSH ENVIRONMENT

Salt-marshes are intertidal environments that are distinguished from neighboring tidal mud or sand flats by a covering of halophytic vegetation (Chapman, 1960; Redfield, 1972; Adam, 1978). Temperate salt-marsh environments have provided a wealth of valuable information concerning Holocene sea-level change. The utility of salt-marshes stems from their intimate linkage with the tidal frame, coupled with pronounced vertical zonations of flora and fauna, which permit the identification of sub-environments from within the intertidal zone. The development of salt-marshes, and their relationship with RSL, is highly complex, mediated by minerogenic sediment supply, plant productivity, tidal range, and wind-wave climate (Harrison and Bloom, 1977; Pethick, 1981, 1992; Allen, 1990, 1995, 2000; French, 1993). A full review of these complex morphosedimentary systems is beyond the scope of this paper, but excellent recent overviews of Holocene salt-marshes from northwestern Europe are provided by Allen (2000, 2003). Here, attention is focused on the features of salt-marsh evolution that pertain to the reconstruction of RSL change in general and the use of foraminifera in particular.

1.2.1 Marsh Surface Elevation

Foraminifera are used to provide information on the elevation of a salt-marsh surface relative to the local tidal frame. A salt-marsh grows vertically by the accretion of minerogenic sediment, primarily derived from the marine environment, and the accumulation of organogenic sediment, principally generated by above and below ground salt-marsh plant productivity (Allen, 2000). Marsh surface elevation determines the extent, frequency and duration of tidal inundation that, in turn, controls both the absolute and relative contributions of these sediment sources. Consequently, a strong feedback loop exists in which marsh surface elevation controls, and is controlled by, tidal inundation characteristics. In a general sense, this results in salt-marsh evolution towards a dynamic equilibrium with the external controlling factors of minerogenic sediment supply, tidal range and RSL.

Northeastern North American salt-marshes, such as those in Nova Scotia, Maine, Connecticut, Massachusetts, Delaware, Virginia and North Carolina have provided a wealth of Holocene sea-level data (e.g. Redfield and Rubin, 1962; Kaye and Barghoon, 1964; Redfield, 1967; Belknap and Kraft, 1977; Scott and Medioli, 1978, 1980a; van de Plassche and others, 1989; 1992, 1998, 2002, 2003, 2004; Smith and others, 1984; Williams 1989; van de Plassche, 1991, 2000, 2001; Scott and Leckie, 1990; Thomas and Varekamp, 1991; Varekamp and others, 1992; Gehrels, 1994, 1999, 2000; de Rijk, 1995a, b; Hippensteel and others, 2000, 2002; Spencer,

2000; Gehrels and others, 1996, 2002, 2005; Edwards and others, 2004a, b; Culver and Horton, 2005; Roe and van de Plassche, 2005; Horton and others, 2005a; Horton and Culver, in press). Many of these systems are profoundly different to their counterparts in northwest Europe, such as the British and Irish marshes considered here. This difference is principally concerned with the relative importance of organogenic versus minerogenic sedimentation. In Connecticut, for example, salt-marsh growth is dominated by organogenic sedimentation and preservation is so high that over 70% of plant fibers remain identifiable many centuries after burial (Hill and Shearin, 1970). As a consequence, the high marsh surface accumulates comparatively rapidly and is capable of keeping pace with rising RSL during the late Holocene. This is reflected by sequences containing meters of high marsh peat that have accumulated over the last 3000 to 4000 years (e.g. Thomas and Varekamp, 1991; Gehrels, 2000; van de Plassche, 2000). In contrast, British salt-marshes are highly inorganic, particularly during the late Holocene, and the supply of minerogenic sediments exerts the dominant control on their growth. Consequently, accumulation rates are most rapid in low elevation settings and decrease asymptotically with increasing marsh surface elevation and decreasing tidal inundation (Pethick, 1981; Allen, 1990, 1993, 1996, 2000, 2003; French, 1993; French and others, 1995). Well-vegetated, highest marsh surfaces therefore accumulate most slowly and are under-represented in late Holocene sedimentary sequences. Whilst much sea-level information has also been derived from marshes along the Pacific coast of North America (e.g. Scott, 1976; Atwater, 1987; Scott and others, 1990, 1996; Patterson, 1990; Jennings and Nelson, 1992; Long and Shennan, 1994; Guilbault and others, 1996; Nelson and others, 1996; Shennan and others, 1999; Patterson and others, 2005; Hamilton and Shennan, 2005a, b; Hamilton and others, 2005), these records are influenced by tectonic processes and are not considered here.

These differences in marsh characteristics have implications for the modern behavior of intertidal foraminifera (e.g. infaunal activity as outlined in Section 2.4) and for the application of transfer function reconstructions to the construction of RSL records (Section 4). Consequently, care must be taken when extrapolating the results of this predominantly British-based assessment to studies in strongly contrasting environments, and we attempt to highlight region-specific results when they arise.
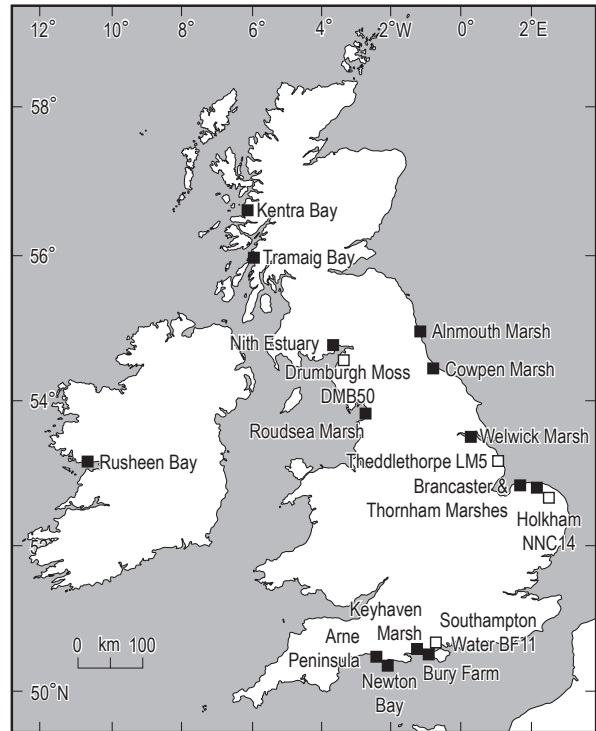
FIGURE 1. Location map showing the study sites in the British Isles. Black squares indicate sites at which surface foraminiferal data were collected, whilst white squares represent locations that provided fossil material.
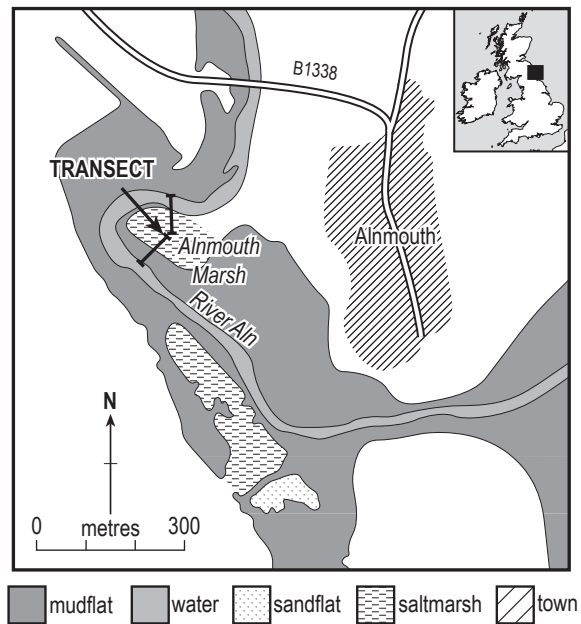
FIGURE 2. Location map of Alnmouth Marsh showing the surface foraminiferal survey transect. Key applies to all location maps.
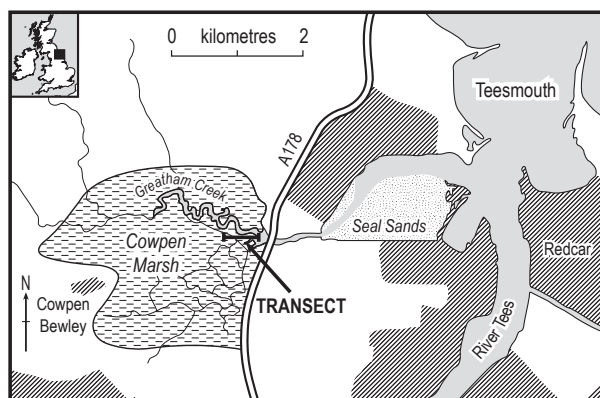
FIGURE 3. Location map of Cowpen Marsh showing the surface foraminiferal survey transect.
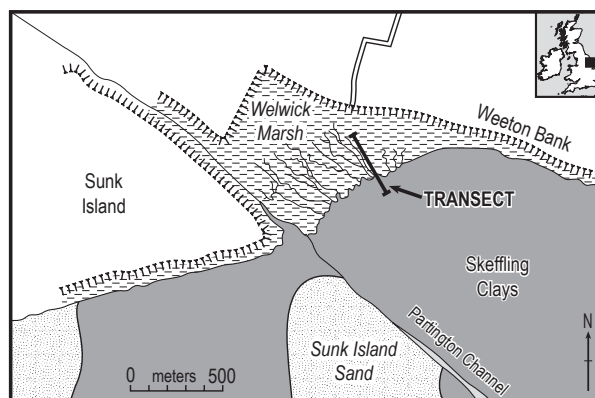
FIGURE 4. Location map of Welwick Marsh showing the surface foraminiferal survey transect.
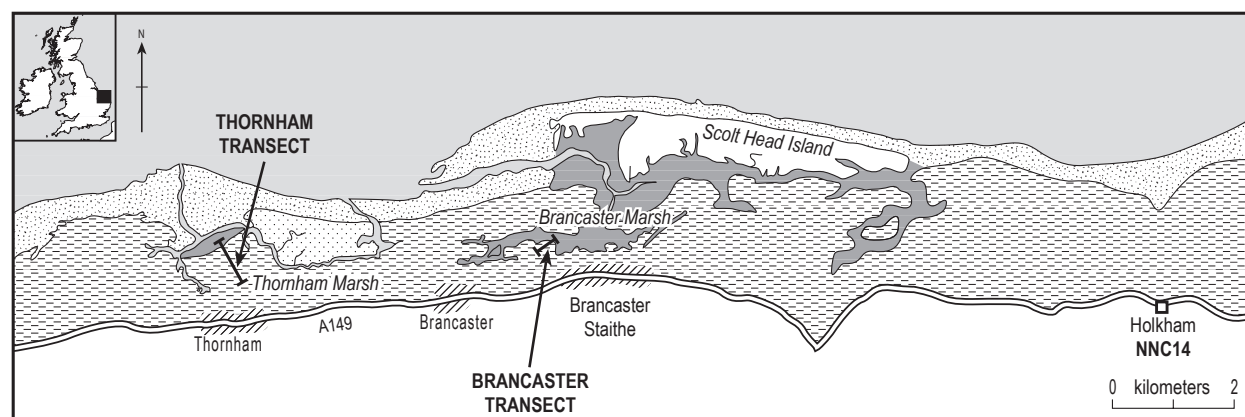
FIGURE 5. Location map of Thornham and Brancaster marshes showing the surface foraminiferal survey transects. Fossil material was recovered from Holkham (core NNC17).

Study area	Tidal Range	Salinity	No.	Site description
Alnmouth Marsh, Northumberland	macro (4.2m)	10-30	20	Between coastal dunes and the Aln estuary
Cowpen Marsh, Tees estuary	macro (4.6m)	15-25	31	Within a small tidal creek connecting to the Tees estuary
Welwick Marsh, Humber estuary	macro (6.4m)	5-35	20	North shore around the mid reach of the Humber estuary
Thornham Marsh, Norfolk	macro (6.0m)	15-25	24	At the west end of the barrier system along the Norfolk coast
Brancaster Marsh, Norfolk	macro (6.0m)	15-25	23	Behind the barrier system along the Norfolk coast
Bury Farm, Southampton Water	macro (4.0 m)	5-15	16	Upper reaches of the Southampton Water estuary
Keyhaven Marsh, Solent	meso (2.1m)	10-30	13	Behind a coastal spit in The Solent
Newton Bay, Poole Harbour	micro (1.6 m)	20-30	6	A small embayment in the lee of Furzey Island
Arne Peninsula, Poole Harbour	micro (1.2 m)	15-25	12	A small embayment in the lee of Round and Long Islands
Roudsea Marsh, Morecambe Bay	macro (8.4 m)	5-25	14	East shore adjacent to Roudsea Wood Nature Reserve
Nith Estuary, Solway Firth	macro (8.4 m)	5-25	13	East shore around the mid reach of the Nith estuary
Tramaig Bay, Jura	micro (1.4 m)	>30	8	A small embayment with little freshwater input
Kentra Bay, Argyll	macro (4.2 m)	>30	7	A sizeable embayment with little freshwater input
Rusheen Bay 1, Galway Bay	macro (4.5m)	10-30	9	Western side of a tidal creek connecting to Rusheen Bay
Rusheen Bay 2, Galway Bay	macro (4.5m)	10-30	20	Eastern side of a tidal creek connecting to Rusheen Bay

TABLE 1. Characteristics of study areas, number of sampling stations (No.) and measured annual salinity range of overlying water (cf. Figure 1-13).

1.3 DESCRIPTION OF STUDY SITES

Our investigations span fifteen study areas located on the east (n = 5), south (n = 4) and west (n = 4) coasts of Great Britain, and west coast of Ireland (n = 2) (Fig. 1, Table 1). These investigations were supported by a number of research projects conducted from 1994 to present. The study areas experience a wide range of tidal conditions and are situated in a variety of coastal settings ranging from back barrier to estuarine environments. This variety in environmental settings is desirable, since variations in coastal environments through time may mean that a single modern environment is not an appropriate analogue for fossil sites (e.g. Scott and Medioli, 1980a; Horton and Edwards, 2005).

1.3.1 East Coast of Great Britain

Five study areas are located on the east coast of Great Britain, fringing the North Sea. Alnmouth Marsh lies on the north-east coast of England in Northumberland, to the east of Alnwick, between Amble and Seahouses (Fig.

2). The River Aln flows into the sea at Alnmouth and the river mouth is bordered to the north by the village of Alnmouth and to the south by Alnmouth Dunes. The salt-marsh extends south into Alnmouth Dunes on their landward side. It is approximately 350 m in width and displays a succession from tidal flat to high marsh. The estuary at Alnmouth has a macrotidal regime of 4.2 m and salinity ranges from 10 to 30.

Cowpen Marsh lies on the north side of the Tees Estuary (Fig. 3). This estuary has a macrotidal range of 4.6 m during spring tides, and salinity varies significantly between tides as a result of the high volume of freshwater output from the Tees catchment (5 to 35). Cowpen Marsh is approximately 400 m in width and displays a succession from tidal flat through low marsh to high marsh.

Welwick Marsh is a remnant of the once extensive area of marshes that fringed the north side of the Humber Estuary (Fig. 4). The estuary is a classic example of a macrotidal estuary (tidal range of 6.4 m). A wide range of salinity is observed within the estuary (5 to 35) due to the large amount of freshwater input from the
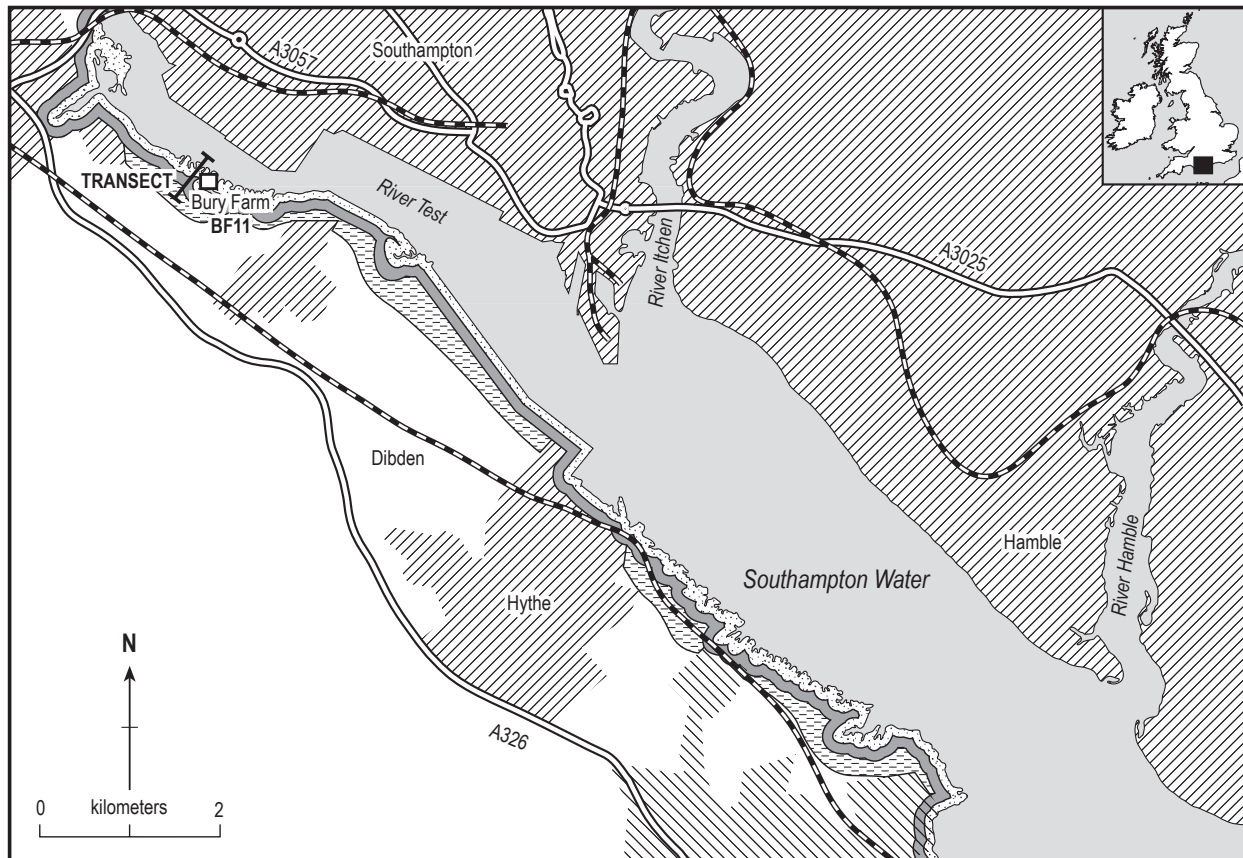
FIGURE 6. Location map of Bury Farm showing the surface foraminiferal survey transect. Fossil material was recovered at Bury Farm (core BF11).

catchment. Welwick Marsh is approximately 500 m wide and possesses tidal flat and low and middle marsh environments. The absence of a high marsh is due to an embankment at the landward edge of the marsh.

The final two east coast sites at Thornham and Brancaster marshes (Fig. 5) are located on the North Norfolk coast and possess similar tidal ranges (6.0 m) and salinities (5 to 30). The coastline is composed of extensive back-barrier tidal flats. Thornham Marsh has developed beyond the west end of the gravel barriers and is approximately 1 km wide. It covers a broad range of environments including tidal flat and low, middle and high marshes. Brancaster Marsh is approximately 150 m in width and can be divided into middle and low marshes and tidal flat environments. An embankment at the landward edge of the marsh is responsible for the absence of a high marsh.

1.3.2 South Coast of Great Britain

Four sites are located on the south coast of England. Bury Farm is situated in the upper reaches of Southampton Water, which has a macrotidal range (4.0 m) and relatively low salinities (5 to 15) due to freshwater drainage from its tributaries (Fig. 6). The marsh is around 100 m wide, although deeply dissected by salt-marsh creeks. The salt-marsh consists of a high and middle marsh which

is connected to the lower lying tidal flat area by a mud ramp. The salt-marsh platform is currently eroding, and this accounts for the absence of a clear lower marsh sub-environment.

The second south coast site, Keyhaven Marsh, is located south of Lymington (Fig. 7). The salt-marsh has formed in the protection of Hurst Spit, a large gravel barrier that provides shelter from south-westerly wind and waves. The marsh is approximately 200 m wide and can be divided into tidal flat, low and middle marsh environments. The absence of a high marsh is due to an embankment at the landward edge. The tidal range is mesotidal (2.1 m) and salinity is between 10 and 30.

Newton Bay is located in the south-eastern part of Poole Harbour, between Cleaval and Goathorn Points (Fig. 8). The area is largely protected by Brownsea, Furzey and Green islands although a sandy beach is evident on the more exposed, western shore. The marsh is around 50 m wide, backed by a small bank, and is currently experiencing erosion as a consequence of *Spartina* die-back. Newton Bay has a microtidal range (1.6 m) and relatively high salinities (20 to 30).

The final south coast site, Arne Peninsula, is also located within Poole Harbour approximately 3 km from Newton Bay (Fig. 8). It possesses a microtidal range (1.2 m) and a complex hydrographic character. Freshwater inputs to the estuary are limited and as a result salinity
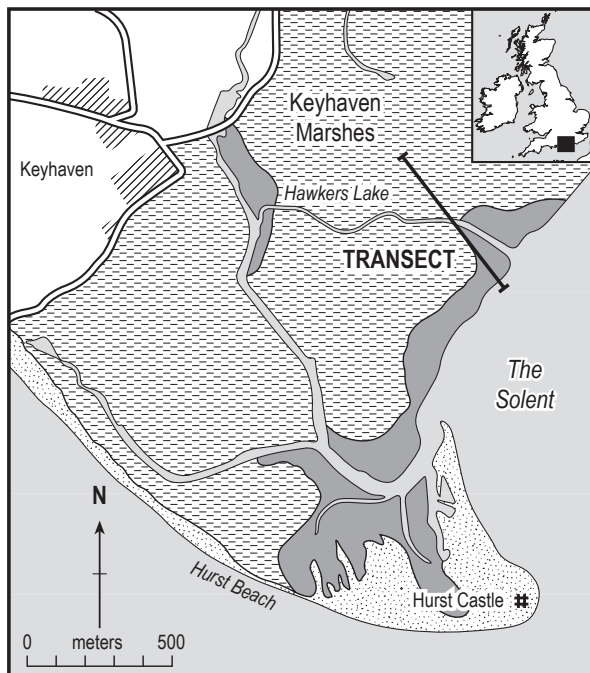
FIGURE 7. Location map of Keyhaven Marsh showing the surface foraminiferal survey transect.
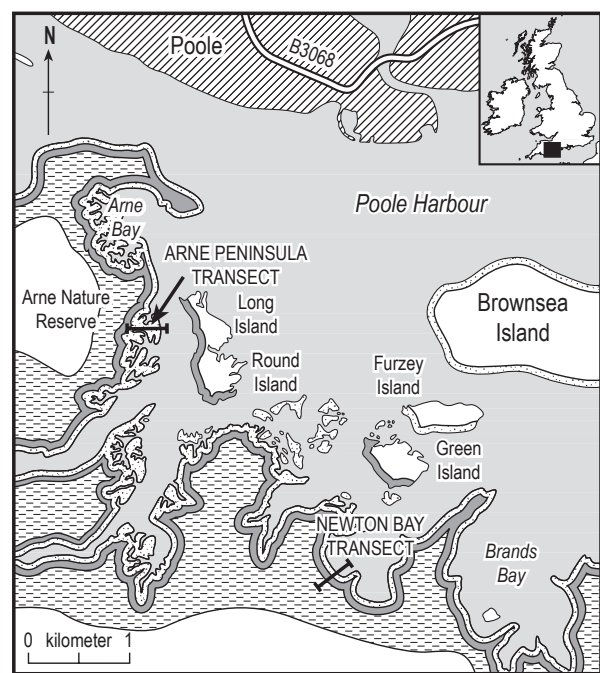
FIGURE 8. Location map of Newton Bay and Arne Peninsula showing the surface foraminiferal survey transects.
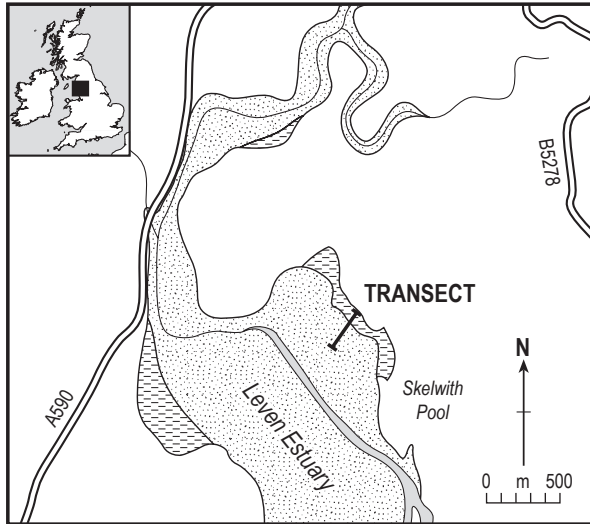
FIGURE 9. Location map of Roudsea Marsh showing the surface foraminiferal survey transect.
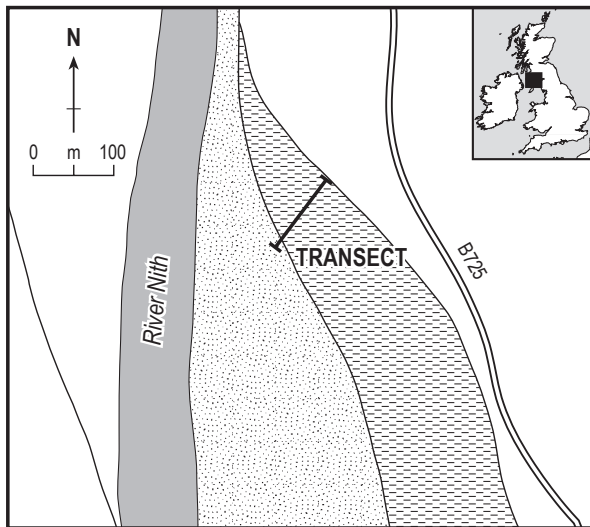
FIGURE 10. Location map of Nith Estuary showing the surface foraminiferal survey transect.

FIGURE 11. Location map of Tramaig Bay showing the surface foraminiferal survey transect.
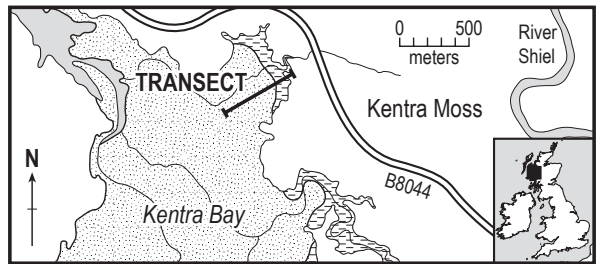
FIGURE 12. Location map of Kentra Bay showing the surface foraminiferal survey transect.

is moderate (15 to 25). The salt-marsh is around 130 m wide and displays a well-developed floral succession grading from woodland to low marsh and tidal flat.

1.3.3 West Coast of Great Britain and West Coast of Ireland

Four study areas are located on westerly facing coastlines. Roudsea Marsh is located towards the head of the Leven Estuary in the northern part of Morecambe Bay (Fig. 9). The marsh is 200 m wide and displays a full range of intertidal environments. Hydrologically,

the marsh is influenced predominantly by discharges of freshwater from the Windermere catchment and seawater from the Irish Sea. Salinity varies between 5 to 25 during high spring tides, when the tidal range is 8.4 m.

The Nith estuary is one of the main estuaries draining from the north shore of the Solway Firth (Fig. 10). Its position in the inner Solway Firth accounts for the macrotidal environment with a tidal range of 8.4 m. The high freshwater output of the Nith combined with the large tidal amplitude produces a wide range of salinities (5 to 25). The study site extends from the eastern shore of the estuary across a salt-marsh, which is only 30 m
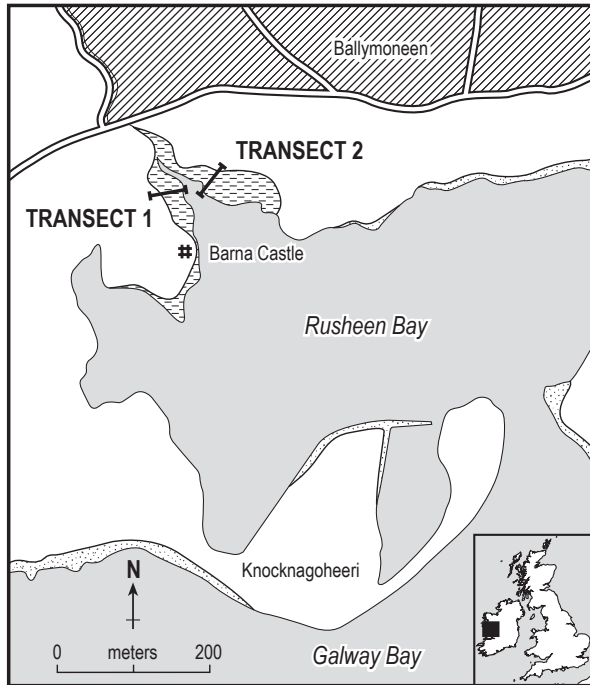
wide. The seaward edge is bounded by a small cliff (1 m). The landward edge of the marsh progrades into a narrow upland zone and is bounded by a coastal road.

Tramaig Bay and Kentra Bay are situated in west Scotland. Tramaig Bay is a small, semi-circular tidal basin on the northeast coast of the Isle of Jura (Fig. 11). It is protected by rock outcrops and is connected to the Sound of Jura via a narrow inlet. The basin is microtidal (1.4 m) and displays a vegetational succession from pioneer salt-marsh through to mature, flat and poorly drained freshwater fen. Due to the small output of freshwater from the upland, salinity within the basin reflects that of the sea water with little tidal variation (> 30).

Kentra Bay is protected from waves by rocky outcrops and a narrow entrance. The study site is located on the northeast fringe of Kentra Bay (Fig. 12), is 120 m wide and covers a range of environments from tidal flat to raised bog (upland) from which acidic runoff drains through the marsh into the Bay. The amount of freshwater running into the Bay is minimal and seems to have little effect upon the salinity of the incoming tides which is usually as high as 33. The predicted range of tides is macrotidal (4.2m).

The two study sites on the west coast of Ireland are located in Rusheen Bay, a sheltered marsh area of

Galway Bay (Fig. 13). The first transect encompasses high and middle marshes, which are separated from the tidal flat by a steep sided bank. The second transect covers the full range of environments from high marsh to tidal flat. Transects one and two are located on the western and eastern sides of a small tributary in Rusheen Bay, respectively. Both sites are 150 m wide and salinity varies between 5 to 25 during high spring tides. These are macrotidal areas with a tidal range of 4.5 m.

2. THE MODERN DISTRIBUTION OF BRITISH INTERTIDAL FORAMINIFERA

The successful use of salt-marsh foraminifera to reconstruct sea level requires a detailed and accurate understanding of their modern distributions and of their relationship to the environmental variables responsible for shaping these patterns (e.g. Phleger and Walton, 1950; Phleger, 1954, 1955; 1965a, b, 1970; Phleger and Ewing, 1962; Lutze, 1968; Scott, 1976, Scott and Medioli, 1978, 1980a; Patterson, 1990; Thomas and Varekamp, 1991; Gehrels, 1994, 2000, 2002; Varekamp and others, 1992; Hayward and others, 1999, 2004a; Horton, 1999; Horton and others, 1999a, b, 2000, 2005; Edwards and Horton, 2000; Hippensteel and others, 2000; Gehrels and others, 2000, 2001, 2005; Horton and Edwards, 2001, 2005; Martin and others, 2003; Edwards and others, 2004a, 2004b; Gehrels and Newman, 2004; Hayward and others, 2004a; Patterson and others, 2004, 2005; Horton and Culver, in press). In the following sections we examine three key issues associated with the study of modern foraminifera in the wider context of sea-level research programs: the most appropriate assemblage constituents (live, dead and/or total) for use in sea-level reconstruction; the potential influence of seasonality in salt-marsh foraminifera-based reconstructions; and the significance of infaunal foraminifera as possible sources of error. Finally, we describe the distribution of foraminifera within the intertidal zones of the fifteen study sites.

2.1 STUDYING INTERTIDAL FORAMINIFERA

Processing methods can introduce errors in quantitative microfossil analysis (Scott and others, 2001). Therefore, it is important to develop a foraminiferal sampling protocol that will facilitate the evaluation of intertidal foraminifera as sea-level indicators.

2.1.1 Sample Collection in the Field

We collected modern sediment samples from cross-marsh transects covering, where possible, the complete range of sub-environments from tidal flat to high marsh. Sample stations were placed at equal vertical intervals or at marked changes in topography or floral community. All stations were surveyed relative to the appropriate national datum. The sampling frequency and interval varied between marshes reflecting the underlying objective of the individual research projects involved. Cowpen Marsh was sampled at approximately two-weekly intervals for a twelve-month period. Welwick, Thornham and Brancaster marshes were sampled four times during a twelve-month period (once in each season). The remaining study areas were sampled once around the time of spring tide. The seasonal measurements are expressed as annual averages and combined with the single measurements to produce the modern foraminiferal dataset.

The collection of modern samples follows Scott and Medioli (1980a), de Rijk (1995a) and Scott and others (2001). The standard sample volume is 10 cm^3 (10 cm^2 by 1 cm thick). This volume allows comparison with similar studies (e.g. Phleger and Walton, 1950; Phleger, 1954, 1955; 1965a, b, 1970; Phleger and Ewing, 1962; Lutze, 1968; Scott, 1976, Scott and Medioli, 1980a; de Rijk, 1995a; Horton, 1999; Horton and others, 1999a, b, 2000, 2005b; Edwards and Horton, 2000; Gehrels and others, 2000, 2001, 2005; Horton and Edwards, 2001, 2005; Edwards and others, 2004a, 2004b; Gehrels and Newman, 2004; Horton and Culver, in press; Tobin and others, 2005). Since the surface material can be root bound and difficult to penetrate, a small hand-held corer with sharpened, serrated edges was developed following the guidelines of Scott and Medioli (1980a). The sampler is turned into the surface of the intertidal zone to avoid compaction and subsequently retrieved by pulling back while supporting the sample with a knife. The sampler is generally suitable for sampling cohesive sediments such as salt-marsh or tidal flat deposits; it is less satisfactory for clean sands and gravels (Murray, 1991). In the field, each sample is placed into ethanol or formalin with the protein stain rose Bengal and sealed in vials or bags. After processing in the laboratory, all samples are stored in buffered ethanol and refrigerated to prevent bacterial oxidation of the foraminiferal tests.

Rose Bengal is used extensively to differentiate living from dead foraminifera (Walton, 1952; Scott and Medioli, 1980b; Murray, 1991; Murray and Bowser, 2000). Protoplasm is stained bright red whereas test walls and organic linings 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, 2000; Horton and Edwards, 2003). However, Boltovskoy and Lena (1970) observed protoplasm in tests collected weeks and even months earlier. Furthermore, it is necessary to check that red staining is not caused by clusters of bacteria or other organisms using the test as a refuge (Murray, 1991). Rose Bengal remains superior to other staining techniques such as heat saturated or heat acetylated Sudan black B. These techniques are hampered by similar problems and are more time consuming than the use of rose Bengal (Murray, 1991; Scott and others, 2001).

A 2 cm^3 or 5 cm^3 sample volume was used for foraminiferal analysis from fossil samples. One centimeter slices were cut with a sharp knife at specific sampling intervals from augers, cores or monolith tins. The sampling interval used depends upon the lithostratigraphy, biostratigraphy, potential selective preservation, infaunal occurrence and reworking of foraminifera. Foraminifera should be sampled from the core immediately, or the core placed in cold storage, to preserve the foraminiferal tests. Wang and Chappell (2001) noted that foraminifera from some environments may disappear if sediment is exposed at room temperature for a few days.

2.1.2 Sample Preparation and Identification in the Laboratory

Conventional preparation techniques of modern and fossil foraminiferal samples are inadequate to isolate foraminifera in sediments with a high organic component (de Rijk, 1995a, b; Lehmann and Rottger, 1997). A solid crust of fine organic material is produced when the sediment is washed, sieved and dried. The crust cannot be broken without the destruction of the tests. De Rijk (1995a) and Horton (1997) evaluated numerous other techniques and concluded that the use of a wetsplitter (Scott and Hermelin, 1993) provides a reliable method for splitting the foraminiferal sample. Each sample is wet sieved through 500 mm and 63 mm sieves and decanted. The greater than 500 mm and decanted fraction is examined before being discarded. After preparation, the wetsplitter puts the remaining sample in suspension with approximately 2.5 liters of water, which may then be divided into eight equal parts (or multiples thereof). This procedure maximizes the number of samples that may be processed whilst minimizing loss or damage to

foraminiferal tests and maintaining a representative sub-sample (Gehrels, 1994). Samples are counted wet under a binocular microscope at typical magnifications of x40 to x50. This wet-counting method facilitates the detection of the rose Bengal stain and prevents the drying out of the organic residue, which can result in consolidation or "pancaking," a phenomenon that is often irreversible (Scott and Medioli, 1980a; Scott and others, 2001).

The taxonomy follows Murray (1971, 1979, 2000b) and de Rijk (1995a). The identifications were confirmed by comparison with primary and secondary type specimens lodged in The Natural History Museum, London, UK. In light of the fact that the foraminiferal data employed in this paper have been compiled from a range of analysts over the course of a number of years, we have adopted a conservative approach to taxonomic sub-division to ensure consistency in data quality. In many cases this necessitates the grouping of minor species at the genus level (e.g. *Quinqueloculina* spp.) and the combination of possible species or ecophenotypes under a single species name (e.g. *Ammonia* spp.). It is possible that a more detailed sub-division of taxa will provide more subtle information on environmental conditions (e.g. Hayward and others, 2004b). To this end we present an updated taxonomy for intertidal foraminifera from Great Britain and Ireland (Appendix 2), which we hope will facilitate more refined studies in the future.

2.2 FORAMINIFERAL ASSEMBLAGE CONSTITUENTS

There is much debate about which assemblage constituents to use for foraminiferal population studies. Published works on modern foraminifera report in terms of live (biocoenosis), dead (thantocoenosis) or total (live plus dead) assemblages (e.g. Jorissen and Wittling, 1999). Many researchers state that the total assemblages most accurately represent general environmental conditions because they integrate seasonal and temporal fluctuations (Buzas, 1965; 1968; Scott and Medioli, 1980b; Scott and Leckie, 1990; Jennings and others, 1995; de Rijk, 1995a; Tobin and others, 2005). However, Murray (1982, 1991, 2000a) suggested that the use of total assemblages disregards changes that will affect live populations after their death. Furthermore, since thicker vertical samples will contain larger dead assemblage contributions, the total assemblage is also influenced by sampling strategy. Murray (1971) stated that only live populations can be used to interpret environmental conditions. Nevertheless, only detailed observation over

a considerable period of time can be used to determine all aspects of a population (Buzas, 1968; Swallow, 2000). Many of these studies have concentrated on agglutinated foraminiferal species occupying salt-marsh areas of the intertidal zone. Thus, Horton (1999) undertook seasonal and post-depositional analyses of both agglutinated and calcareous foraminiferal species, occupying not only salt-marsh environments of the intertidal zone but also tidal flat and sand flat environments. He concluded that the dead assemblage is the most appropriate constituent if the whole intertidal zone is to be used. In the following section, we expand upon these published results of Horton (1999), which are based on a detailed survey of the intertidal zone at Cowpen Marsh, Tees Estuary, Great Britain.

2.2.1 Method

Horton (1999) collected samples at two-weekly intervals for a period of twelve-months from selected intertidal environments of Cowpen Marsh, Tees Estuary. Methods followed the guidelines set out in Section 2.1. Here, we re-examine the live, dead and total foraminiferal assemblages collected over this twelve-month period to determine their relationships.

2.2.2 Results

The foraminiferal dead assemblage of Cowpen Marsh remains relatively stable during the twelve-month period, despite significant seasonal fluctuations in the live population (Fig. 14). The dead assemblage ranges from 6215 individuals in May 1995 to 10264 individuals in July 1995 with a coefficient of variance (V_c) of 0.14. In contrast, the live population fluctuates between 1240 individuals in February 1996 and 7768 individuals in July 1995 with a V_c of 0.36. This produces a total assemblage
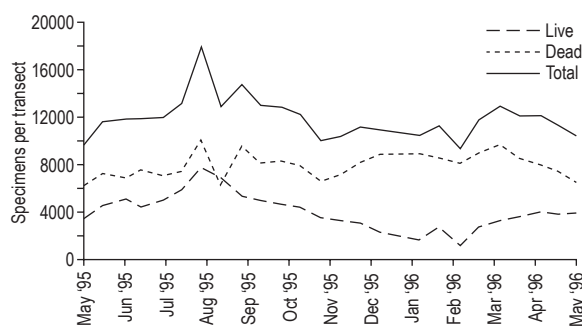
FIGURE 14. Number of live, dead and total foraminiferal specimens for all species from Cowpen Marsh from 1st May 1995 to 3rd May 1996.
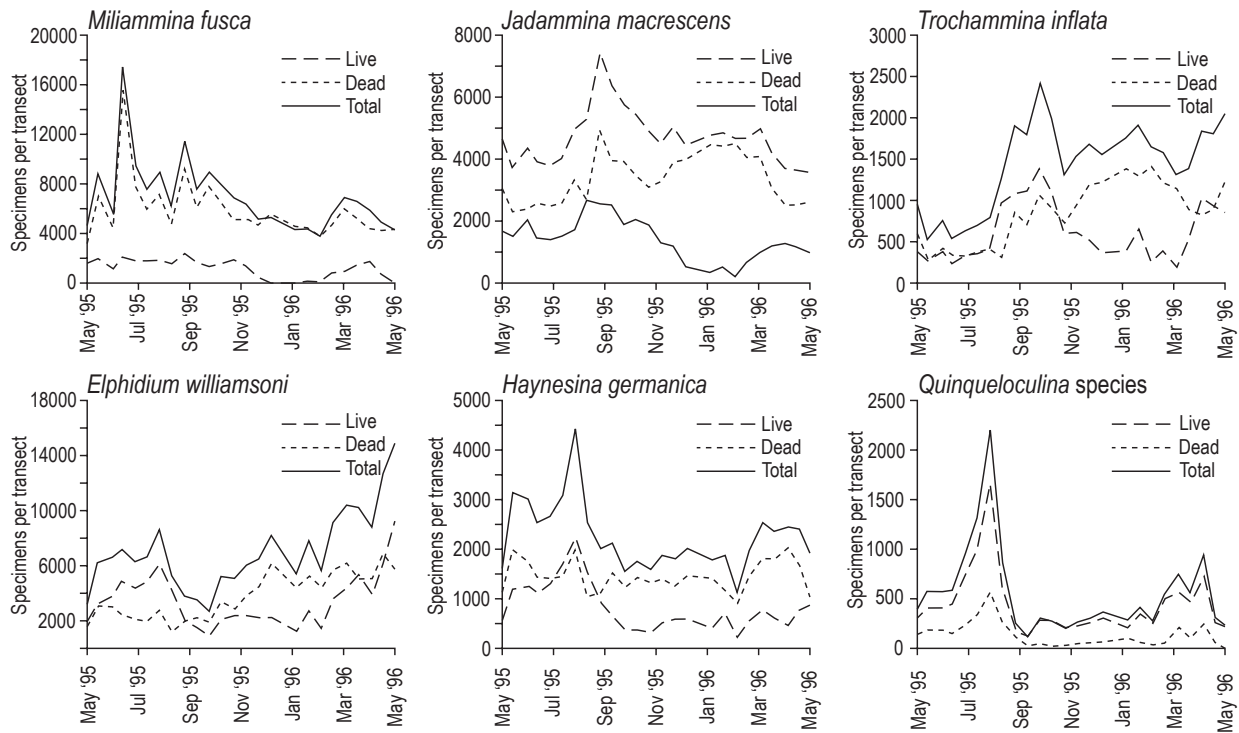
FIGURE 15. Number of live, dead and total specimens of six foraminiferal species from Cowpen Marsh from 1st May 1995 to 3rd May 1996.
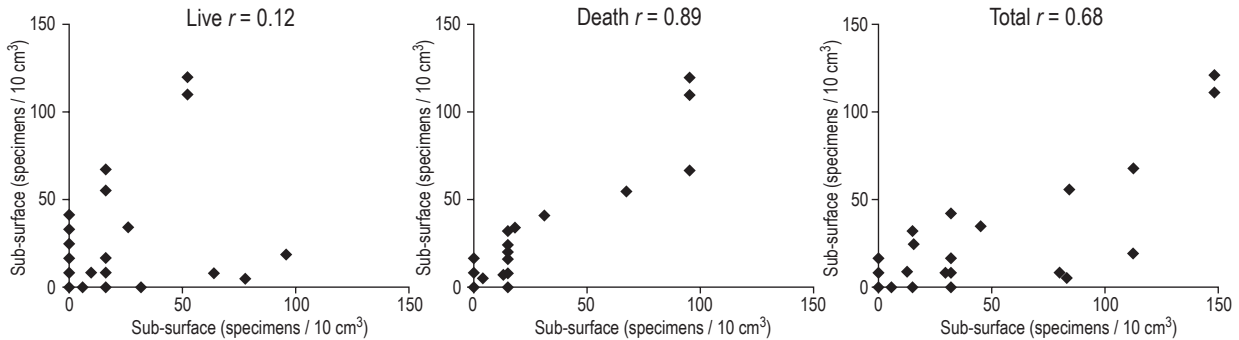
FIGURE 16. Scatter plots and correlation coefficients (r) showing the relationship between surface and sub-surface assemblages when considering the: (a) live population; (b) dead assemblage; and (c) total assemblage.

fluctuating between 9464 individuals in February 1996 and 18032 individuals in July 1995 with a V_c of 0.15.

Analyses of the relative abundance of six selected foraminiferal species from Cowpen Marsh reveal that the composition of the foraminiferal dead assemblage remains relatively stable (Fig. 15). The fluctuations of the live calcareous and agglutinated species are more pronounced than for the dead foraminifera. For example, the abundance of living *Haynesina germanica* ranges from 256 (21%) to 2280 (29%) individuals per transect with a V_c of 0.58, whilst the total abundance ranges from

1200 (13%) to 4289 (25%) individuals per transect with a V_c of 0.28 in February 1996 and July 1995. In contrast, the abundance of dead *H. germanica* ranges from 954 (13%) in February 1996 to 2064 (24%) individuals per transect in April 2004 with a V_c of 0.21.

The study was further extended to determine which modern assemblage constituents are the most appropriate for paleoenvironmental reconstructions. Surface and sub-surface samples were collected from the high, middle and low marsh, and tidal flat environments of Cowpen Marsh. Sub-surface samples were collected at a depth of

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7 cm; virtually all infaunal activity within Cowpen Marsh occurred above this depth (Horton, 1997). The scatter plot (Fig. 16) and Pearson's correlation coefficient ($r = 0.89$) show a positive linear correlation between sub-surface and surface dead assemblages. The dead assemblage fluctuates little between sub-surface and surface because the majority of calcareous species are minor contributors to dead surface assemblages in intertidal environments. In contrast, the live population ($r = 0.12$) and total assemblage ($r = 0.68$) in intertidal environments show non-linear relationships between the sub-surface and the surface. The live and total assemblages of the surface sample incorporate living calcareous species which can represent over 40% of the assemblage. However, post-depositional changes (e.g. dissolution; Green and others, 1993) result in calcareous species being removed and the sub-surface assemblage becomes dominated by agglutinated species.

2.2.3 Discussion and Summary

Foraminiferal dead assemblages differ from live populations due to life processes and post-depositional changes. The twelve-month study of dead foraminiferal assemblages described here indicates that they are in equilibrium with the depositional environment in which they are found. Dead assemblages do not exhibit the seasonal fluctuations seen in live populations. Furthermore, sub-surface assemblages, that are the foci of paleoenvironmental reconstructions, accurately reflect the dead surface assemblage, indicating that taphonomic processes are minimal (Goldstein and Watkins, 1999; Patterson and others, 1999; Hippensteel and others, 2002, Martin and others, 2003; Horton and others, 2005b; Culver and Horton, 2005; Horton and Murray, 2006).

2.3 SEASONAL DISTRIBUTION OF FORAMINIFERA

Seasonal variations in foraminiferal assemblages have been documented in many studies (Buzas, 1965, 1968; Jones and Ross, 1979; Scott and Medioli 1980b; Alve and Murray, 1995, 1999, 2001; Murray and Alve, 1999, 2000; Swallow, 2000; Horton and Edwards, 2003; Murray 2003; Duchemin and others, 2005; Horton and others, 2005b; Horton and Murray, 2006). Indeed, Buzas (p. 11, 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 modern assemblage sampled on any one occasion may

or may not be in equilibrium with the environment or be typical of assemblages over a longer time period. This is an important issue for any study that seeks to use surface assemblages as modern analogues for past conditions recorded in a fossil sequence. Section 2.2 demonstrates that dead assemblages are less influenced by seasonal fluctuations than live populations, but an important question remains concerning the extent to which any variation in dead assemblage may influence reconstructions derived from modern distributions. Horton and Edwards (2003) illustrated that, over the course of one year, seasonal variations of modern dead foraminiferal assemblages at Cowpen Marsh modify the elevation and range of their vertical assemblage zones. In this paper we further investigate the seasonal variability of dead assemblages using data from three additional marshes located on the east coast of Great Britain.

2.3.1 Method

Foraminiferal sampling and preparation followed the guidelines set out in Section 2.1. We use cluster analyses of the foraminiferal samples collected at three-monthly intervals for a period of twelve-months from Welwick, Thornham and Brancaster marshes to classify the vertical distribution. The elevation of each station within the cluster zones is analyzed to determine the vertical zonation of the intertidal environment for each three-month period (see Section 2.5 for further details of foraminiferal assemblages and cluster analyses).

2.3.2 Results

Cluster analysis of each three-monthly foraminiferal dead assemblage from Welwick, Thornham and Brancaster marshes divides the intertidal zone into two parts (I and II) on the basis of species and sample composition (Fig. 17). The first one of these is an agglutinated assemblage that is restricted to the vegetated marsh, whilst the second is predominantly a calcareous assemblage that typifies the tidal flats of the intertidal zone. The vertical zonation of each study area varies during the year in response to the seasonality of foraminiferal distributions, and this variation results in changes to the elevation of the boundary between zones I and II. This boundary is at its lowest elevation in the spring months (Welwick = 2.95 m OD; Thornham = 2.15 m OD; Brancaster = 2.48 m OD) when agglutinated species such as *Jadammina macrescens* and *Balticammina pseudomacrescens* extend further down the marsh. The maximum elevation of this

boundary occurs in either the summer (Welwick = 3.37 m OD; Thornham = 3.09 m OD) or autumn (Brancaster = 3.23m OD) months when calcareous species such as *H. germanica* and *Ammonia* spp. are found in high abundances at higher elevations.

FIGURE 17. Seasonal variations of elevational ranges of three-monthly cluster zones from (a) Welwick, (b) Thornham and (c) Brancaster marshes. The unconstrained cluster analysis is based on unweighted Euclidean distance, and uses foraminiferal dead assemblages. Only samples with counts greater than 40 individuals and species that contribute 5% of the dead assemblage are included.

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2.3.3 Discussion and Summary

The results presented above demonstrate that a modern sample taken in one three-month period can significantly under-estimate or over-estimate the boundary between foraminiferal zones by as much as 0.94 m. Hence, the reliability of cluster zones as indicators of former sea levels can only be assessed following a consideration of the seasonal errors affecting the altitude of their upper and lower boundaries. Uncertainties arising from the large vertical excursions in zonal boundaries are compounded by the limitations inherent in the assemblage zone approach to RSL reconstruction. Edwards and others (2004a) discuss these limitations with regard to the spatial variability of assemblage zone composition, elevation and vertical range. Principal among these problems is the variable resolution with which RSL changes can be examined. This is caused by the fact that changes can be identified only when the boundary between assemblage zones is crossed.

Horton and Edwards (2003) investigated the influence of seasonality further by developing monthly foraminiferal transfer functions using the Cowpen Marsh data (see Section 3 for further information on transfer functions). They 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. Horton and Edwards (2003) conclude that an investigation of modern salt-marsh 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.

2.4 THE SIGNIFICANCE OF INFAUNAL FORAMINIFERA IN BRITISH AND IRISH SALT-MARSHES

The most commonly collected sampling depth for studies of the modern distribution of foraminifera is the uppermost one or two centimeters of sediment (e.g. Scott and Medioli, 1980a, b; Jennings and Nelson, 1992; Gehrels, 1994; de Rijk, 1995a, b; Horton, 1999; Horton and others, 1999a, b, 2003, 2005b; Edwards and
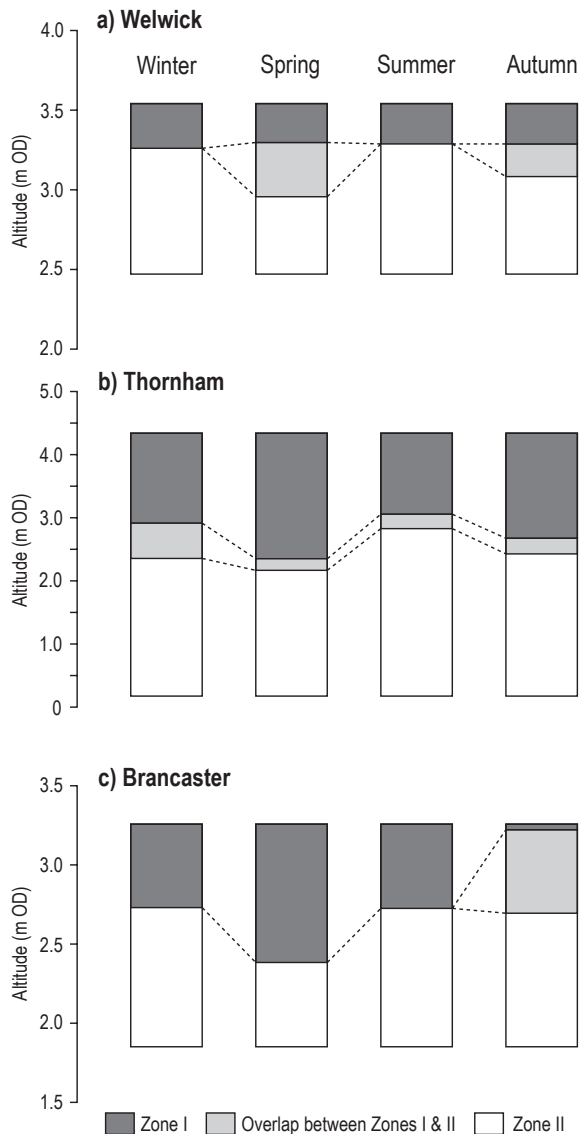
others, 2004a; Duchemin and others, 2005; Tobin and others, 2005). This sampling procedure assumes that intertidal foraminifera are primarily epifaunal. However, infaunal foraminifera have been reported in a variety of salt-marshes. Infaunal occurrences may change the composition of dead assemblages that accumulate in sub-surface sediments (Akers, 1971; Goldstein and Harben, 1993; Kitazato, 1994; Goldstein and Kuhn, 1995; Ozarko and others; 1997; Goldstein and Watkins, 1998; Saffert and Thomas 1998; Patterson and others 1999; Hippensteel and others, 2000; Culver and Horton, 2005; Duchemin and others, 2005). Akers (1971) reported rose Bengal stained agglutinated foraminifera at depths of 30 to 35 cm in Beaufort salt-marsh, North Carolina. Goldstein (1988) further reported rose Bengal-stained foraminifera in sub-surface sediments at depths of 8 cm. Goldstein and Harben (1993) found the infaunal *Arenoparrella mexicana* to be virtually absent in surface sediments but abundant in sub-surface assemblages. The deepest records of living marsh foraminifera were noted by Saffert and Thomas (1998) at 50 cm in New England and at 60 cm by Hippensteel and others (2000) in Delaware salt marshes. Duchemin and others (2005) concluded that the use of distributional models exclusively based on superficial assemblages must be corrected by considering infaunal taxa. In contrast, in one of the few studies from Great Britain and Ireland, at Cowpen Marsh, live foraminifera are restricted to the top 3 cm of marsh sediments (Horton, 1997, 1999).

In this paper we further investigate the significance of infaunal foraminifera in the sub-surface sediments from the intertidal zone of Rusheen Bay, Ireland. In addition, we will elucidate the relationship between living foraminifera and the apparent Redox Potential Discontinuity (RPD). In fine-grained coastal areas, when there is oxygen in the overlying water column, the near

FIGURE 18. Relative abundance of live foraminiferal species per 10 cm³ versus depth from short cores of the high marsh, middle marsh, low marsh and tidal flat of Rusheen Bay. The shaded bar indicates the depth of the Redox Potential Discontinuity.

surface sediment will have a higher reflectance value relative to hypoxic or anoxic sediment underlying it. This is because the oxidized surface sediment contains particles coated in ferric hydroxide, while the suphidic sediments below the oxygenated layer are grey to black. The boundary between the colored ferric hydroxide surface sediment and underlying grey to black sediment is defined as the apparent RPD. If RPD levels can be obtained, the depth of the oxidized zone is determined.

2.4.1 Method

We collected surface and sub-surface samples from four intertidal environments (high, middle and low marshes, and tidal flat) at Rusheen Bay. Sub-surface samples were taken at 2 cm intervals from 0 to 16 cm depth. Foraminiferal sampling and preparation followed the guidelines set out in Section 2.1. A Sediment Profile Imagery Camera (Aquafact Ltd; Barry, 2000) was used to examine RPD levels.

2.4.2 Results

Ten living foraminiferal species are identified from the four environments. Two agglutinated species (*J. macrescens* and *Trochammina inflata*) and two calcareous species (*Elphidium incertum* and *H. germanica*) dominate the live population. The highest number of living foraminifera for each of these environments is observed in the surface sample (0 to 1 cm depth), which indicates that they are primarily epifaunal (Fig. 18). In total, an average of 92% of all living foraminiferal species are found in the surface samples. However, there is a gradual increase in the proportion of infaunal foraminifera from high marsh (3%) to tidal flat (13%). Indeed a small live population of *Glabratella milletti* and *Lagena* species is found at depths of 10 to 12 cm in the tidal flat environment. The RPD levels of each environment range from 2 cm within the high and middle marsh to 5 cm within the tidal flat (Fig. 18).

2.4.3 Discussion and Summary

These results suggest that the intertidal foraminifera of Rusheen Bay live primarily in epifaunal habitats. The Sediment Profile Imagery Camera indicates that the sediments beneath the vegetated marsh have a thin oxygenated layer that extends to a depth of 3 cm, and yet virtually all living foraminifera are found in the uppermost centimeter of sediment. The tidal flat
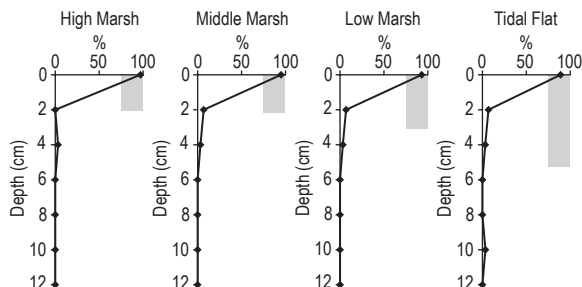
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environment is associated with a sandier substrate and a thicker oxygenated layer (5 cm). These environments possess the highest numbers of infaunal foraminifera although, once again, most live individuals are recovered from the top 1 cm. The elevated numbers of *Glabratella milletti* and *Lagena* species at depth could be due to an 'oxygen oasis' around which living foraminifera may cluster (Goldstein and Harben, 1993) or simply the result of bioturbation, whereby living foraminifera bypass the surface through biogenic subduction or by falling into tubes or burrows (Green and others, 1993).

These results are in good agreement with previously reported infaunal distributions from British estuarine environments. Castignetti (1996) states that, in a seasonal study of 8 cm short-cores from the Plym estuary, 97% of stained individuals are found in the top centimeter of sediment. Similarly, Horton (1997, 1999) illustrate that the intertidal foraminifera of Cowpen Marsh live primarily in the top 1 cm. Alve and Murray (2001) also note that in the Hamble estuary, the majority of living foraminifera are restricted to the top 0.25 cm of sediment whilst the redox boundary was located at around 1 cm depth. They conclude that the redox boundary is not the main limiting factor in down-core abundance, and this inference is supported by the results from Rusheen Bay. It is therefore likely that the foraminifera are responding to the availability of algae (food), which is strongly controlled by light and clearly limited to the sediment surface. The general lack of consensus concerning the infaunal character of individual species is likely to be due, in part, to the fact that these are spatially and temporally variable, reflecting seasonal and local environmental conditions and chance bioturbation (Buzas and others, 1993; de Stigter and others, 1998; Patterson and others, 2004; Culver and Horton, 2005; Tobin and others, 2005).

2.5 FORAMINIFERAL DISTRIBUTIONS

In this section we provide a synthesis of foraminiferal dead assemblages collected from fifteen intertidal study areas situated on the east, south and west coasts of Great Britain, and west coast of Ireland. (Fig. 1 and Table 1). We have identified 84 dead species from 236 sampling stations. The relative percentages and total counts at every site together with environmental data (where available) are presented in Appendix 3.

FIGURE 19. Relative dead abundance of four principal foraminiferal species from Alnmouth Marsh. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.

2.5.1 East Coast of Great Britain

Alnmouth has a diverse foraminiferal assemblage with thirty-one species identified; indeed this site has the highest diversity of any of the east coast sites. The assemblages are dominated by one agglutinated species, *Jadammina macrescens*, and three calcareous species, *Cibicides lobatulus*, *Elphidium williamsoni* and *Haynesina germanica* (Fig. 19). The landward edge of the transect has a near-monospecific *J. macrescens* assemblage (98%; 0 m along the transect) with the

FIGURE 20. Relative dead abundance of four principal foraminiferal species from Cowpen Marsh. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.

lowest total count (422 individuals/10 cm^3). The relative abundance of *J. macrescens* rapidly declines 150 m along the transect to be replaced by a diverse calcareous assemblage. *E. williamsoni* (38%) and *H. germanica* (48%) reach their maximum relative abundances 290 m and 330 m along the transect, respectively. *C. lobatulus* rapidly increases in relative abundance at the seaward edge of the transect, with values greater than 57% between 366 m and 380 m.

Cowpen Marsh also has a diverse foraminiferal assemblage with twenty-eight species identified. The

FIGURE 21. Relative dead abundance of two principal foraminiferal species from Welwick Marsh. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.

assemblage consists mainly of three agglutinated species (*J. macrescens*, *Miliammina fusca* and *Trochammina inflata*) and one calcareous species (*H. germanica*) (Fig. 20). *J. macrescens* and *T. inflata* dominate the high and middle marsh, with a monospecific *J. macrescens* assemblage at the upper limit of the high marsh (0 m along the transect). The transition to low marsh corresponds with an increase in the relative abundance of *M. fusca* (36%). The percentages of agglutinated species rapidly decrease at the transition between low marsh and tidal flat to be replaced by a more diverse calcareous assemblage, dominated by *H. germanica*. This species gradually increases in relative abundance throughout the tidal flat zone to a maximum of 53% 202 m along the transect.

Twenty-two foraminiferal species have been identified from the intertidal environment of Welwick Marsh. One agglutinated species (*J. macrescens*) and one calcareous species (*H. germanica*) dominate the assemblages. These species represent over 85% of the dead assemblage at this site (Fig. 21). *J. macrescens* dominates from 0 m to 101 m along the transect with a maximum percentage of

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FIGURE 22. Relative dead abundance of four principal foraminiferal species from Thornham Marsh. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown

FIGURE 23. Relative dead abundance of four principal foraminiferal species from Brancaster Marsh. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.

77%. The transition between the middle and low marsh corresponds to a rapid decrease in the relative abundance of this taxon. It is subsequently replaced by calcareous taxa such as *H. germanica*, *Ammonia* spp. and *E. williamsoni*. *H. germanica* dominates much of the low marsh and tidal flat zone with a maximum abundance of 90% 237 m along the transect; indeed the relative abundance of this taxon exceeds 72% from 217 to 302 m along the transect.

The study of the intertidal zone of Thornham Marsh has identified twenty-three dead foraminiferal species. The assemblages are dominated by two agglutinated species, *J. macrescens* and *T. inflata*, and two calcareous

species, *Ammonia* spp. and *H. germanica* (Fig. 22). *J. macrescens* and *T. inflata* show a bimodal distribution across the transect. They dominate the high and middle marshes with a monospecific *J. macrescens* assemblage at the landward limit of the intertidal zone. The transition between the middle and low marsh corresponds with a decrease in the relative abundance of *J. macrescens* and *T. inflata* and an increase in calcareous species. However, the relative abundances of these agglutinated taxa increase again between 706 m and 804 m along the transect, where there is a rise in marsh elevation. The intertidal zone from middle marsh to tidal flat is dominated by the calcareous species *Ammonia* spp. and

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FIGURE 24. Relative dead abundance of four principal foraminiferal species from Bury Farm. The total count of the dead assemblage (per 10 cm³), elevation, tidal levels and floral zonations are shown.

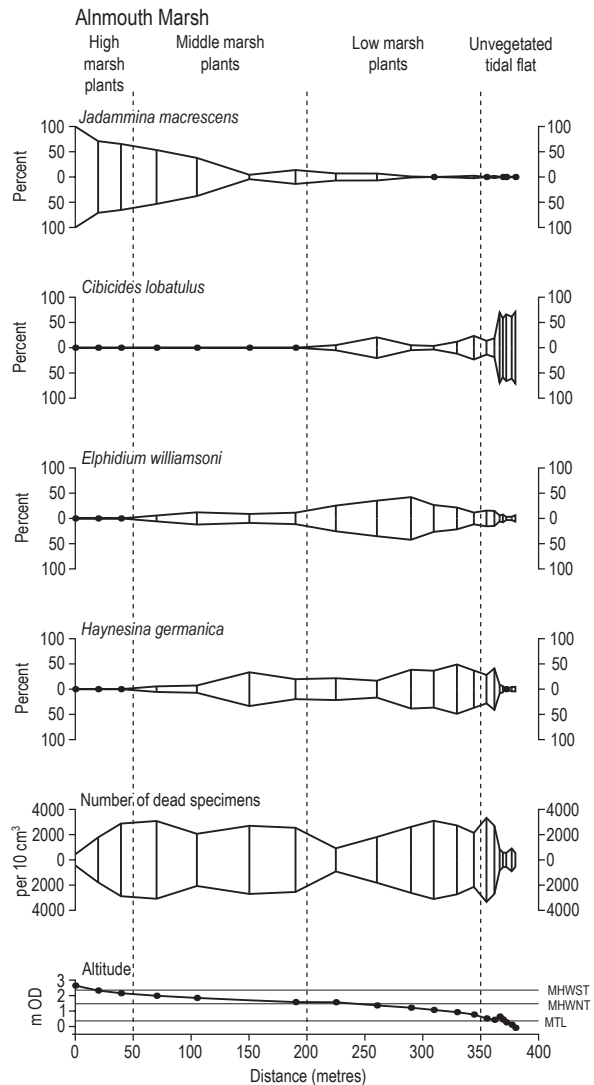

FIGURE 25. Relative dead abundance of four principal foraminiferal species from Keyhaven Marsh. The total count of the dead assemblage (per 10 cm³), elevation, tidal levels and floral zonations are shown.

H. germanica. The maximum relative abundance of *H. germanica* (37%) occurs within the low marsh, 584 m along the transect. The relative abundance of *Ammonia* spp. increases along the transect from high marsh to tidal flat; the maximum abundance (71%) occurs at the seaward edge of the transect (949 m).

Twenty-four dead foraminiferal species have been identified from the intertidal zone of Brancaster Marsh. The foraminiferal dead assemblages are characterized by three agglutinated species, *J. macrescens*, *M. fusca* and *T. inflata*, and one calcareous species, *H. germanica* (Fig. 23). The agglutinated species dominate the middle marsh, representing over 70 % of the dead assemblage

for the majority of stations between 0 m and 63 m along the transect. The relative abundance of all agglutinated species decreases at the transition between low marsh and tidal flat. This corresponds with a decline in the foraminiferal concentration to 226 dead individuals/10 cm³. The agglutinated species are replaced by a more diverse calcareous assemblage, dominated by *H. germanica*. This species increases in relative abundance throughout the tidal flat zone to a maximum of 73% of total dead foraminifera at the seaward edge of the transect (94 m along the transect).
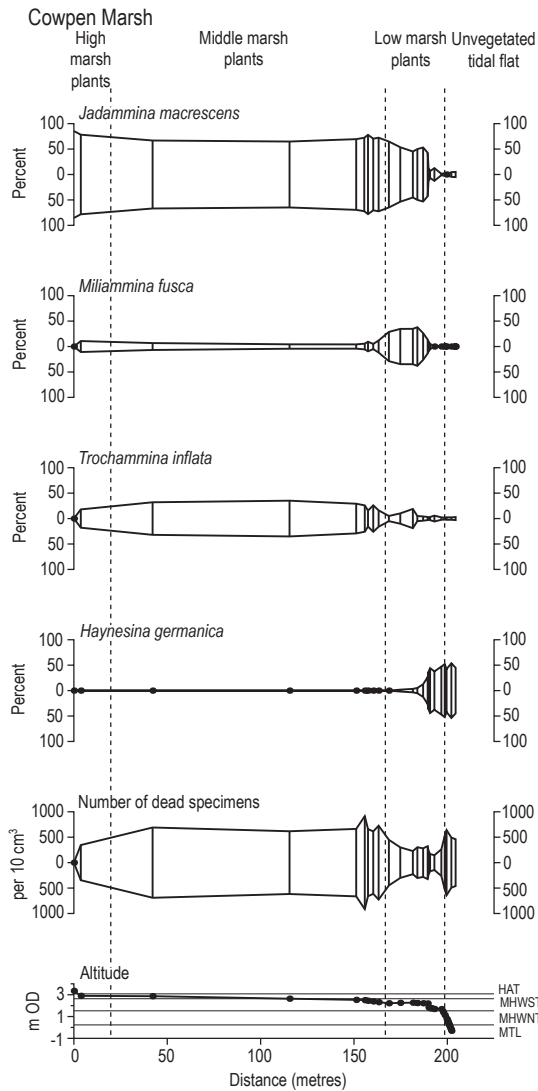
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Newton Bay

FIGURE 26. Relative dead abundance of three principal foraminiferal species from Newton Bay. The total count of the dead assemblage (per 10 cm³), elevation, tidal levels and floral zonations are shown.

2.5.2 South Coast of Great Britain

Twenty-one foraminiferal species are present at Bury Farm. The assemblages are dominated by three agglutinated and one calcareous species (Fig. 24). The landward limit of the marsh is dominated by *J. macrescens* with a maximum relative abundance of 93%. This species is replaced within the middle and low marshes by *M. fusca* and to a lesser extent by *T. inflata*, which coincides with the maximum foraminiferal concentration of 991 individuals/10 cm³ 114 m along the transect. The agglutinated species are replaced by calcareous taxa such as *Ammonia* spp., which have a maximum relative abundance of 28% 128 m along the transect.

Keyhaven Marsh has a low diversity with only eight species recorded. Of these species, *J. macrescens*, *M.*
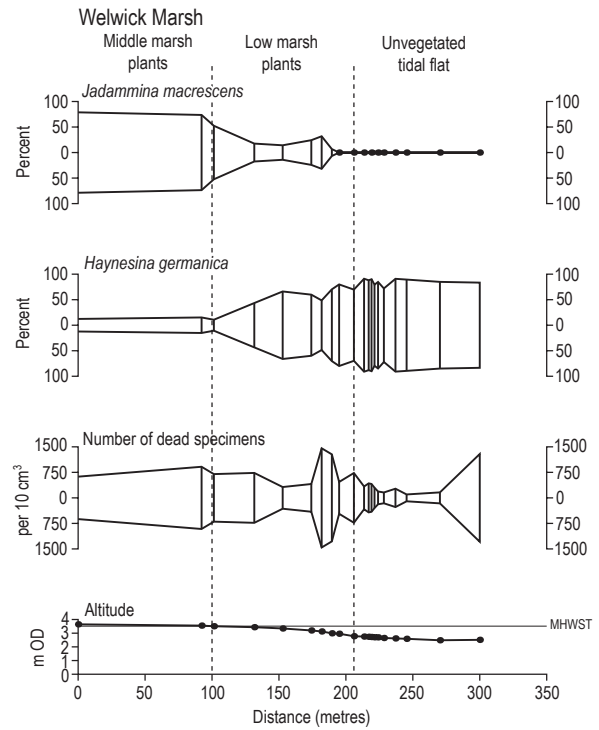
Arne Peninsula

FIGURE 27. Relative dead abundance of four principal foraminiferal species from Arne Peninsula. The total count of the dead assemblage (per 10 cm³), elevation, tidal levels and floral zonations are shown.

fusca, *T. inflata* and *Ammonia* spp. dominate the dead assemblage (Fig. 25). Agglutinated species dominate the marsh zone with maximum percentages of *J. macrescens* (60%), *M. fusca* (82%), and *T. inflata* (32%) occurring 0 m, 110 m and 180 m along the transect, respectively. Calcareous species, notably *Ammonia* spp., dominate the tidal flat zone, which coincides with a rapid increase in foraminiferal concentrations to 5012 individuals/10 cm³ at the seaward edge of the transect (190 m).

Newton Bay also has a low diversity of foraminifera
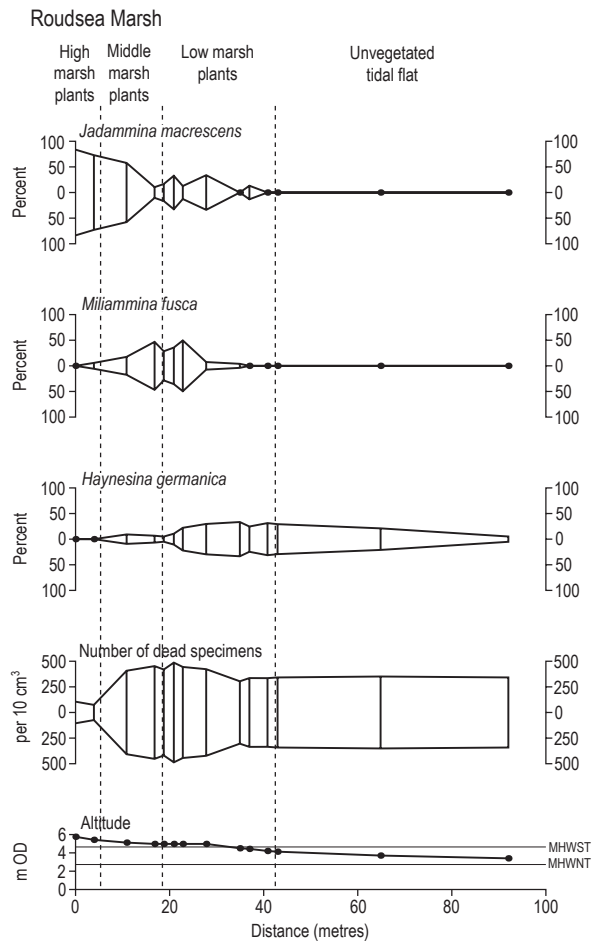
FIGURE 28. Relative dead abundance of three principal foraminiferal species from Roudsea Marsh. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.
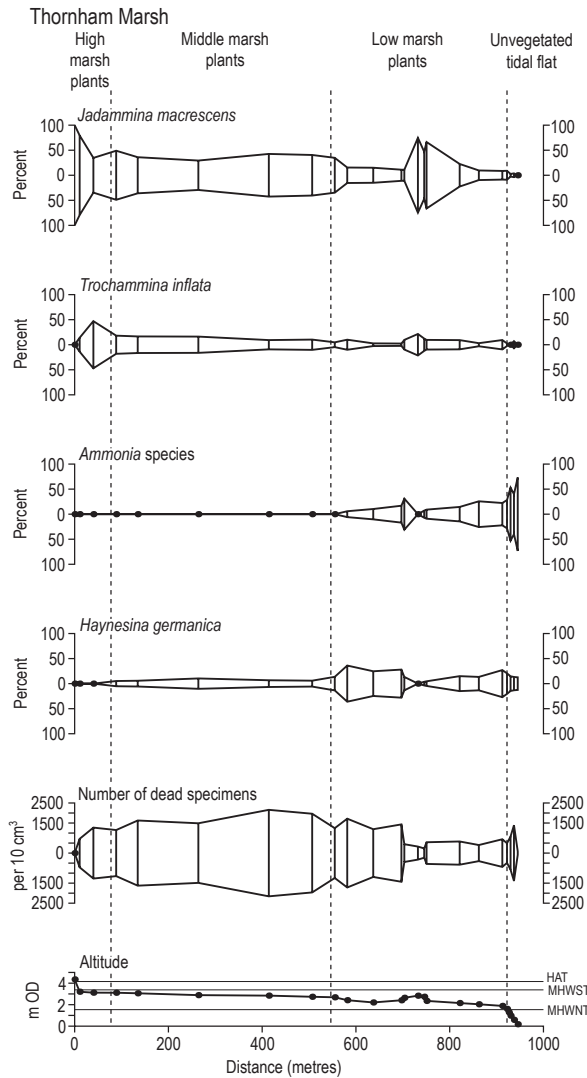

FIGURE 29. Relative dead abundance of three principal foraminiferal species from Nith Estuary. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.

with only nine species identified. The assemblage is dominated by agglutinated species such as *J. macrescens*, *M. fusca* and *T. inflata* (Fig. 26). The relative abundance of *J. macrescens* increases along the transect reaching 64% at the seaward edge. Both *M. fusca* and *T. inflata* reach their maximum abundances (39% and 32%, respectively) within the low marsh zone.

Twenty-four foraminiferal species are recorded along the transect at Arne Peninsula; the highest diversity for the south coast sites. The assemblages are dominated by *J. macrescens*, with lesser percentages of *Haplophragmoides* spp., *M. fusca*, *Ammonia* spp. and *H. germanica* (Fig. 27). The marsh is typified by an agglutinated assemblage. *J. macrescens* has a bi-modal distribution with a monospecific assemblage at the landward limit of the marsh and a high relative abundance (78%) 108 m along the transect. The

maximum abundance of *M. fusca* (50%) is found 6 m along the transect. The agglutinated assemblage gives way to a calcareous assemblage characterized by *Ammonia* spp. and *H. germanica*, which have maximum relative abundances of 27% and 38%, respectively.

2.5.3 West Coast of Great Britain and West Coast of Ireland

Roudsea Marsh has the highest diversity of all study sites with fifty-three foraminiferal species identified from the intertidal environment, although the dead assemblage is dominated by just two agglutinated species, *J. macrescens* and *M. fusca*, and one calcareous species, *H. germanica* (Fig. 28). *J. macrescens* dominates the high marsh with percentages greater than 50%; however, this species is replaced by *M. fusca* within the middle and
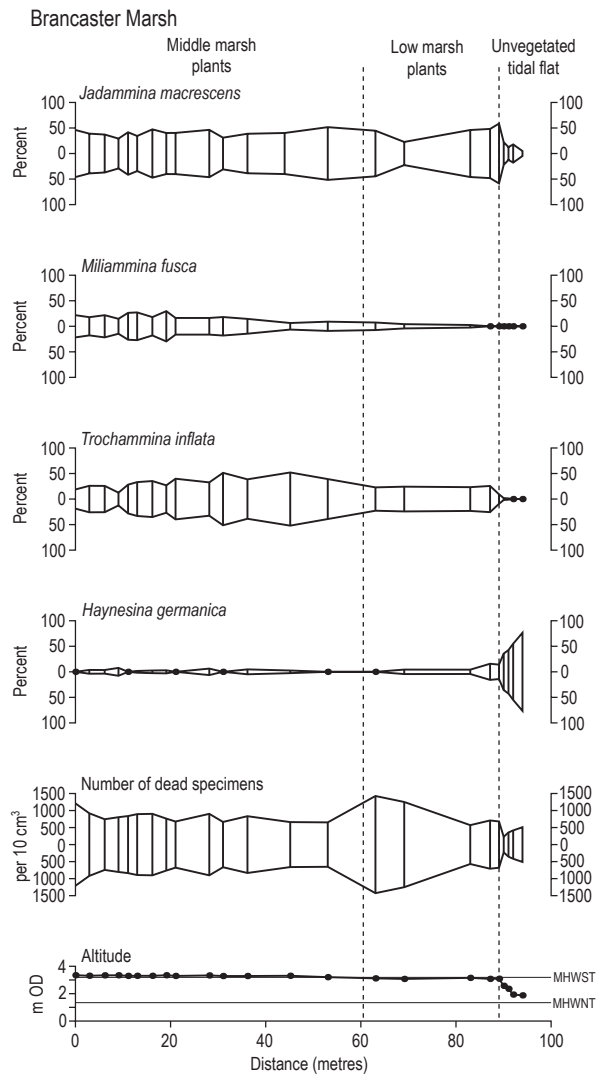
23
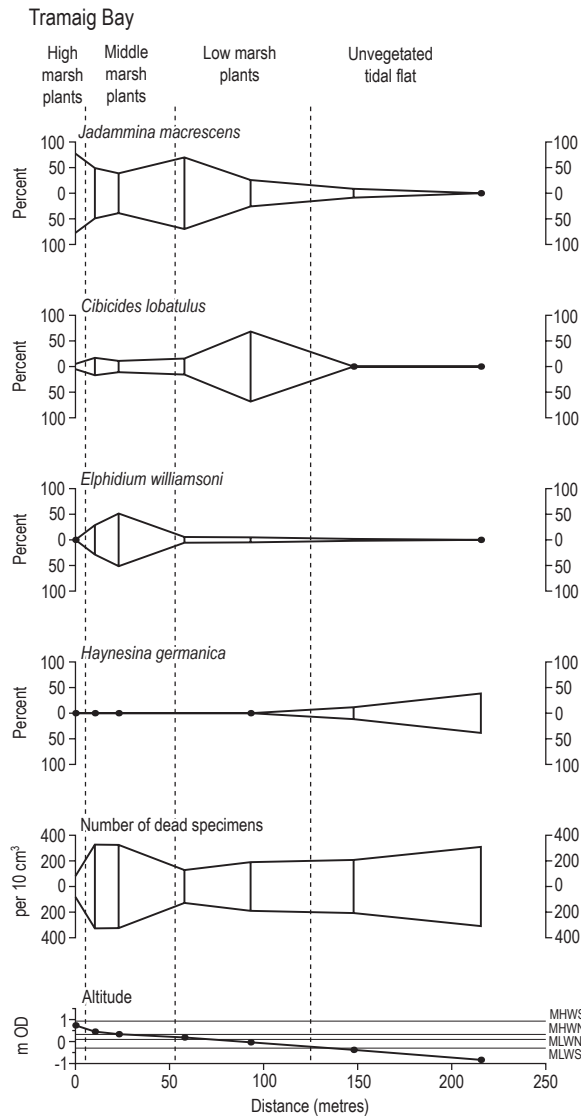
Tramaig Bay

FIGURE 30. Relative dead abundance of two principal foraminiferal species from Tramaig Bay. The total count of the dead assemblage (per 10 cm³), elevation, tidal levels and floral zonations are shown.
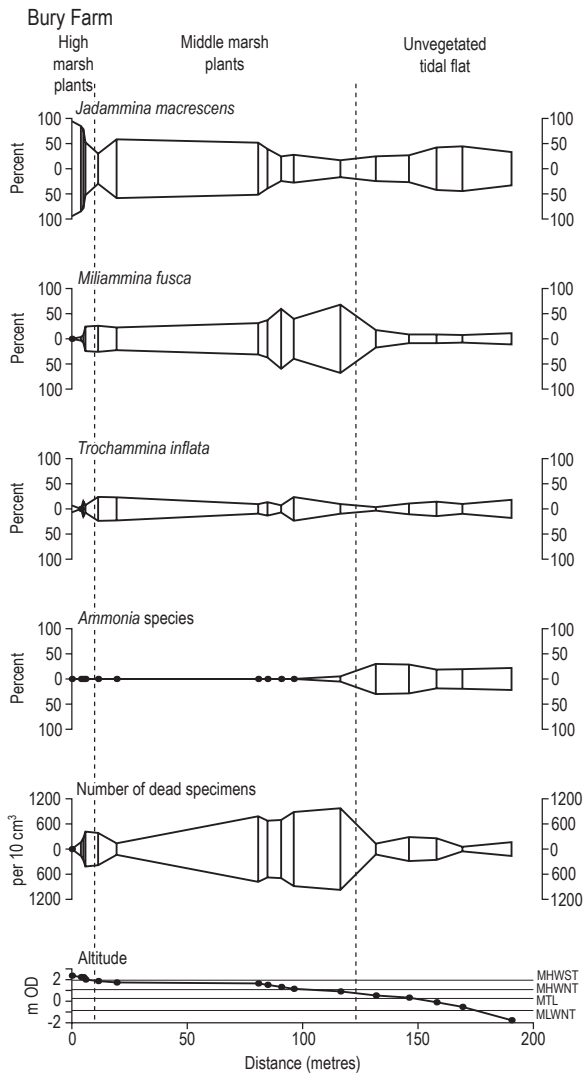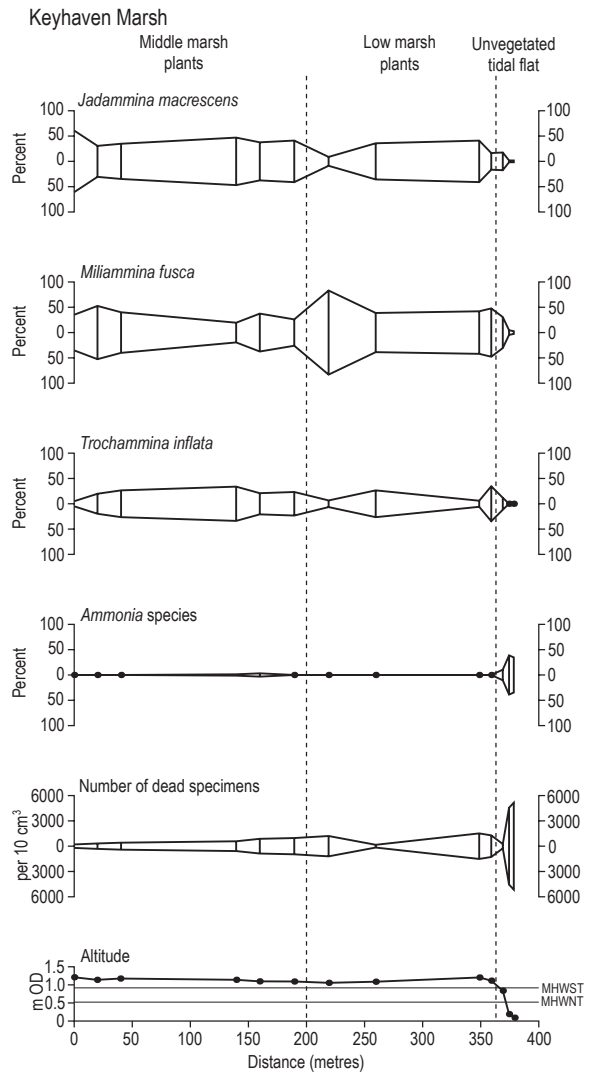
Kentra Bay

FIGURE 31. Relative dead abundance of four principal foraminiferal species from Kentra Bay. The total count of the dead assemblage (per 10 cm³), elevation, tidal levels and floral zonations are shown.

is substituted by *M. fusca*, which reaches its maximum relative abundance (64%) 7 m along the transect. This section also has the highest species concentration; 2112 individuals/10 cm³ 10 m long the transect. The change from low marsh to tidal flat coincides with an increase in the relative contribution of calcareous species; *H. germanica* reaches a maximum relative abundance of 35% at the seaward edge of the transect (30 m).

Thirty-three species have been encountered across the transect of Tramaig Bay, Jura. The landward edge of the transect within the salt-marsh is dominated by *J. macrescens* (76%, 0 m along the transect), which is first replaced by *T. inflata* (49%, 23 m along the transect) and subsequently by *M. fusca* (68%, 93 m along the transect). Calcareous taxa such as *C. lobatulus* characterize the intertidal flat (Fig. 30) with a maximum relative abundance of 35% at the seaward edge of the transect (215 m).

Kentra Bay has the lowest species diversity of all the study areas with only four foraminiferal species found; the assemblage is dominated by *J. macrescens* and *E. williamsoni* (Fig. 31). The former species dominates the first 82 m of the transect with relative abundances

low marsh zones (greater than 28%, 17 to 48 m along the transect). Calcareous species, such as *H. germanica*, supplant the agglutinated foraminifera for the remainder of the transect.

Thirty-seven foraminiferal species have been identified from the transect across the salt-marsh and tidal flat of the Nith Estuary. *J. macrescens*, *M. fusca* and *H. germanica* dominate the assemblages (Fig. 29). A near monospecific assemblage of *J. macrescens* is found at the landward edge of the transect (98%), within the high marsh. As the transect changes to middle and low marsh, *J. macrescens*

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FIGURE 32. Relative dead abundance of three principal foraminiferal species from Rusheen Bay, Transect 1. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.
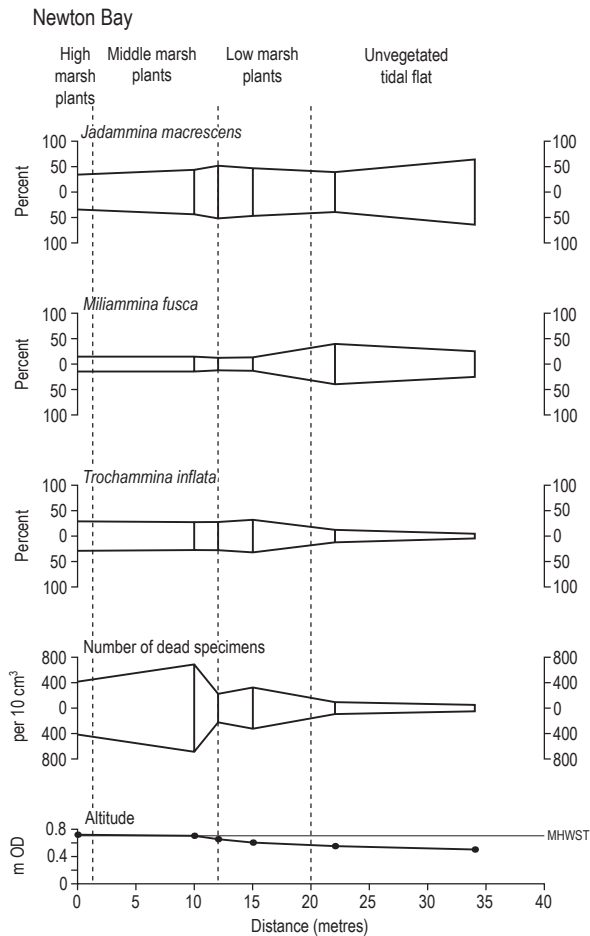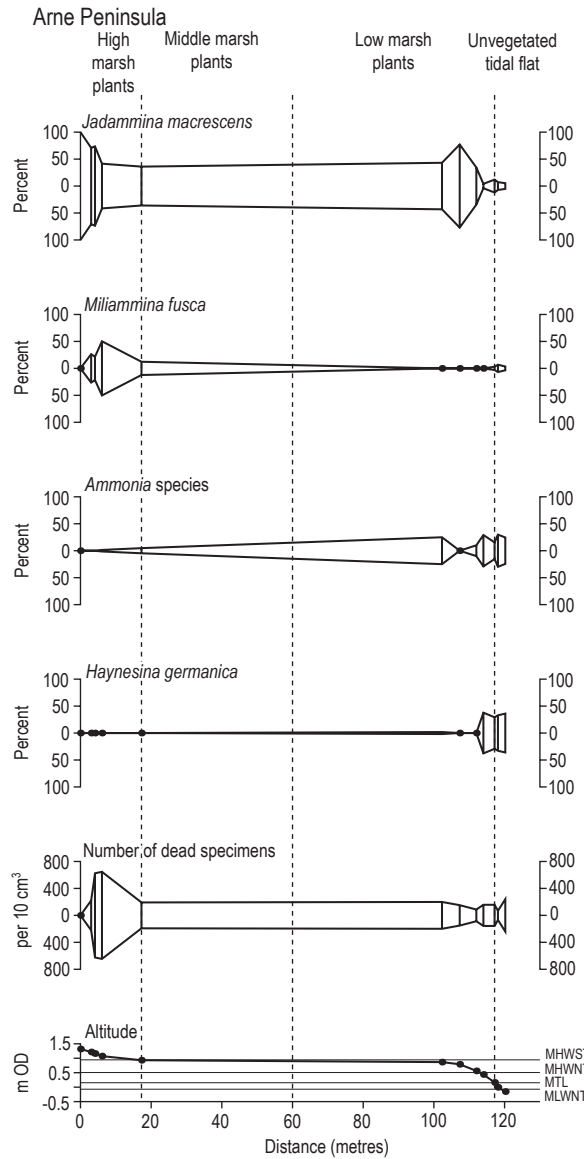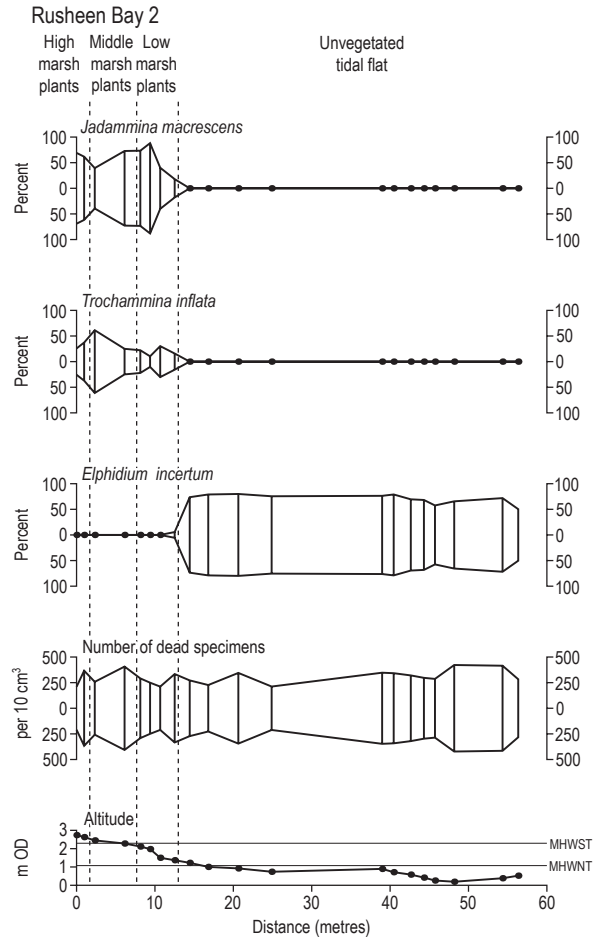
FIGURE 33. Relative dead abundance of four principal foraminiferal species from Rusheen Bay, Transect 2. The total count of the dead assemblage (per 10 cm^3), elevation, tidal levels and floral zonations are shown.

greater than 59%. The seaward portion of the transect is occupied by the latter species with a monospecific assemblage between 120 m and 160 m.

Ten foraminiferal species are present on Transect I of Rusheen Bay. The salt-marsh floral zone is dominated by *J. macrescens* with a maximum relative abundance of 89% at the landward edge of the transect (Fig. 32). The transition between salt-marsh and tidal flat corresponds with a rapid increase in calcareous species such as *H. germanica* and *E. incertum*. Eleven foraminiferal species have been identified from the second transect of Rusheen Bay. The assemblages are dominated by the agglutinated species *J. macrescens* (maximum of 89%, 9 m along the transect) and *T. inflata* (maximum of 59%, 2 m along the transect) within the salt-marsh floral zone, and the

calcareous species *E. incertum* (maximum of 80%, 41 m along the transect) within the tidal flat (Fig. 33).

2.5.4 The Vertical Distribution of Salt-marsh Foraminifera in Great Britain and Ireland

To detect, describe and classify the vertical distribution of foraminifera at each site we use two multivariate methods: unconstrained cluster analysis; and detrended correspondence analysis (DCA). Unconstrained cluster analysis based on unweighted Euclidean distance, using no transformation or standardization of the percentage data, is used to classify modern samples into more-or-less homogeneous faunal zones (clusters). DCA is an ordination technique and is used to represent samples as

25
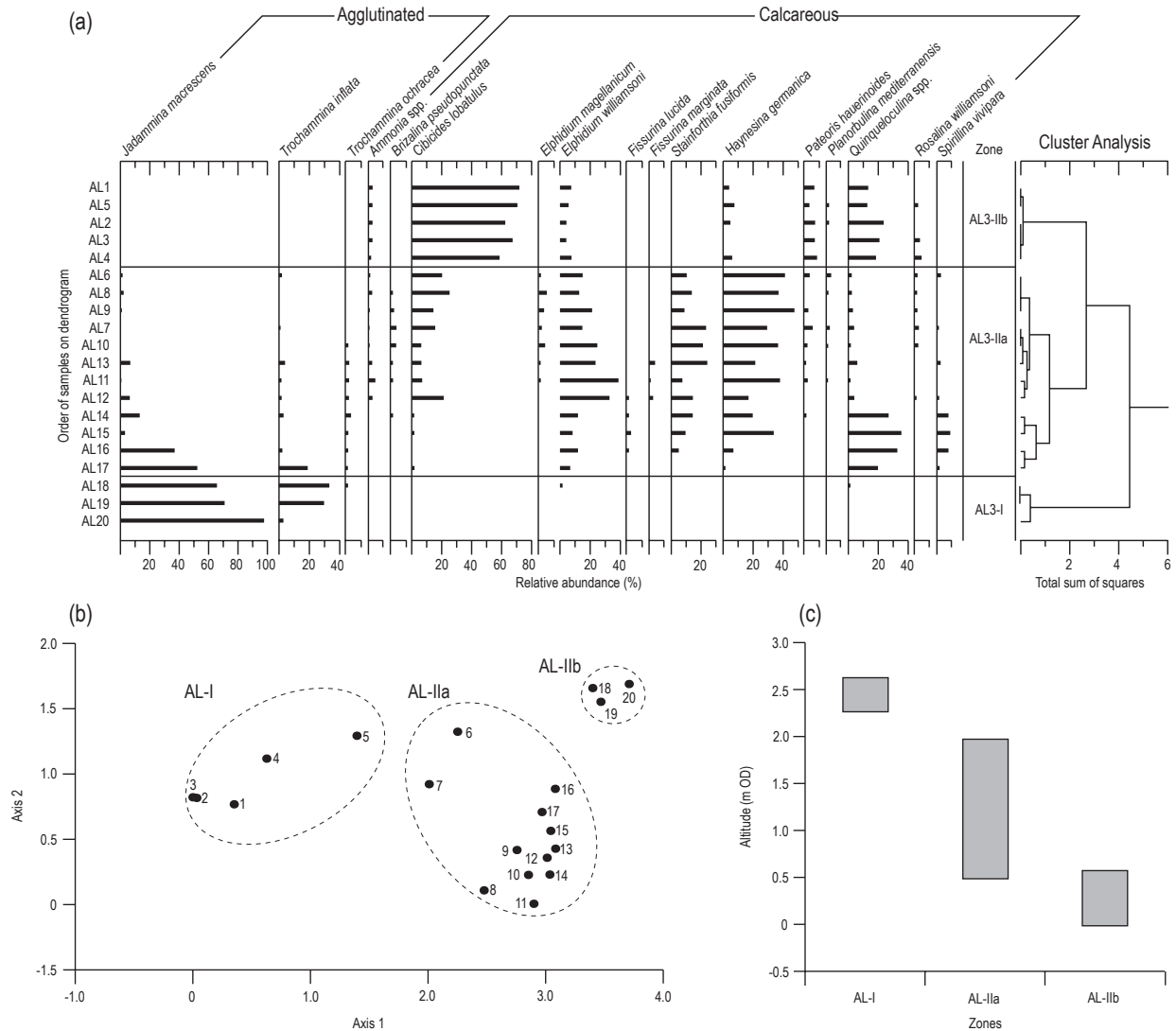
FIGURE 34.(a) Unconstrained cluster analysis based on unweighted Euclidean distance (b) detrended correspondence analysis and (c) vertical zonation of foraminiferal dead assemblages (%) from Alnmouth Marsh. Only samples with counts greater than 40 individuals and species that contribute 5% of the dead assemblage are included.

points in a multi-dimensional space. Similar samples are located together and dissimilar samples are separated. Birks (1986, 1992) stressed the complementary nature of the cluster analysis and ordination techniques. Cluster analysis is effective in classifying the samples according to their foraminiferal assemblage, but DCA gives further information about the pattern of variation within and between groups. This is important as the precise boundaries between clusters can be arbitrary. Using this combination of techniques we objectively delimit faunal zones on the basis of sample clusters that are mutually exclusive in ordination space. The elevation of each

station within the reliable clusters determines the vertical zonation of each intertidal environment.

For the statistical analyses (this section and all others) we remove all samples that have counts of less than 100 individuals and all species groups that contribute less than 5% of any assemblage (Patterson and Fishbein, 1989; Fatela and Taborda, 2002). Exceptions to this are the high marsh, monospecific assemblages of *J. macrescens*, which are retained because of their widespread occurrence and characteristic low species diversity and abundance (Scott and Medioli, 1978, 1980a; Gehrels, 1994; Horton and Edwards 2005; Edwards and others, 2004b; Horton
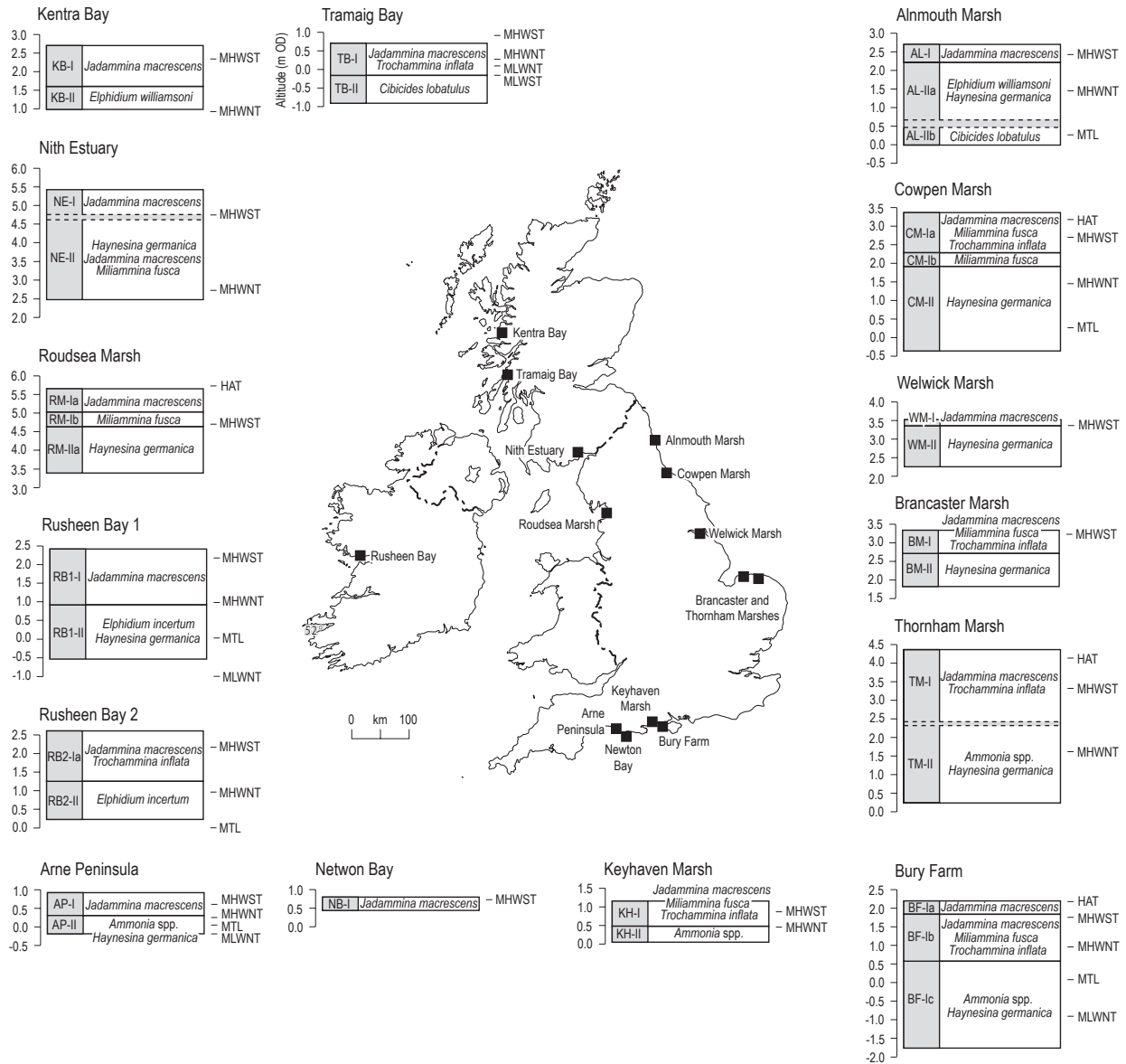
FIGURE 35. Summary foraminiferal assemblages and faunal zones determined by unconstrained cluster analysis based on unweighted Euclidean distance and detrended correspondence analysis for the fifteen study areas. Dashed lines and shaded areas indicate overlapping boundaries. Altitude (m OD) and tidal levels are shown.

and Culver, in press). Figure 34 shows an example of the cluster and DCA analyses of foraminiferal dead assemblages from Alnmouth Marsh. Other cluster and DCA figures are available from the authors.

Fourteen of the fifteen study sites exhibit a vertical zonation (Fig. 35). The exception is Newton Bay, which does not show any clear sequence of foraminiferal change at the marsh. This may simply be due to the small vertical range of the samples analyzed (24 cm)

that, in turn, reflect the low tidal range, low elevation and limited spatial extent of the vegetated marsh surface. In addition, complications may have been introduced by erosion and transport of sediment within Newton Bay. This marsh is currently experiencing erosion enhanced by the die-back of *Spartina*, which is releasing considerable volumes of previously trapped sediment back into the marine system. Distinct depressions, partially vegetated by sparse stands of *Spartina*, are associated with very

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wet, unconsolidated, fine-grained sediment, which may be recently deposited or mobile.

The remaining study sites can be generally divided into agglutinated assemblages that are restricted to the vegetated marsh and calcareous assemblages that dominate the tidal flats. Faunal Zone Ia is found at three of the fifteen study sites (Cowpen and Roudsea marshes, and Bury Farm), within the high to middle marsh zone around or above mean high water spring tide (MHWST). Zone Ia is characterized by a low diversity, agglutinated assemblage dominated by *J. macrescens* with little variability between sites. Other agglutinated species such as *M. fusca* and *T. inflata* may be co-dominant with *J. macrescens*, although their relative abundances are more site-specific. Similar faunal zonations have been documented in other temperate and tropical marshes. In Britain, Coles (1977) and Coles and Funnell (1981) studied the central Broadlands, identifying a high salt-marsh zone dominated by *J. macrescens* and *T. inflata* with minor influences from *Haplophragmoides* spp. Boomer (1998) and Funnell and Boomer (1998) distinguished a high marsh faunal zone dominated by *J. macrescens* and *T. inflata* in the North Norfolk salt-marshes, and a similar zone is also recorded in the Severn estuary by Haslett and others (1997). In the latter study, Haslett and others (1997) suggest that this zone only extends up to MHWST, above which all foraminifera are absent.

Murray (1991) distinguished *J. macrescens* and *T. inflata* associations in high marsh environments of Europe based on the work of Phleger (1970), Pujos (1976) and Le Campion (1970). Similarly, Patterson (1990) identified *J. macrescens* as the major species of the high and middle marshes of the Fraser River delta in British Columbia, although *T. inflata* is co-dominant with *J. macrescens* in samples from sites with decreased freshwater input from the Fraser River.

In contrast, many studies of tropical mangroves found low abundances of *J. macrescens* at the landward edge of the intertidal zone. Brönnimann and others (1992), Brönnimann and Whittaker (1993) and Horton and others (2005b) found assemblages of *A. mexicana* in mangrove sediments of the Fiji, Malay Archipelago and Indonesia, respectively. Assemblages dominated by *T. inflata* have been identified by Haslett (2001) and Horton and others (2003) at the landward limit of mangrove distributory channels from the Great Barrier Reef coastline, Australia. Barbosa and others (2005) found similar assemblages in the marshes and mangroves of south-southeastern Brazil.

Alnmouth, Cowpen and Thornham marshes, Arne

Peninsula and Nith Estuary exhibit near monospecific assemblages (≥ 98%) of *J. macrescens* at the landward limit of the high marsh. Similar monospecific faunal assemblages have been well-documented from marshes of north-eastern North America (Scott, 1976; Scott and Medioli, 1978, 1980a; Gehrels, 1994; Edwards and others, 2004a; Horton and Culver, in press). However, the assemblages from the remaining study sites of this paper and others did not identify this faunal zone. Scott and Leckie (1990) argued that the elevational range of assemblage zones at Great Sippewissett salt-marsh, Massachusetts, restricted the zone and the sampling regime undertaken. Patterson (1990) concluded that the limited number and precision of samples did not permit the clear differentiation of faunas at the upper edge of the high marsh from lower elevation faunas. Edwards and others (2004a) suggested that monospecific *J. macrescens* zones are not found in all modern temperate intertidal environments because of disturbance at the rear of salt-marshes due to human activities such as embankments, roads and other structures.

Cowpen and Roudsea marshes, and Bury Farm exhibit a Faunal Zone Ib, which is a middle to low marsh zone around or below MHWST that is dominated by *M. fusca* in association with low frequencies of calcareous species. Many other researchers have also observed a lower salt-marsh subzone (Coles, 1977; Scott and Medioli, 1978, 1980a; Coles and Funnell, 1981; Smith and others, 1984; Patterson, 1990; Scott and others, 1990; Gehrels, 1994; Horton and Culver, in press). On the western Atlantic seaboard, Scott and Medioli (1980a), Smith and others (1984) and Scott and others (1990) based a lower subzone on increased abundances of *M. fusca* and species characteristic of tidal flat environments. Similarly, on the Pacific coast, Scott (1976), Patterson (1990) and Scott and others (1996) divided the low marsh faunal zone into higher and lower subzones. Many studies have identified high abundances of *M. fusca* in mangrove zones in Fiji, Malay Archipelago, southwest Australia, Brazil, New Zealand, northern Australia, the Great Barrier Reef coastline and Indonesia (Brönnimann, and others, 1992; Brönnimann and Whittaker, 1993; Yassini and Jones, 1995; Debenay and others, 1998, 2000; Hayward and others, 1999, 2004a; Wang and Chappell, 2001; Horton and others, 2003, 2005). Horton and others (2005b) found an assemblage dominated by *M. fusca* and a minor calcareous component in the mangroves of Indonesia. In tropical or sub-tropical environments of northern Australia, Wang and Chappell (2001) note an intertidal zone where brackish water species such as

M. fusca dominate. Further, studies from Brazil suggest that agglutinated species (e.g. *M. fusca* and *A. mexicana*) are dominant in mangrove zones (Debenay and others, 1998, 2000; Barbosa and others, 2005).

The remaining twelve of the study areas did not possess any subzones of Zone I. Similarly, Scott and Leckie (1990), Jennings and Nelson (1992) and Jennings and others (1995) did not identify a boundary within Zone I at the Great Sippewissett salt-marsh, Massachusetts, and the Oregon tidal marshes, respectively. They concluded that the number of samples and the accuracy of sample elevations were inadequate to identify any subzones.

A tidal flat zone (Faunal Zone II) is found below MHWST, consisting of a high diversity calcareous assemblage with taxa such as *H. germanica*, *Ammonia* spp., *E. williamsoni* and *Quinqueloculina* spp. The relative abundance of agglutinated species is typically low, although the composition of the tidal flat assemblages displays considerable variation between study areas. For example, only one calcareous species, *E. williamsoni*, is identified in the tidal flat environment of Kentra Bay. We believe other calcareous species are not preserved because the intertidal environment of Kentra Bay is subject to acidic runoff from a raised bog, which enhances the dissolution of calcareous foraminifera (Green and others, 1993).

Similar intertidal studies from Europe also identified tidal flat faunal zones dominated by calcareous species (Phleger, 1970; Pujos, 1976; Coles, 1977; Coles and Funnell, 1981; Murray, 1991, Boomer, 1998; Funnell and Boomer, 1998). Woo and others (1997), Buzas and others (2002) and Horton and Culver (in press) identified calcareous assemblages consisting of *Ammonia*, *Elphidium* and *Quinqueloculina* species in the lagoons of the Indian River, Florida, the Delmarva Peninsula, Virginia and the Outer Banks, North Carolina, respectively. However, some studies from North America have not identified low marsh and tidal flat faunal zones because most taxa found in the middle and lower marshes extend into the tidal flat area (Scott and Medioli, 1980a; Williams, 1989; Patterson, 1990; Scott and Leckie, 1990). For example, Patterson (1990) identified a *M. fusca* zone which ranged from the lower part of the lower marsh (0 to 40 cm above mean tide level (MTL) through much of the elevational range of the tidal flat (0 to 80 cm below MTL). Calcareous faunal zones are common in many tropical and sub-tropical locations (Debenay and others, 2000; Wang and Chappell 2000; Horton and others, 2003, 2005b; Woodroffe and others, 2005), although the composition of assemblages differ.

At Alnmouth Transect three we have identified two subzones of Zone II: Zone AL3-IIa has a high diversity calcareous assemblage; and Zone AL3-IIb is dominated by *C. lobatulus*. This further illustrates the exceptionally localized nature of some distributions. Although *C. lobatulus* is a marine species, high abundances are occasionally found within the tidal flat as live *C. lobatulus* clings to firm substrates such as seaweeds, tunicates, shells and rocks, in areas subject to disturbance. Hence, dead tests may be transported in high numbers into estuary mouths (Murray, 1979; Duncan, 2000).

2.6 SUMMARY AND CONCLUSIONS

Scott and Medioli (1978, 1986) state that assemblages of agglutinated salt-marsh foraminifera are the most accurate sea-level indicators on temperate coastlines and that the assemblages exhibit a strong correlation with elevation above MTL. Furthermore, these assemblages are well preserved, easily detectable in fossil deposits and occur in high numbers (100 to 200 individual per cm^3), thereby providing a good statistical base for quantitative paleoenvironmental interpretations. However, the use of foraminifera to determine former sea levels requires the precise establishment of their modern distributions and controlling environmental variables, coupled with an understanding of any post-depositional changes that may alter these relationships.

The series of studies presented above produced three results that are incorporated in the foraminiferal sampling system of this paper:

1. A twelve-month study of modern foraminifera from Cowpen Marsh indicates that the dead assemblage provides the most reliable dataset for studying patterns of foraminiferal distributions. In contrast to the live populations or total assemblages, the dead assemblages exhibit less seasonal variability. Furthermore, sub-surface assemblages, which are the foci of paleoenvironmental reconstructions, accurately reflect dead assemblages accumulating at the surface;

2. Despite the conclusion that dead assemblages are less susceptible to seasonal fluctuations than live populations, seasonal studies from Welwick, Thornham and Brancaster marshes show that the vertical boundaries between dead assemblage zones still vary during a single annual cycle in response to variations in the foraminiferal distributions. Consequently, the reliability of dead foraminiferal assemblages as indicators of former sea levels can only be assessed following a consideration of the vertical errors introduced by this seasonality in

distribution. This fact, coupled with the inherent spatial variability in assemblage zone composition, elevation and vertical range, means that the assemblage zone approach to sea-level reconstruction is prone to unquantified and potentially significant error;

3. The intertidal foraminifera of Rusheen Bay live primarily in epifaunal habitats. This result, coupled with other observations from the UK, suggest that the foraminifera of the 0-1 cm interval can serve as the model upon which British and Irish fossil marsh deposits can be related to former sea levels. These results appear to contrast strongly with some studies from North America that indicate significant infaunal habitats in certain salt-marshes. Whilst these differences may reflect the relative ease with which foraminiferal tests can be transported within the sediment column, or the availability of food, they appear to have no clear relationship to oxygen levels;

4. The foraminiferal assemblages from British and Irish salt-marshes exhibit a vertical zonation of species that is similar to those in other mid-latitude, cool temperate intertidal environments. However, there are inter-site differences in the precise composition of assemblage zones, their elevations and vertical ranges. Multivariate analyses separate the intertidal zone into two parts: first, an agglutinated assemblage that is restricted to the vegetated marsh; and second, a high diversity calcareous assemblage that occupies the mudflats and sandflats of the intertidal zone. At three of the fifteen study sites, the agglutinated assemblage can be subdivided further into a high and middle marsh zone (Ia) dominated by *J. macrescens* with differing abundances of *T. inflata* and *M. fusca*, and a low marsh zone (Ib) dominated by *M. fusca*. The calcareous assemblage consists of species such as *Ammonia* spp., *E. williamsoni* and *H. germanica*. At Alnmouth Marsh the calcareous assemblage is subdivided into two zones with a lower zone (IIb) occupied by *C. lobatulus*, which reflects the introduction of 'exotic' material into low intertidal contexts.

3. DEVELOPING FORAMINIFERAL TRANSFER FUNCTIONS FOR SEA-LEVEL RECONSTRUCTION

In Section 2 we presented a range of evidence that demonstrates salt-marsh foraminifera from the British Isles, in common with their counterparts from North America and elsewhere, are vertically zoned with respect to elevation. Spatial variability in the composition, elevation and vertical range of these zones provides fundamental constraints on the application of an assemblage zone approach to the reconstruction of former RSL (Gehrels and others, 2001; Edwards and others, 2004a). In this section we present an alternative methodology that employs statistical tools, known as transfer functions, to describe the relationships among intertidal foraminifera and the environmental variables controlling their distribution. Since our target variable is sample elevation, we first examine the relative capacity this has to explain the observed vertical distributions of modern intertidal foraminifera. We then describe the methodology associated with developing transfer functions capable of estimating elevation from foraminiferal assemblages. We illustrate this by compiling a transfer function based on the modern distributions of intertidal foraminifera from the North Sea coast of England and use this to reconstruct paleomarsh-surface elevations from core material. Finally, we examine the potential range of sediments that can be interrogated using this methodology and the spatial applicability of local to regional transfer functions.

3.1 CONTROLS ON FORAMINIFERAL DISTRIBUTIONS

There are differing opinions regarding the influence of elevation on foraminiferal distributions. The work of Scott and Medioli (1980a, 1986) and others (Scott and Leckie, 1990; Horton and others, 1999a, b; 2003) suggests a strong vertical zonation of foraminiferal species from both temperate and tropical intertidal zones. This concept (Scott and Medioli, 1980a, 1986; Scott and others, 2001) implies that all environmental variables determining foraminiferal distribution are related to tidal submergence, and that this, in turn, is correlated with marsh surface elevation. Accordingly, foraminifera of the salt-marsh are distributed in clearly identifiable vertical zones. In contrast, de Rijk (1995a, b) and de Rijk and Troelstra (1997) suggest that the salinity of the porewater mainly governs foraminiferal distribution in the Great Marshes, Massachusetts, USA. These authors argue that, in contrast to the salt-marshes mentioned above, the topography of the Great Marshes does not slope progressively seaward but displays an irregular high marsh surface. Consequently, the salinity gradient is not controlled by marsh elevation and no vertical zonation is found. However, the studies of de Rijk (1995a, b) and de Rijk and Troelstra (1997) concentrated on the agglutinated foraminiferal species occupying the

high marsh area of the intertidal zone. In this section we employ Canonical Correspondence Analysis (CCA) to test the hypothesis that foraminiferal dead assemblages are related to elevation using annual foraminiferal dead assemblages and environmental data (loss on ignition (LOI), clay fraction (ca. grain size), pH and salinity) from the mudflat and salt-marsh environments of the intertidal zone of Cowpen Marsh.

3.1.1 Method

CCA is a multivariate technique that relates community composition to known variations in the environment (ter Braak, 1986, 1987; ter Braak and Verdonschot, 1995). The technique is an extension of correspondence analysis, an ordination technique which displays the main trends of variation of a multi-dimensional dataset in a reduced space of a few, linearly independent dimensions. Ordination axes are typically interpreted with reference to external knowledge and/or environmental data. This two-step approach (ordination followed by environmental gradient identification) is termed 'indirect gradient analysis' by ter Braak (1986). In CCA, ordination axes are chosen in the light of known environmental variables by imposing the extra restriction that the axes be linear combinations of these variables. This technique is known as 'direct gradient analysis' (ter Braak, 1986) and community variations can be directly related to environmental variations. The independence and relative strength of the major environmental gradients were estimated using a series of partial CCAs (Borcard and others, 1992) to separate the total variation of foraminiferal data into components representing: first, the unique contributions of individual environmental variables; second, the contribution of covariance between variables; and third, the unexplained variance. When CCA and partial CCA are used, canonical eigenvalues provide measures of the amount of variation accounted for by environmental variables. The statistical significance of partial CCAs was determined using a Monte Carlo permutation test. The processes were based on computations made with the CANOCO program, release 4.51 (ter Braak and Smilauer, 1997-2003).

3.1.2 Results

The CCA sample-environment and species-environment biplots are shown in Figure 36. CCA axes one (eigenvalue = 0.76) and two (eigenvalue = 0.08) explain 71% of the total variance in the foraminiferal

data and 93% of the species-environment relationship (Table 2). The lengths of the environmental arrows approximate their relative importance in explaining the

Axis	1	2	3	4	Total inertia
Eigenvalues	0.76	0.08	0.04	0.02	1.18
Species-environment correlations	0.98	0.78	0.74	0.63	
Cumulative percentage variance:					
-of species data	64.3	71.4	74.7	76.4	
-of species environment relationship	83.9	93.3	97.6	99.7	
Sum of all eigenvalues					1.18
Sum of all canonical eigenvalues					0.90

Table 2. Summary of CCA and DCA results from annual foraminiferal dead assemblages of four modern field sites.
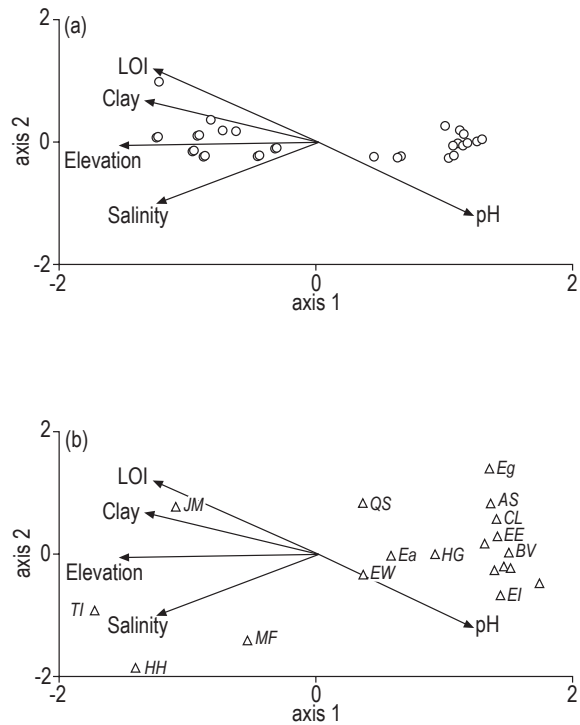
Figure 36. Canonical Correspondence Analysis biplots of (a) sample-environment and (b) foraminiferal species-environment from Cowpen Marsh. Species abbreviations: AS = *Ammonia* spp.; EW = *Elphidium williamsoni*; HG = *Haynesina germanica*; JM = *Jadammina macrescens*; MF = *Miliammina fusca*; QS = *Quinqueloculina* spp.; and TI = *Trochammina inflata*. Environmental abbreviations: LOI = loss on ignition. Only samples with counts greater than 40 individuals and species that contribute 5% of the dead assemblage are included.

(a)

(b)
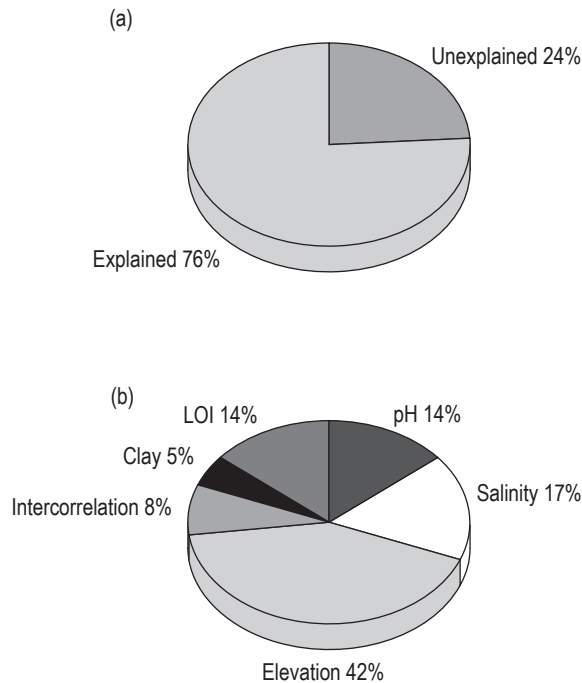
FIGURE 37. Pie charts showing the total variation of the foraminiferal training set of Cowpen Marsh in: (a) explained and unexplained portions; and (b) components representing the unique contributions of elevation, salinity, LOI, vegetation cover, pH, clay fraction and intercorrelations among gradients.

variance in the foraminiferal data and their orientation shows their approximate correlations to ordination axes and other environmental variables. Intra-set correlations of environmental variables with axes one and two show that elevation and clay fraction are highly correlated with axis one and that LOI, salinity and pH show a joint correlation with axes one and two (Fig. 36a). Axis one, therefore, reflects the major gradient from high marsh plotted on the left (high LOI, clay fraction, elevation and salinity, and low pH) to tidal flat plotted on the right (low LOI, clay fraction, elevation and salinity, and high pH). On the species-environment biplot the position of species projected perpendicularly onto environmental arrows approximates their weighted average optima along each environmental variable (Fig. 36b). Therefore, species characteristic of a particular environment may be identified. For example, agglutinated species *J. macrescens*, *M. fusca* and *T. inflata* (high and middle marsh: LOI, clay fraction, elevation and salinity, and low pH) and calcareous species *Ammonia* spp. and *H. germanica* (tidal flat: LOI, clay fraction, elevation and salinity, and high pH) are found on the left and right-

hand side of the figure, respectively.

The six environmental variables account for 76% of the explained variance in the foraminiferal data (Fig. 37). Partial CCAs show that the total explained variance is composed of 42% (elevation), 17% (salinity), 14% (LOI), 14% (pH) and 5% (clay fraction). The associated Monte Carlo permutation tests (p = 0.02, 499 permutations under reduced model) indicate that all these variables except for clay fraction are highly significant. Therefore, each of these gradients accounts for a significant proportion of the total variance in the foraminiferal data.

3.1.3 Discussion and Summary

CCA and partial CCAs of the foraminiferal and environmental data from Cowpen Marsh support the hypothesis that foraminiferal dead assemblages are related to elevation and hence tidal submergence. These results suggest that the distribution of foraminifera in the intertidal zone is usually a direct function of elevation with the duration and frequency of intertidal exposure as the most important factors. The high inter-correlation between variables indicates the elevational gradient cannot be considered completely independent. In reality, the structure of foraminiferal assemblages is more likely to be jointly affected by many linear or non-linear related factors (e.g. Buzas, 1969; Bé, 1977; Buzas and others, 1977). This is to be expected because the other variables are dependent on the frequency of tidal flooding. Similar inter-correlations among variables have been observed during the production of other modern marsh foraminiferal (Horton and others, 1999b, 2003; Horton and Edwards, 2001, 2003, 2005, Horton and Culver, in press) and diatom datasets (Jones and Juggins, 1995; Gasse and others, 1997; Zong and Horton, 1999; Sawai and others, 2004a, b).

3.2 TRANSFER FUNCTIONS: THE THEORY

Given that the distribution of salt-marsh foraminifera is strongly influenced by surface elevation, we can use foraminifera as 'proxies' for elevation, providing a suitable means of converting faunal data into environmental (i.e. elevation) data can be found. A transfer function quantifies this relationship between the environmental variable of interest and the environmental proxy so that the former may be expressed as a function of the latter (Fig. 38). Transfer functions were pioneered by Imbrie and Kipp (1971) and are routinely employed in a wide range of paleoecological studies to achieve

Foraminiferal data   Elevation

Modern data 1 ——————→ *m* taxa   1

$$Y \qquad\qquad X$$

n   *n*
Samples   Samples

Fossil Data 1 ——————→ *m* taxa   1
                                          X_0
$$Y_0 \qquad\qquad$$ Unknown,
                                        to be
                                      reconstructed

t   *t*
Samples   Samples
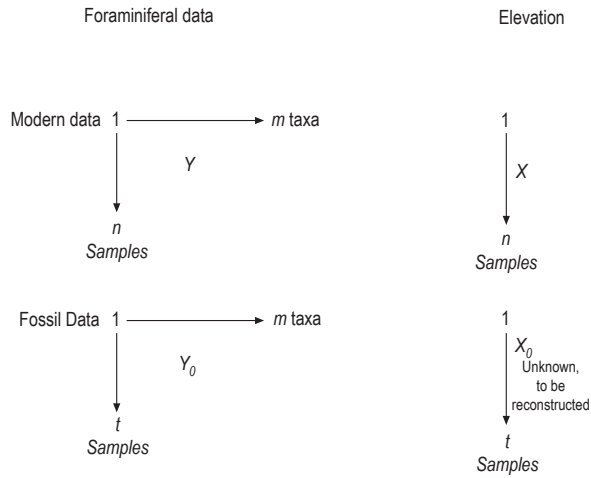
FIGURE 38. Principles of quantitative paleoenvironmental reconstruction showing Xo, the unknown environmental variable to be reconstructed from fossil assemblage Yo, and the role of the modern training set consisting of modern biological data Y (i.e., foraminifera) and environmental data X (i.e., elevation) (modified from Birks, 1995).
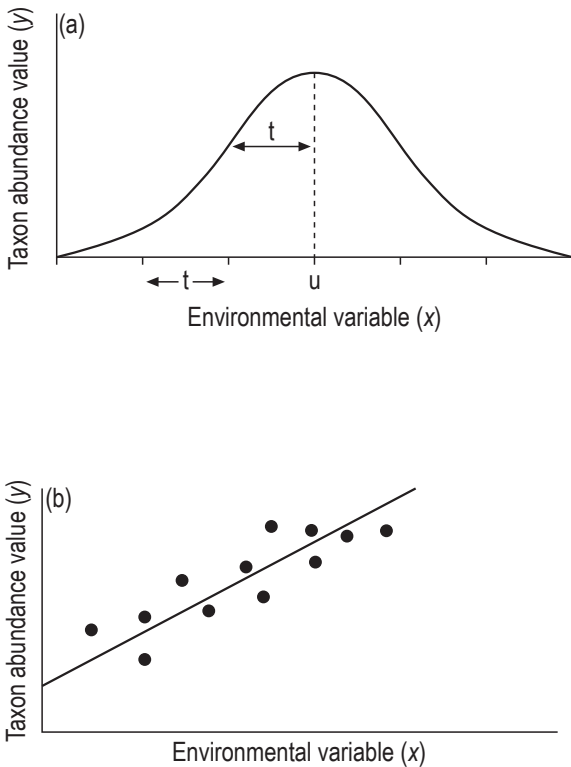
FIGURE 39. Theoretical species-environment response models. (a) Gaussian unimodal and (b) linear relationship between the abundance (y) of a species and an environmental variable (x). Abbreviations for ecological parameters are: u = optimum; and t = tolerance (modified from Birks, 1995).

this type of transformation (e.g. Jones and Juggins, 1995; Gasse and others, 1997; Zong and Horton, 1999; Charman, 2001; Malmgren and others, 2001; Noon and others, 2001; Rosén and others, 2003; Sawai and others, 2004 a, b; Telford and others, 2004; Hamilton and Shennan, 2005a; Hamilton and others 2005; Kucera and others, 2005; Telford and Birks, 2005; Horton and others, 2005b). Birks (1995) outlines the general application of transfer functions to paleoenvironmental reconstruction, and here we concentrate on their use as it relates to salt-marsh foraminifera and sea-level reconstruction (Horton and others, 1999b; 2003; Edwards and Horton, 2000; Gehrels, 2000; Gehrels and others, 2001, 2002, 2004, 2005; Horton and Edwards, 2001, 2003, 2005; Edwards and others, 2004b; Patterson and others, 2004, 2005; Boomer and Horton, 2006). The foraminiferal transfer function methodology can be conveniently sub-divided into three stages: training set compilation; fauna-environment regression; and (fossil) sample calibration.

3.2.1 Modern Analogues – Compiling a Training Set

Modern data that are used to develop a transfer function are termed a 'training set'. In this instance, the training set comprises a series of foraminiferal samples with associated elevational data. An ideal training set will contain foraminiferal assemblages that represent all environmental conditions encountered in the fossil sequence under investigation. Modern sampling, therefore, aims to locate a wide range of modern analogues that can, on uniformitarian grounds, be used to make inferences about past conditions.

The composition of the modern training set has the potential to significantly influence the performance of the resulting transfer function. Important questions regarding training set compilation include: the number of samples to be collected; the elevation range over which samples should be recovered; and the spatial scales across which survey results can be combined into a single dataset. To control the random component arising from sampling variability, the sample size should be as large as is practical (affordable in terms of collection time, analysis and cost). To our knowledge, there are no clear guidelines indicating a minimum sample size for transfer function training sets. However, predictions based on smaller training sets will be more prone to error, since the range of modern analogues will be restricted and spatial variability is likely to be under-represented (Griffith and Amrhein, 1997). In this publication, training set sizes

range from 55 up to over 200 samples, and no simple relationship between sample size and transfer function performance is noted (see Section 3.7).

The strongest relationship between foraminiferal assemblage and elevation is expressed in the highest samples at the upper limit of marine influence, where *J. macrescens* is commonly found to the exclusion of all other taxa. With decreasing elevation, the driving forces behind vertical zonation (namely period of subaerial exposure or extremes in temperature/salinity, etc.) weaken, whilst complicating factors such as sediment transport or reworking increase. Intuitively, this means that there is likely to be a fundamental lower limit below which foraminiferal assemblages cease to relate to elevation in a consistent, systematic manner. This issue is investigated in Section 3.6.

Since the transfer function approach considers modern analogue environments rather than local assemblage zones, the spatial scale over which meaningful analogous environments can be found is not immediately clear. Similarly, the potential impact that spatial differences in training set constituents may have on transfer function reconstructions is also unquantified. We explore both these issues in more detail in Section 3.5.

3.2.2 Regression Analysis – Deriving Ecological Response Functions

The second stage in the transfer function approach is to empirically model the relationship between the elevation of a number of samples and the relative abundances of foraminiferal taxa contained within them, in order to derive 'ecological response functions'. This is achieved by regression, either expressing the foraminiferal data as a function of elevation (the classical approach), or vice versa (the inverse approach). The statistical details of each approach need not concern us here, but it is worth noting that inverse approaches tend to perform best when considering samples from the middle of the environmental gradient, whilst classical approaches may have better predictive abilities at environmental extremes when extrapolation is required (ter Braak, 1995).

Within each approach, a range of statistical methods are available to derive the required ecological response functions. These are differentiated on the basis of their underlying taxon-environment response model (Birks, 1995; Telford and others, 2004; Telford and Birks, 2005). For our purposes, we can distinguish between two methods: those using a unimodal response model that assumes individual foraminiferal taxa have a

Gaussian distribution along the environmental gradient, peaking in abundance at a preferred (optimal) elevation; and those employing a linear response model in which relative foraminiferal abundance increases or decreases with elevation (Fig. 39).

Given these theoretical differences in species response, it is important to select the model that best describes the distribution of foraminifera within the training set. This can be achieved by using detrended canonical correspondence analysis (DCCA), which provides a means of gauging the extent to which assemblage composition changes along the environmental gradient (Birks, 1995). Detrending by segments and using non-linear rescaling means that the length of DCCA axis one can be used as an estimate of gradient length in standard deviation (SD) units. Unimodal response models are most appropriate for describing training sets with data spanning more than 2 SD units (Birks, 1995).

3.2.3 Calibration – Producing Estimates of Paleomarsh Surface Elevation

In the final stage of the transfer function approach, fossil foraminiferal assemblages from sediment samples are 'calibrated' to produce estimates of paleomarsh-surface elevation by applying the ecological response functions derived in the second stage of the process. Once the elevation of the paleomarsh surface has been estimated, changes in RSL can be inferred by the combination of lithostratigraphic and chronostratigraphic data. A variety of methods have been employed to combine these data, and we examine the contribution transfer functions can make to these in Section 4.

A number of assumptions are inherent in the calibration process, and the degree to which these are valid will influence the reliability of the resultant elevation estimates. Principal among these is the assumption that elevation remains the dominant control on foraminiferal distributions, and that other environmental variables do not exert a strong or changeable influence through time. The results presented in Section 3.1 show that other variables influence foraminiferal distributions and may introduce scatter into the elevation-foraminifera data. Therefore, for paleoenvironmental reconstructions, it must be assumed that the joint distribution of these variables with elevation is the same in both the training and fossil sets (Birks, 1995). Le and Shackleton (1994) assessed this assumption using simulated biological species data. Their simulations show that transfer functions do have potential pitfalls regarding their sensitivity to joint

distributions. However, they concluded that if used with caution, they are reliable working methods when applied within the calibration range.

A second important assumption in the context of salt-marsh foraminifera is that the composition of the modern foraminiferal assemblages are representative of those found in sub-surface sediments. Taphonomic process including infaunal foraminiferal activity, post-depositional destruction of tests, or transport and reworking may violate this assumption and introduce error into reconstructions (e.g. Hippensteel and others, 2002, Martin and others, 2003; Duchemin and others, 2005). Some issues relating to this are considered in Section 2.4 and Section 3.6. Comparison of the composition of fossil assemblages with those contained within the training set can serve to highlight samples that have experienced post-depositional change, and this can be achieved via the matching analogue technique (Section 3.4.5).

3.3 STANDARDIZING WATER LEVELS

Throughout the preceding discussion, we have referred to the 'environmental variable' of interest as sample elevation expressed relative to the tidal frame. Strictly speaking, elevation is not a real environmental variable, but rather a proxy for flooding frequency and hydroperiod / duration of subaerial exposure. Ideally, tide-gauges and data loggers should be deployed on all study marshes to accurately determine local hydrographic conditions and tidal wave deformation across the marsh surface (van der Molen, 1997). At present these data are unavailable for Great Britain and Ireland and, given the extent of public access to many study areas, would require careful installation and monitoring to prevent disturbance. In the future, such information may improve the resolution of reconstructions by reducing scatter in the modern taxa-elevation data. At present, in the absence of such data, tidal information is derived from neighboring established tide gauges reported in the Admiralty Tide Tables (2003). Under these conditions, sample elevation can be considered a general indicator of flooding frequency, and in the development of previous microfossil transfer functions by Gehrels and others (2001), environmental variables based on both elevation and flooding frequency produced comparable results.

Since sites with differing tidal ranges are combined to form single training sets, it is necessary to standardize the elevation of each sample to take these differences in vertical range into account. This is achieved by converting the elevation of each sample to a standardized

water level index (SWLI):

$$SWLI = \left[\frac{Alt_{ab} - MLWS}{MHWST_b - MLWST_b} \right] \quad (Eq. 1)$$

where Alt_{ab} is the altitude of sample a at site b (measured in m OD); $MLWST_b$ is the mean low water spring tide level at site b (m OD); and $MHWST_b$ is the mean high water spring tide at site b (m OD).

A comparison of constructed tidal levels using Equation 1 indicates that the procedure is reliable (Horton, 1997). Brancaster and Thornham marshes show analogous linear relationships between SWLI and flooding frequency, with the Pearson's correlation coefficients (r) exceeding the critical value at the 1% significance level. Alternative variants of SWLI, employing different tidal parameters, have been used by other authors in a number of studies (e.g. Horton and others, 1999a, b, 2000; Edwards and others, 2004b). Here, MHWST and MLWST are used because they improve correlations with tide levels when considering lower elevation environments, and data availability via the Admiralty Tide Tables (2003) is greater than for extreme tidal levels (e.g. highest and lowest astronomical tide).

3.4 AN EXAMPLE TRANSFER FUNCTION FROM THE NORTH SEA COASTLINE OF GREAT BRITAIN

To illustrate the process of transfer function development and application as outlined in Section 3.2, we present the various stages of the methodology in developing a foraminiferal transfer function from the North Sea coastal dataset (Cowpen, Welwick, Thornham and Brancaster marshes), which consists of an unscreened training set of 110 samples and 32 species. These data are first assessed for quality and screened, and an appropriate response model determined. The screened dataset is then regressed in an iterative process to infer the ecological response functions. The resultant transfer function is applied to a fossil sequence, and finally some estimates of its performance are presented.

DCCA analysis is conducted using the CANOCO program, release 4.51 (ter Braak and Smilauer, 2003), with SWLI (ca. elevation) as the only environmental variable (Birks, 1995). Transfer function regression and calibration is conducted using the C2 program, version 1.4 (Juggins, 2004). An assessment of modern analogues

is made using the program MAT, version 1.1 (Juggins, 1997).

3.4.1 Initial Data Screening

The modern training set consists of foraminiferal species groups expressed as relative abundances, and associated elevations expressed as SWLIs. When combining foraminiferal data collected from different sites and examined by various analysts, an important first step is to ensure that a consistent taxonomy has been employed and to rationalize the species groups present. In the case of the North Sea coast dataset, the same analyst examined all sites and training set compilation is a simple combination of data.

Prior to analysis, all data are screened to ensure that the samples employed in the statistical analysis are of appropriate size and composition (see Section 2.5.4). This procedure results in a screened dataset of 110 samples and 19 species groups. Only one characteristic salt-marsh species, *Balticammina pseudomacrescens*, is removed as part of this process. The majority of the other taxa excluded are typical shelf species that may be transported into estuaries and deposited on tidal flats, or occasionally washed onto marsh surfaces during higher energy conditions. Examples of these include genera such as *Bolivina*, *Bulimina*, *Cassidulina* and *Lagena*.

3.4.2 Response Model and Transfer Function Selection

Detrended canonical correspondence analysis (DCCA) is performed on the screened dataset to determine whether a linear or unimodal model is most appropriate as outlined in Section 3.2.2. The gradient length of axis one is 3.16, indicating that a unimodal response model will most reliably describe the species distributions. It is worth noting that despite the recent development of artificial neural networks (e.g. Malmgren and others, 2001); unimodal species-environment response models are considered the most robust reconstruction method (Telford and others, 2004; Telford and Birks, 2005).

In an idealized situation, the distribution of all salt-marsh foraminiferal species will be solely controlled by their elevation. In reality, whilst foraminiferal distributions vary most strongly with elevation, other environmental variables, such as salinity, also exert an influence (Section 3.1). These additional factors introduce scatter into the one-to-one relationship between observed and predicted elevation that characterize the

ideal scenario above. Whilst not negating the validity of the vertical relationship, they reduce the precision with which reconstructions can be made. Ultimately, if the influence of these other variables becomes dominant, the scatter introduced will be so great that no meaningful predictions can be made. In the context of sea-level research, we can think of the strong vertical relationship between foraminifera and tide level as the desired 'signal', whilst the influence of additional variables may be thought of as 'noise'.

The need to maximize the elevation signal recommends the use of a statistical technique known as weighted averaging partial least squares regression and calibration (WA-PLS) (ter Braak and Juggins, 1993; Birks, 1995). This is a modification of a unimodal method 'weighted averaging' (WA). Weighted averaging considers the variance along a single environmental gradient such as elevation, and has previously been employed to develop transfer functions based on British foraminifera (Horton and others, 1999; Edwards and Horton, 2000; Gehrels and others, 2001). Each foraminiferal species is assigned an ecological optimum, reflecting its 'preferred' elevation, and an ecological tolerance, describing the range of elevations over which it may be found. As outlined above, where an additional environmental variable, such as salinity, exerts an influence on the composition of a foraminiferal assemblage, scatter is introduced into the plot of observed versus predicted values, and this departure from the ideal one-to-one relationship is termed the 'prediction residual'. WA-PLS improves predictions by using any structure present in the WA residuals and, in effect, considers the influence of additional environmental variables such as salinity (ter Braak and Juggins, 1993).

In order to effectively assess the predictive abilities of the transfer function, it is important to use cross-validated performance indices, since the 'apparent' measures, coefficient of determination (r^2) and root mean squared error (RMSE), use the whole dataset to develop the transfer function and test its performance. Jack-knifed or 'leave-one-out' measures (ter Braak and Juggins, 1993) are a simple cross-validation approach where the reconstruction procedure is applied n times using a training set of (n - 1). In each of the n predictions, one sample is omitted in turn and the transfer function, based on the remaining (n - 1) samples in the training set, is applied to the omitted sample. This produces a predicted value and, by subtracting this from the observed value, generates a prediction error for the omitted sample ($RMSEP_{jack}$) (Birks, 1995). In addition, r^2_{jack} can be

calculated for each observed value when the sample is included in the test set but excluded from the training set. Jack-knifing measures are reliable indicators of the true predictive ability of the transfer functions as they are less-biased by sample re-substitution (Dixon, 1993).

$RMSEP_{jack}$ is a measure of the overall predictive abilities of the training set. It does not provide sample-specific errors for each fossil sample, as the observed value is not known for the fossil samples (Birks, 1995). Bootstrapping can be used to derive a standard error of prediction (SE_{pred}) (Birks and others, 1990; Line and others, 1994). This is interpreted, following Birks and others (1990), as a sample-specific root mean squared error of prediction for individual fossil and modern samples. SE_{pred} for an environmental variable in the past can vary from sample to sample depending upon the composition of the fossil assemblage and thus the presence or absence of taxa with a particularly strong signal for the environmental variable of interest (Birks, 1995). Bootstrapping for the estimation of sample specific errors has been implemented for WA-PLS (Birks and others, 1990; Line and others, 1994).

3.4.3 Transfer Function Development

WA-PLS produces as many components as there are variables or samples. The first component maximizes the covariance between the vector of weighted averages and the environmental variable of interest (elevation). Subsequent components are chosen to maximize the same criterion but must be uncorrelated to earlier components (Birks, 1995). The choice of component for the transfer function depends upon the prediction statistics ($RMSEP_{jack}$, and r^2_{jack}) and the principle of parsimony; that is, the lowest component that gives an acceptable model (e.g. Horton and others, 2003). On this basis, component two is selected for the North Sea example, since it performs significantly better than component one (in terms of jack-knifed errors), with only modest improvements thereafter (Table 3). Figure 40 shows the relationship between observed and foraminifera-estimated elevation using component two, and illustrates the strong performance of the initial regression (r^2_{jack} = 0.73; $RMSEP_{jack}$ = 7.53).

A second phase of screening now takes place to remove samples or species that have the potential to produce erroneous reconstructions. Any large, heterogeneous foraminiferal training set will inevitably contain some samples that show a poor statistical relationship with SWLI. They have a poor fit because other environmental

Estimated errors		
Component	RMSE	r^2
1	7.69	0.69
2	6.66	0.77
3	6.23	0.79

Prediction errors		
Component	RMSEP	r^2
1	8.28	0.66
2	7.53	0.73
3	7.80	0.74

TABLE 3. Statistics summary of the performance of weighted averaging partial least squares (WA-PLS) for unscreened east coast training set.
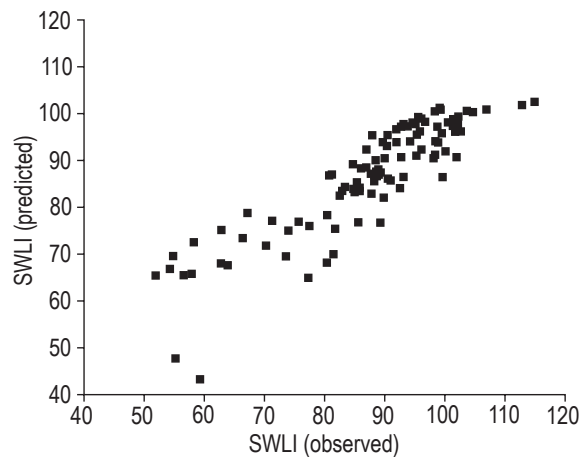
FIGURE 40. Scatter plot showing the initial (unscreened) relationship between observed SWLI (as measured during the surveys) and predicted SWLI (produced by the WA-PLS transfer function) derived from the North Sea coast dataset.

factors may become dominant in influencing the assemblage, or the composition of the assemblage may have been altered by factors such as transport or differential preservation. Samples with a poor fit will have a high residual distance from the first ordination axis constrained by SWLI. Such samples can decrease the predictive ability of the estimated transfer function coefficients. They should, therefore, be identified and removed from the training set (Gasse and others, 1997; Jones and Juggins, 1995). It is common practice to screen samples with an absolute residual (observed minus predicted) greater than the standard deviation of SWLI in the training set (Jones and Juggins, 1995). Screening removes the lowest two samples from Cowpen Marsh which, given their low elevation, have an increased

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likelihood of containing an allochthonous component.

The issue of allochthonous material is central to the screening of certain species at this stage of the analysis (e.g. Racca and others 2003). The use of foraminifera as proxies for elevation rests on the assumption that dead assemblages are formed in-situ by the accumulation of foraminifera living in restricted subzones that are controlled by environmental variables correlated with elevation. Where an allochthonous component is present in the assemblage, this should contribute only minor species (that will be screened out), or comprise a faunal signature that is characteristic of the elevation at which it is deposited. Intuitively, allochthonous material will become increasingly significant with decreasing elevation, and will be typified by a range of taxa that reflect neighboring sub-tidal environments. Inspection of the predicted species optima, coupled with an understanding of the ecology of salt-marsh and nearshore foraminifera, allows an assessment to be made of species (and samples) that are especially susceptible to transport and may result in erroneous reconstructions if included in the modern dataset. The influence of post-depositional modification is considered in more detail in Section 3.6.

In the case of the North Sea coast dataset, *Brizalina* and *Trochammina ochracea* display highly variable distributions with a tendency to cluster in the upper salt-marsh. The former is a marine, shelf taxon that is commonly transported into estuaries and is likely to have been washed onto the marsh surface shortly before the modern transect was taken. Calcareous taxa such as this will dissolve in acidic high marsh environments (Scott and Medioli, 1980a, b; Green and others, 1993), and therefore will not be incorporated into the fossil dataset. Whilst it is unlikely that they would be encountered in core material, it is still safest to screen these species out to avoid potential confusion with lower (though clearly minerogenic) samples. Conversely, *T. ochracea* is agglutinated and has the potential to be preserved within salt-marsh sequences (e.g. Shennan and others, 1999; Scott and others, 2001). This species is an epiphytic shelf species that lives attached to rocky or pebbly substrates, but may also cling to seaweed (Murray, 1971). Its very high species optimum is likely to reflect its transport and deposition on to the marsh around the strandline where seaweed collects after the retreat of the tide. Since this species may be found at both ends of the elevation gradient, it cannot be considered as diagnostic and should be screened from the training set. Whilst *T. ochracea* is recorded in fossil sediments, it is commonly present in very low abundances.

Estimated errors		
Component	RMSE	r^2
1	7.38	0.69
2	6.13	0.79
3	5.96	0.80
Prediction errors		
Component	RMSEP	r^2
1	7.93	0.66
2	6.86	0.75
3	7.02	0.75

TABLE 4. Statistics summary of the performance of weighted averaging partial least squares (WA-PLS) for screened (2nd Iteration) east coast training set.
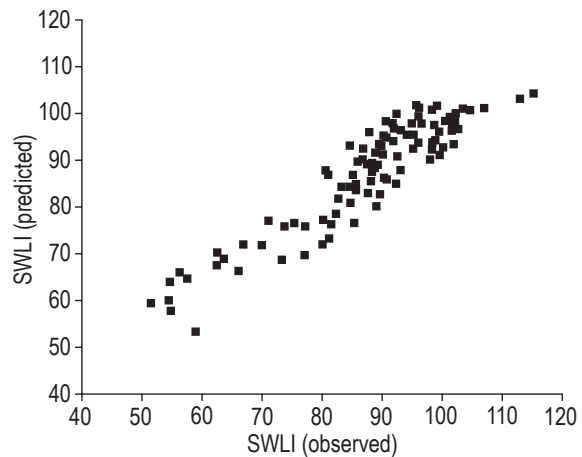
FIGURE 41. Scatter plot showing the screened relationship between observed SWLI (as measured during the surveys) and predicted SWLI (produced by the WA-PLS transfer function) derived from the North Sea coast dataset.

A selection of calcareous shelf species is associated with the lowest elevation samples in all marshes. Whilst the precise composition of these assemblages may vary in space and time, their presence is ubiquitous and consistent, being indicative of low marsh to tidal flat environments. These species are combined into a single group, termed 'exotics', that effectively functions as a low marsh to tidal flat 'species', and may be used by the transfer function to increase its resolving power below the middle marsh. In the case of the North Sea coast training set, this 'exotic' group comprises *Cibicides* species, some *Elphidium* species (such as *E. margaritaceum*), *Stainforthia fusiformis*, *Pateoris hauerinoides*, and *Spirillina* species.

The screened and rationalized training set is used to

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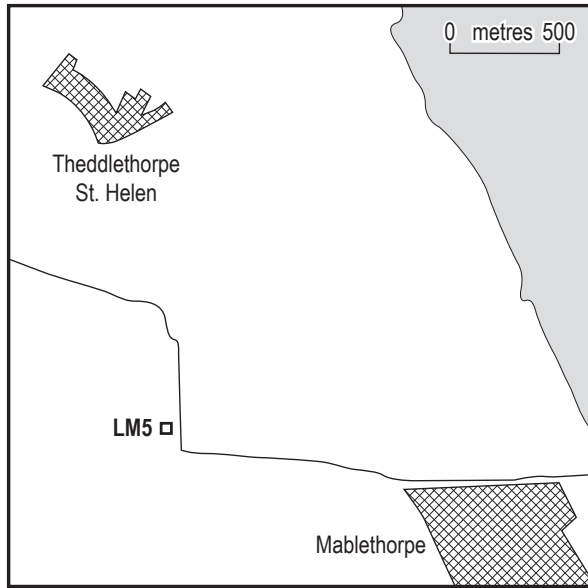
FIGURE 42. Location map of Theddlethorpe showing the site of core LM5.

develop a second iteration of the transfer function, and the results are summarized in Figure 41 and Table 4. The screened data improve transfer function performance assessed in terms of r^2 (0.75; component two) and RMSEP (6.86; component two).

3.4.4 Transfer Function Application

Calibration is achieved via the C2 program and is used to predict SWLI on the basis of fossil foraminiferal assemblages from sediment cores. To illustrate this, an example sediment core from the North Sea coast (core LM5) is used to provide foraminiferal data for calibration. Core LM5 was collected 2 km southeast of Theddlethorpe and approximately 350 m west of the Gas Terminal on the Lincolnshire coast (Fig. 42). The lithostratigraphy consists of a diamicton of stiff clay at the base of the core (Fig. 43). Directly overlying the diamicton is a thin, well-humified peat found at a depth of 1295 cm to 1287 cm. The peat is overlain by an olive-grey silty clay with dispersed organic remains and numerous bivalve
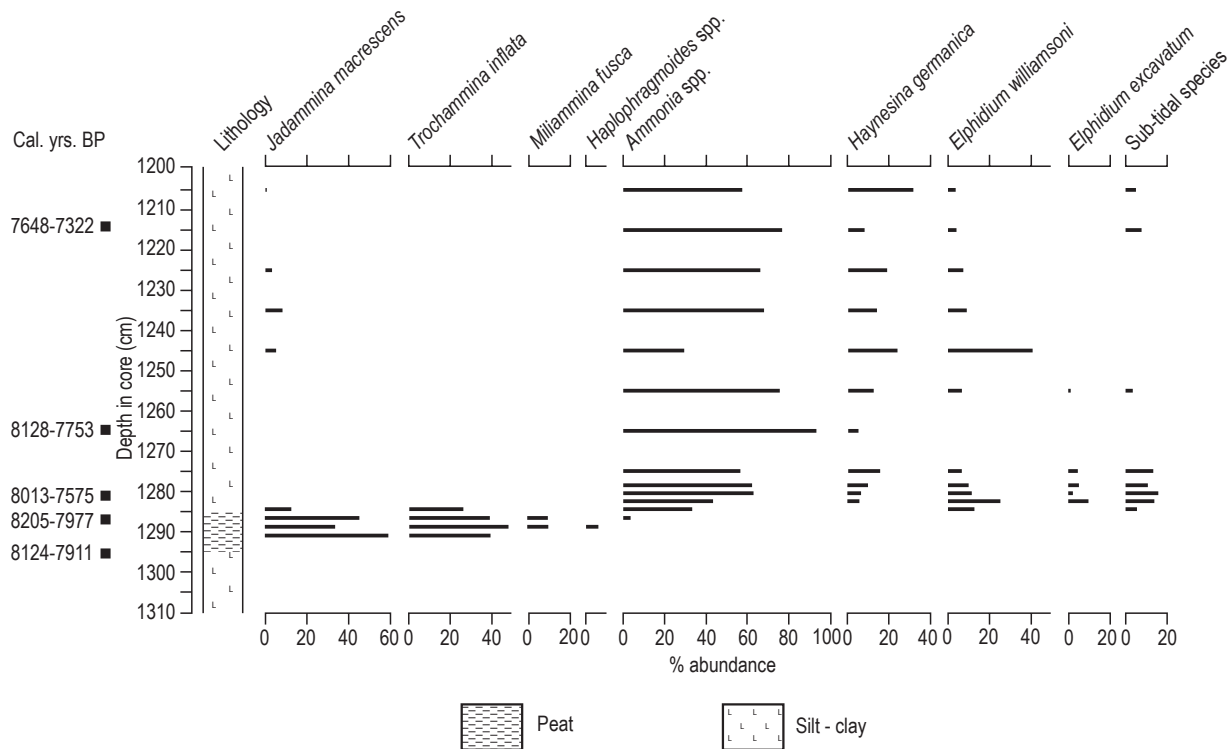
FIGURE 43. Theddlethorpe, core LM5. Foraminiferal abundance is calculated as the percentage of dead foraminiferal tests. Radiocarbon dates (expressed in calibrated years BP using the 95% confidence limits for the probability option) are shown.

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fragments. The upper and lower contacts of the peat are gradational. The foraminiferal data indicate a transition within the peat from a freshwater (no foraminifera) to a salt-marsh environment (associated with an assemblage dominated by two characteristic salt-marsh species, *J. macrescens* and *T. inflata*). The overlying silty clay is dominated by a calcareous foraminiferal assemblage, indicative of an estuarine or tidal flat environment.

Prior to calibration, the fossil foraminiferal data are rationalized to conform to the training set characteristics, primarily by combining the 'exotic' species into a single species group. The North Sea coast transfer function is used to calibrate the fossil assemblages from core LM5. SWLI estimates are provided using cross-validated WA-PLS predictions from component 2, whilst the error range is derived by bootstrapping (1000 cycles). The results are summarized in Figure 44 and Table 5. The maximum tide level reconstructed by the transfer function occurs at a
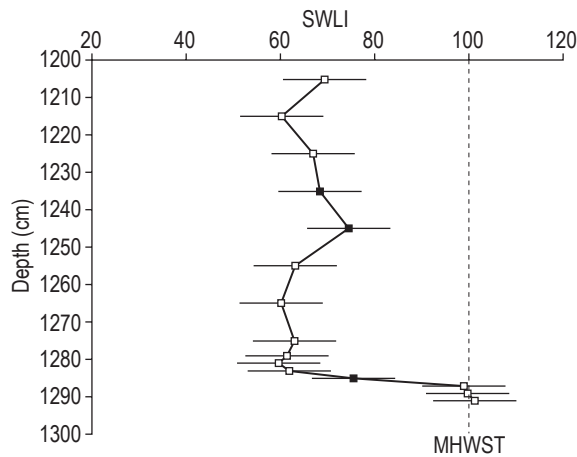
FIGURE 44. WA-PLS reconstruction for Theddlethorpe, core LM5 using the North Sea coast dataset.
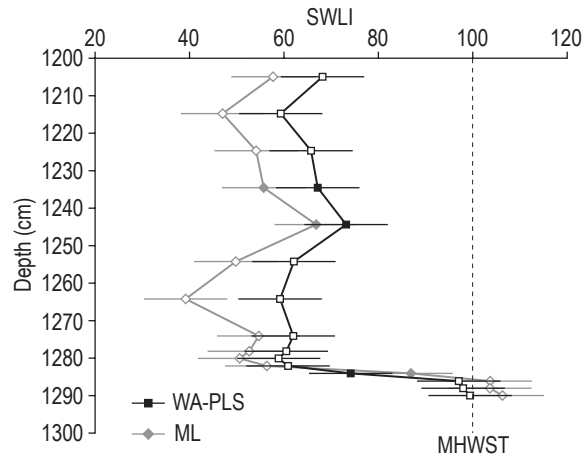
FIGURE 45. Comparison of reconstructions for core LM5 using both WA-PLS (squares) and ML (diamonds) for the North Sea coast dataset. Samples with 'no modern analogues' are plotted as filled symbols.

Sample depth (m)	Sample altitude (m OD)	SWLI	Error	Min. DC	Analogue	Elevations (m relative to MTL)
1205	-10.05	69.33	8.61	0.14	Good	-11.36 m ± 0.52 m
1215	-10.15	60.28	10.04	0.07	Good	-10.92 m ± 0.60 m
1225	-10.25	66.80	9.31	0.14	Good	-11.41 m ± 0.56 m
1235	-10.35	68.32	9.46	0.28	No close	-11.60 m ± 0.57 m
1245	-10.45	74.57	7.29	0.32	No close	-12.07 m ± 0.44 m
1255	-10.55	63.13	9.99	0.12	Good	-11.49 m ± 0.60 m
1265	-10.65	60.16	11.49	0.13	Good	-11.41 m ± 0.69 m
1275	-10.75	63.07	8.60	0.03	Good	-11.68 m ± 0.52 m
1279	-10.79	61.41	9.03	0.04	Good	-11.62 m ± 0.54 m
1281	-10.81	59.81	9.02	0.07	Good	-11.55 m ± 0.54 m
1283	-10.83	61.89	7.96	0.11	Good	-11.69 m ± 0.48 m
1285	-10.85	75.51	7.41	0.27	No close	-12.53 m ± 0.44 m
1287	-10.87	99.12	6.69	0.02	Good	-13.97 m ± 0.40 m
1289	-10.89	99.88	6.73	0.08	Good	-14.03 m ± 0.40 m
1291	-10.91	101.42	6.69	0.01	Good	-14.15 m ± 0.40 m

TABLE 5. The standardized water level index (SWLI), bootstrapped error and elevations (expressed relative to MTL) generated by the screened (2nd Iteration) east coast weighted averaging partial least squares (WA-PLS) transfer function for samples from Theddlethorpe, LM5. The critical value (10th percentile) for the dissimilarity coefficients (Min. DC) produced by the modern analogue technique is 0.17. The predicted values of SWLI are converted to estimates of elevation (m relative to MTL) by re-arranging Equation 1, and inputting the appropriate tidal parameters for Theddlethorpe (MHWST = 31.5 m OD; MLWST = -2.85 m OD).

depth of 1291 cm within the basal peat (a SWLI of 101.4 ± 6.7), which is around local MHWST (100). Values decline markedly above the transgressive contact and continue to fall within the silty clay to a minimum SWLI of 59.8 ± 9.0 at a depth of 1281 cm. The predicted values of SWLI can be converted to estimates of elevation by re-arranging Equation 1 and inputting the appropriate tidal parameters for the site from which the fossil sequence was recovered. This back-transformation process results in the elevations (expressed in metres relative to MTL) shown in Table 5.

3.4.5 Assessing Transfer Function Reliability

Whilst the various performance measures, such as RMSEP and r^2, provide some information on the internal consistency of the transfer function, they provide little information on how reliable or 'realistic' the estimated values of SWLI produced by the transfer function are. Ideally, entirely independent transfer functions using different environmental proxies should be used to evaluate which reconstructions are 'ecologically reasonable'. In the context of British and Irish salt-marsh elevation changes, diatoms have the potential to provide this information, but at the cost of conducting an additional suite of time-consuming micropaleontological analysis.

Here, we use two methods to provide an informal assessment of 'reliability'. The first considers how similar the fossil assemblage used to estimate SWLI is to the assemblages used to develop the transfer function. In simple terms, the greater the dissimilarity between a fossil sample and all samples in the training set, the more the transfer function is forced to extrapolate and the more prone the resultant estimate will be to error. For example, samples that have experienced significant post-depositional modification, such as decalcification, may be without modern analogues in the modern training set, and this can serve to identify estimates that should be treated with caution (Edwards and Horton, 2000).

Dissimilarity is calculated using the modern analogue technique (MAT). We calculate the dissimilarity between a fossil sample and the ten most similar modern samples, using the squared chord distance as the dissimilarity coefficient (Prentice, 1980; Overpeck and others, 1985). Fossil samples with coefficients below the tenth percentile are considered to have good analogues in the training set (Birks and others, 1990). For our example core and transfer function, of the 20 fossil assemblages, three do not have matching analogues in the modern training set (Table 5).

In the second approach, we use a different statistical method to generate a second transfer function. Once again, whilst this is an informal approach and will not circumvent fundamental problems in a training set, similar estimates produced by different transfer functions demonstrate that the selection of the statistical technique is not significantly determining the outcome. Here we use Maximum Likelihood (ML) regression and calibration which can be regarded as the most 'statistically rigorous approach to environmental reconstruction' (Birks, 1995). In the ML approach, ecological response curves are modeled for each taxon, and these curves are used in combination to calculate the probability that a given value of elevation would occur for a particular foraminiferal assemblage. The elevation that is associated with the highest probability is the 'Maximum Likelihood' estimate. ML is a useful complementary method to WA-PLS since, whilst it is also appropriate for unimodal datasets, it is a classical approach, whereas WA-PLS is an inverse method (see Section 3.2.2).

A transfer function is developed for ML following the same procedure as outlined above for WA-PLS. Figure 45 shows the reconstructions of ML plotted with those of WA-PLS and demonstrates that they estimate similar values within the error margins of both techniques. Samples with 'no modern analogues' are plotted as black squares. ML estimates slightly larger variations than WA-PLS as would be expected from a 'classical' approach. In addition, both techniques predict similar values for those samples without modern analogues. The largest deviation between the two techniques is for sample 1265 cm, which is characterized by an almost monospecific assemblage of *Ammonia* species. Differences between the two reconstructions reflect the different ways in which each method develops the ecological response functions. Overall, the ML results provide additional support for the statistical reliability of reconstructions derived from WA-PLS transfer functions.

In this simple example, the reconstructions produced by the transfer functions are consistent with those we may expect from 'eye-balling' the data. Whilst this similarity may provide us with some confidence that the transfer function methodology is reliable, it should not be confused with the suggestion that the latter approach is capable of producing results of comparable quality. The transfer function approach involves a transparent, repeatable methodology that is applicable across and range of sedimentary environments and produces estimates with consistent, quantified error terms. In

contrast, visual interpretation of foraminiferal data (e.g. the assemblage zone approach), is subjective and involves sub-division and interpolation that can differ between analysts. In addition, the resulting estimates are of variable precision reflecting the differing vertical ranges encompassed by assemblage zones across the inter-tidal zone (Edwards and others, 2004a). Furthermore, the transfer function approach incorporates the spatial complexity displayed by foraminiferal distributions at the intra- and inter-site scale. This provides a more reliable representation of faunal-environment relationships and maximizes the applicability of these relationships as depositional environments change through time. This cannot be achieved by simply 'eye-balling' datasets, and the latter will tend to underestimate faunal complexity and variability whilst over-estimating the accuracy and precision attached with its reconstructions. The issue of spatial variability is addressed in the following section.

3.5 TRAINING SET COMPOSITION – SPATIAL SCALE AND REPRESENTATIVITY

The reliability of any foraminiferal transfer function for tide level is dependent upon the precise and accurate quantification of the relationship between foraminiferal assemblages and elevation. Compilation of a modern training set endeavors to encompass the full suite of elevations and associated depositional environments that may be encountered in a fossil core, thereby ensuring the maximum number of modern analogues. This search for analogous environments usually begins in the vicinity of the site from which fossil material is recovered. In this way, complications arising from spatial variability in salinity, sediment type, hydrographic regime or foraminiferal assemblage can be minimized. In the absence of statistical methods capable of combining data that exhibit such spatial variability, there is little alternative but to use local data, traditionally in the form of a generalized vertical zonation (e.g. Gehrels, 1994; Allen and Haslett, 2002).

A number of important limitations are associated with this local-scale approach, notwithstanding the considerable problems associated with the use of vertical assemblage zones discussed in Section 2. In the first instance, the idea that modern local data are more representative of past local conditions rests upon the assumption that these environmental variables have not changed significantly through time. For high-resolution studies of limited duration, this may be an acceptable premise, but it becomes increasingly speculative as

the temporal scale of an investigation is increased. In areas that have experienced significant changes in coastal morphology, such as the growth of sand barriers through the Holocene, large changes in variables like wind-wave climate or substrate are to be expected. By extension, sediment cores may be recovered from areas that are now terrestrial, either as a consequence of RSL change, sedimentary processes or reclamation, leaving no source of site-specific data. Perhaps of greater importance, however, is the growing recognition that spatial variability can be significant, even at local scales. Studies employing multiple transects from single sites demonstrated that the precise composition and elevation of certain foraminiferal assemblages depends upon exactly where a sampling transect is located (Scott and Medioli, 1980a; Gehrels, 1994; Edwards and others, 2004a; Horton and others, 2005b).

Having accepted that spatial variability is unavoidable, a reliable method is required to extract elevation information from complex, composite datasets. The transfer function approach is ideally suited to this task since it is not concerned with delimiting vertical assemblages, but rather with the compilation of analogous environments and their associated fauna. In a recent study, Horton and Edwards (2005) compared the performance of a transfer function compiled from the foraminiferal distributions recorded at the adjacent marshes of Thornham and Brancaster, with one developed from 13 sites around Great Britain and Ireland. These transfer functions were used to calibrate foraminiferal assemblages recovered from a core extracted from the Norfolk coastline. The results of this study revealed that the local-scale transfer function produced more precise reconstructions (smaller associated error terms) than the national-scale transfer function. However, whilst both transfer function reconstructions resulted in similar estimates of paleomarsh-surface elevation, the local-scale transfer function estimates were associated with significantly more 'no modern analogue' situations than the national-scale transfer function. Horton and Edwards (2005) concluded that reconstructions derived from the national-scale transfer function are more reliable than those of the local-scale transfer function, since the latter achieves its slight increase in precision at the expense of a significant decrease in predictive power.

Horton and Edwards (2005) noted that one possible explanation for the poorer performance of the local-scale transfer function could be a consequence of the smaller sample size of its training set and the lack of suitable analogous environments. We investigate this issue of

Region	Study Sites	GL	No.	Scr. samples	% Scr.	Key species	Sub-species	RMSE	r^2	r^2_{BOOT}	RMSEP	10th percentile
West	KB, NE, RB1, RB2, RM, TB	2.5	55	0	0.0	AS, EWl, HG, Hs, JM, MF, Qs, TI	Es	9.22	0.73	0.66	11.07	0.17
Northeast	AM, CM, WM	2.6	63	2	3.2	AS, EM, EW, HG, JM, MF, Qs, TI	CL, Es, SF,	5.69	0.81	0.78	6.37	0.12
Southeast	AP, BF, BM, KH, NW, TM	2.7	85	2	2.4	AS, EE, EW, HG, Hs, JM, MF, Qs, TC, TI	CL, Es, ES, Rs	6.97	0.78	0.73	8.04	0.14
National	AM, AP, BM, BF, CM, KB, KH, NE, NW, RB1, RB2, RM, TB, TM, WM,	3.1	203	3	1.5	AS, EE, EM, EWl, HG, Hs, JM, MF, Qs, TC, TI	CL, Es, ES, SF, Rs	8.55	0.71	0.69	8.99	0.21
East	AM, CM, WE, TH, BM	3.2	110	2	1.8	AS, EE, EM, EW, HG, Hs, JM, MF, Qs, TI	CL, Es, SF, PM, SV	6.13	0.79	0.75	6.86	0.17

TABLE 6. The summary statistics, sample sizes and screening details for each quasi-regional averaging partial least squares (WA-PLS) transfer function (GL = Gradient Length). Study site abbreviations: AM - Alnmouth Marsh; CM - Cowpen Marsh; WM - Welwick Marsh; TM - Thornham Marsh; BM - Brancaster Marsh; BF - Bury Farm; KM - Keyhaven Marsh; NB - Newton Bay; AP - Arne Peninsula; RM - Roudsea Marsh; NE - Nith Estuary; TB - Tramaig Bay; KB - Kentra Bay; RB1 - Rusheen Bay 1; and RB2 - Rusheen Bay 2. Species abbreviations: AS = *Ammonia* spp.; CL = *Cibicides lobatulus*; ES = *Eggerelloides scaber*; EE = *Elphidium excavatum*; EM = *Elphidium magellanicum*; Es = *Elphidium* spp. EW = *Elphidium williamsoni*; SF = *Stainforthia fusiformis*; Hs = *Haplophragmoides* spp. HG = *Haynesina germanica*; JM = *Jadammina macrescens*; MF = *Miliammina fusca*; Qs = *Quinqueloculina* spp.; Rs = *Reophax moniliformis*; TC = T*iphotrocha comprimata*; and TI = *Trochammina inflata*.

training set composition by sub-dividing the modern data into three, quasi-regional groups (Table 6). We prefer this sub-division to the groupings presented in Section 2 in order to strike a balance between 'geographic regions' whilst ensuring similar sample sizes. At present, there is a pronounced bias in the modern training sets toward samples from the North Sea coast marshes, and limited data are available from the marshes of southern England. These discrepancies would make it difficult to distinguish 'regional' effects from those due to differences in training set size.

Regional transfer functions based on WA-PLS are developed according to the procedure outlined in Sections 3.2 and 3.4. In addition, we develop a 'multi-regional' transfer function derived from the full training set of 15 sites. The summary statistics, sample sizes and screening details for each transfer function are shown in Table 6. Fossil assemblages from three cores located within the broad regions west (DBM50), north-east (LM5) and south-east (BF11) are calibrated by all the transfer functions and the results discussed below.

3.5.1 Drumborough Moss, Core DBM50 (West Coast)

The raised bog of Drumborough Moss is situated on the south side of Solway Firth, 2.5 km west of Boustead Hill and 1.5 km south of the coast (Fig. 46). The stratigraphy comprises a basal clastic unit comprising

FIGURE 46. Location map of Drumborough Moss showing the site of core DBM50.

sand slit and clay, a thin lower peat, a second clastic unit of silt and clay and a surface peat (Lloyd and others, 1999). The basal clastic unit and much of the basal peat (Fig. 47) are devoid of foraminifera. Just at the top of the peat (366 cm), agglutinated foraminifera (*J. macrescens* and *Haplophragmoides* spp.), indicative of salt-marsh conditions, appear and are soon replaced by the calcareous species, *H. germanica*, and then by a wide range of calcareous species. The foraminifera within the upper clastic unit show several fluctuations in environment; between 306 cm – 290 cm there is a return to salt-marsh conditions with a near 100% assemblage of *J. macrescens* and *T. inflata*. There is a reappearance of calcareous species above 290 cm which are, in turn, replaced by agglutinated species from 200 cm.

Fig. 48 presents the estimates of SWLI generated by the multi-regional and regional transfer functions. All reconstructions show excellent agreement in terms of the patterns and magnitude of inferred changes, and are indistinguishable within the error terms associated with each estimate. The least precise reconstructions are provided by the western transfer function, followed

FIGURE 47. Drumborough Moss, core DBM50. Foraminiferal abundance is calculated as the percentage of dead foraminiferal tests. Radiocarbon dates (expressed in calibrated years BP using the 95% confidence limits for the probability option) are shown.

by the multi-regional, south-eastern and north-eastern transfer functions.

As discussed in Section 3.4.5, reliability of transfer function estimates can be assessed by testing the fossil assemblages for modern analogues within the training set data. The results of this matching analogue technique are summarized in Table 7, and show that whilst the values of the reconstructions are similar, considerable differences in the provision of modern analogues exists between datasets. Of the 26 fossil samples, three are without modern analogues in the 'local' (west coast) training set. Similarly four to five samples are without modern analogues in the north-east and south-east training sets, whilst all samples have good modern analogues in the multi-regional training set.

3.5.2 Theddlethorpe, Core LM5 (North-east Coast)

The process outlined above for the west coast material is repeated for the north-east coast (Fig. 49, Table 8). The reconstructions from core LM5 (see Section 3.4.4 for core description) show greater variation between datasets than was apparent for DBM50, although all exhibit similar patterns of change. These datasets show particularly good agreement for the highest elevation samples at the base of the sequence. Predicted values of SWLI diverge above 1285 cm depth, with the south-east coast dataset resulting in values that are clearly lower than those of the north-east and west coasts. The multi-regional data reconstruct values mid-way between these extremes.

FIGURE 48. WA-PLS reconstruction for Drumborough Moss, core DBM50 using (a) multi-regional, (b) western, (c) north-eastern and (d) south-eastern transfer functions. Samples with 'no modern analogues' are plotted as black squares.

FIGURE 49. WA-PLS reconstruction for Theddlethorpe, core LM5 using (a) multi-regional, (b) western, (c) north-eastern and (d) south-eastern transfer functions. Samples with 'no modern analogues' are plotted as black squares.

Depth (cm)	Multi-region		West		North-east		South-east	
	SWLI	Error	SWLI	Error	SWLI	Error	SWLI	Error
114	102.0	8.9	99.5	10.7	100.2	6.3	106.0	8.1
130	102.7	9.0	101.1	10.7	100.8	6.4	107.4	8.3
146	101.4	8.9	98.1	10.8	99.2	6.3	104.7	7.9
162	101.6	8.9	98.6	10.8	99.3	6.3	105.0	7.9
178	101.2	8.9	97.4	10.9	98.3	6.3	103.9	7.8
194	101.5	8.9	98.3	10.8	99.1	6.3	104.8	7.9
210	92.6	8.9	89.8	11.0	92.4	6.2	93.7	7.8
226	88.5	8.9	87.7	11.1	90.2	6.2	88.5	7.8
242	91.3	8.9	89.2	11.0	91.8	6.2	91.8	7.8
258	89.3	8.9	87.4	11.2	90.7	6.2	89.0	7.8
274	86.8	8.9	85.4	11.6	89.3	6.2	85.6	8.0
290	100.7	8.9	97.3	10.9	98.6	6.3	103.3	7.9
306	102.4	9.0	100.7	10.7	101.2	6.4	107.1	8.3
322	91.0	8.9	90.6	11.2	94.2	6.2	90.2	8.0
331	83.5	9.0	84.6	12.7	85.5	6.2	81.8	8.1
335	84.8	9.0	85.0	12.3	89.0	6.2	81.6	8.2
339	84.8	9.0	85.3	12.0	91.2	6.3	80.1	8.2
343	83.8	9.0	84.3	12.2	89.2	6.2	80.0	8.1
347	82.5	9.0	83.6	12.1	89.3	6.3	77.4	8.2
351	83.1	9.0	82.9	12.4	89.2	6.2	78.8	8.3
355	85.5	9.0	83.1	12.9	89.8	6.2	82.3	8.4
359	95.8	8.9	94.2	11.2	96.2	6.3	95.5	8.0
361	95.1	8.9	93.7	11.2	94.6	6.2	94.5	8.0
363	102.1	8.9	102.1	10.6	99.3	6.4	104.6	8.0
365	102.7	8.9	102.9	10.6	99.3	6.3	104.6	8.0
366	102.1	9.0	103.6	10.7	101.7	6.5	101.9	8.2

TABLE 7. The standardized water level index (SWLI), bootstrapped error generated by multi-regional, western, north-eastern and south-eastern transfer functions for Drumborough Moss, core DBM50. Shaded boxes indicated no-matching analogues.

Depth (cm)	Multi-region		West		North-east		South-east	
	SWLI	Error	SWLI	Error	SWLI	Error	SWLI	Error
1205	72.7	9.6	83.0	11.3	87.9	6.8	61.4	8.7
1215	66.6	10.3	82.4	11.7	86.2	7.3	52.0	9.6
1225	71.4	10.0	84.2	11.4	89.2	7.1	58.5	9.2
1235	72.2	9.9	85.1	11.4	89.5	7.0	60.2	9.2
1245	75.3	9.1	80.6	10.9	81.0	6.5	75.4	8.3
1255	68.1	10.2	82.8	11.6	87.1	7.2	54.2	9.4
1265	66.2	10.9	84.8	12.1	90.8	7.8	47.7	10.4
1275	68.6	9.6	79.8	11.2	81.5	6.8	58.9	8.5
1279	67.4	9.8	80.1	11.3	81.9	6.9	56.9	8.7
1281	65.9	9.8	78.9	11.3	79.5	6.9	56.5	8.7
1283	68.0	9.4	77.2	11.0	75.6	6.7	63.5	8.4
1285	80.0	9.2	85.0	11.0	85.7	6.5	76.1	8.1
1287	100.0	8.9	97.0	11.0	95.2	6.3	101.1	7.7
1289	100.6	8.9	97.3	11.2	94.3	6.4	99.7	7.9
1291	100.8	8.9	96.5	11.1	98.0	6.3	103.1	7.8

TABLE 8. The standardized water level index (SWLI), bootstrapped error generated by multi-regional, western, north-eastern and south-eastern transfer functions for Theddlethorpe, core LM5. Shaded boxes indicated no-matching analogues.

Depth	Multi-region		West		North-east		South-east	
(cm)	SWLI	Error	SWLI	Error	SWLI	Error	SWLI	Error
8	101.8	8.9	99.0	10.7	99.7	6.3	105.4	8.0
16	101.8	8.9	98.9	10.8	99.7	6.3	105.4	8.0
24	101.1	8.9	97.3	10.9	98.6	6.3	103.9	7.9
32	102.7	9.0	101.2	10.7	101.5	6.5	107.6	8.4
40	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
48	102.7	9.0	101.2	10.7	101.5	6.5	107.0	8.3
52	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
56	102.7	9.0	101.7	10.7	101.7	6.5	107.3	8.4
60	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
68	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
76	102.5	9.0	100.7	10.7	101.1	6.4	107.2	8.3
82	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
84								
86	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
88	102.5	8.9	100.6	10.7	100.1	6.3	106.8	8.1
96	102.8	9.0	101.5	10.7	101.7	6.5	107.9	8.4
108	102.8	9.0	101.4	10.7	101.0	6.4	107.3	8.3
120	103.0	8.9	101.7	10.6	100.2	6.4	107.7	8.2
128	102.7	9.0	101.3	10.7	101.5	6.5	107.7	8.4
136	102.5	9.0	100.9	10.7	101.2	6.4	107.3	8.3
148	102.2	8.9	99.8	10.7	99.5	6.3	106.0	8.0
160	102.0	8.9	99.5	10.7	99.9	6.3	105.3	8.0
172	88.4	8.9	87.0	11.2	84.8	6.2	88.5	8.0
184	94.1	8.9	93.9	10.8	90.7	6.2	92.5	7.8
196	101.8	8.9	100.2	10.7	93.9	6.2	102.9	7.7
208	98.6	8.9	96.5	10.7	93.0	6.2	99.0	7.7
220	99.0	8.9	96.8	10.7	93.7	6.2	98.9	7.7

TABLE 9. The standardized water level index (SWLI), bootstrapped error generated by multi-regional, western, north-eastern and south-eastern transfer functions for Southampton Water, core BF11. Shaded boxes indicated no-matching analogues.

Significantly, both the north-east and west coast training sets perform poorly in terms of matching analogues. Of the 15 fossil samples, 12 are without modern analogues in the north-east (local) training set, whilst 11 no-matching analogue situations occur for the west coast data. In contrast, the south-east data have four no modern analogue situations whilst the multi-regional training set has only three. It is possible; therefore, that the north-east and west coast training sets produce transfer functions that underestimate the extent of submergence due to a lack of appropriate modern analogue samples from lower elevation contexts.

3.5.3 Southampton Water, Core BF11 (South-east Coast)

The final test is performed on core material taken from Southampton Water (southern England) at Bury Farm, adjacent to the surface foraminiferal transect shown in Figure 6. The lithostratigraphy consists of a humified basal peat overlain by 140 cm of grey silty clay (Fig. 50). This minerogenic sediment is interrupted by a thin peat band between 85 cm and 80 cm before the grey silty clay sediments return. The upper 35 cm of the sequence is typified by a brown, organic silty clay containing macrofossils of *Spartina*. In contrast to the predominantly minerogenic nature of the sequence, which is suggestive of deposition in or below a low marsh environment, the bulk of the silty clay sequence above 165 cm is devoid of calcareous taxa. Instead, the sequence is dominated by *J. macrescens* (commonly >80%) with some *T. inflata*, suggestive of high marsh deposition.

In common with the previous two cores, the multi-regional transfer function performs best in terms of the fewest samples with no modern analogues in the training set (Fig 51 and Table 9). However, of greater significance is the general inability of any of the transfer functions to discern elevation changes. This undoubtedly reflects
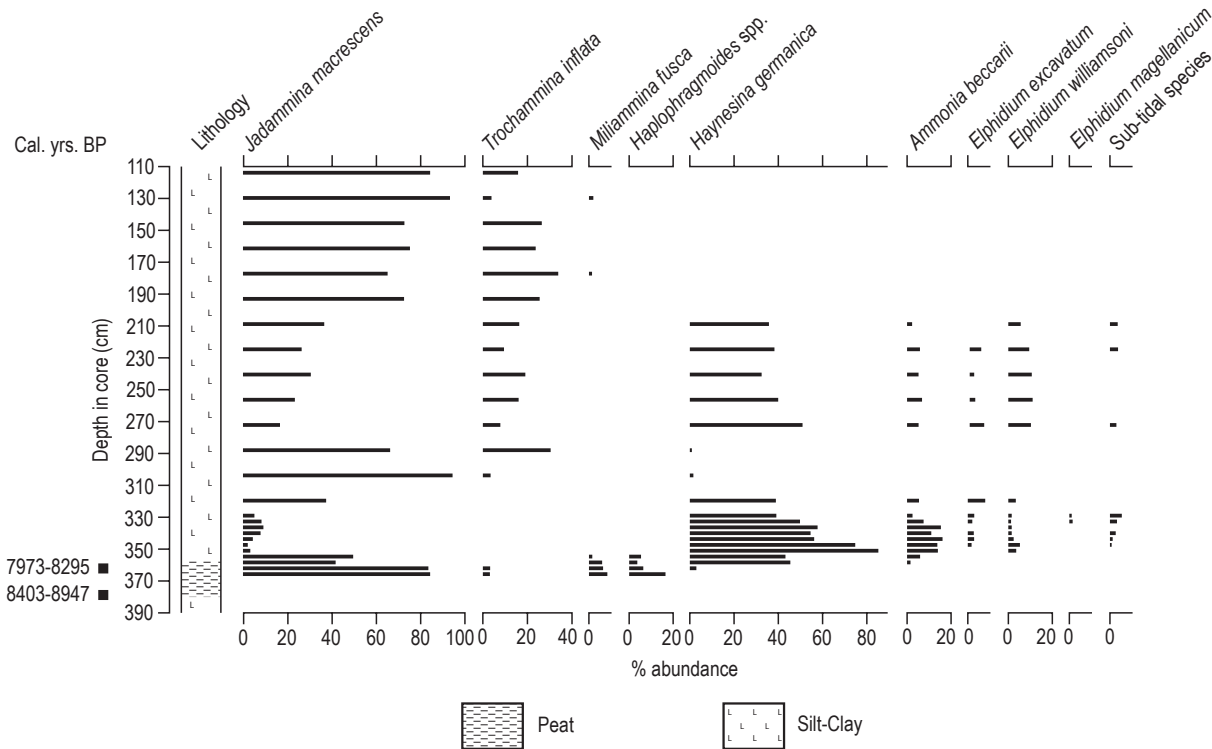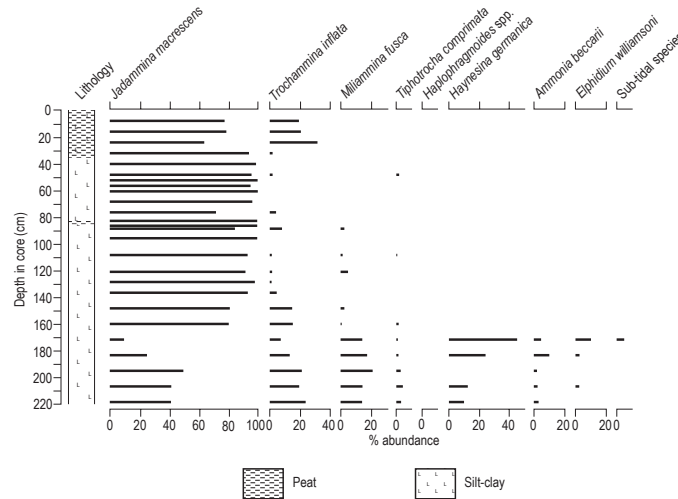
FIGURE 50. Southampton Water, core BF11. Foraminiferal abundance is calculated as the percentage of dead foraminiferal tests. Radiocarbon dates (expressed in calibrated years BP using the 95% confidence limits for the probability option) are shown.
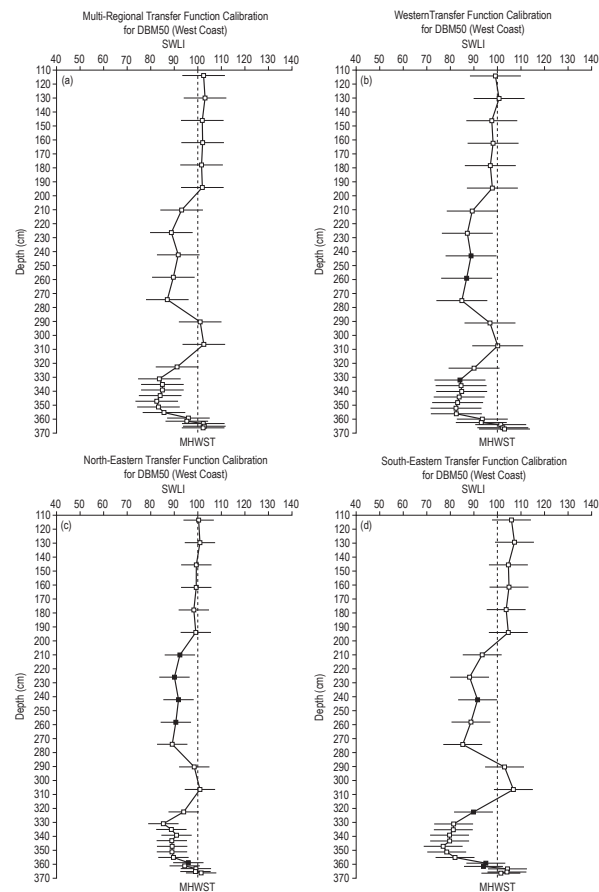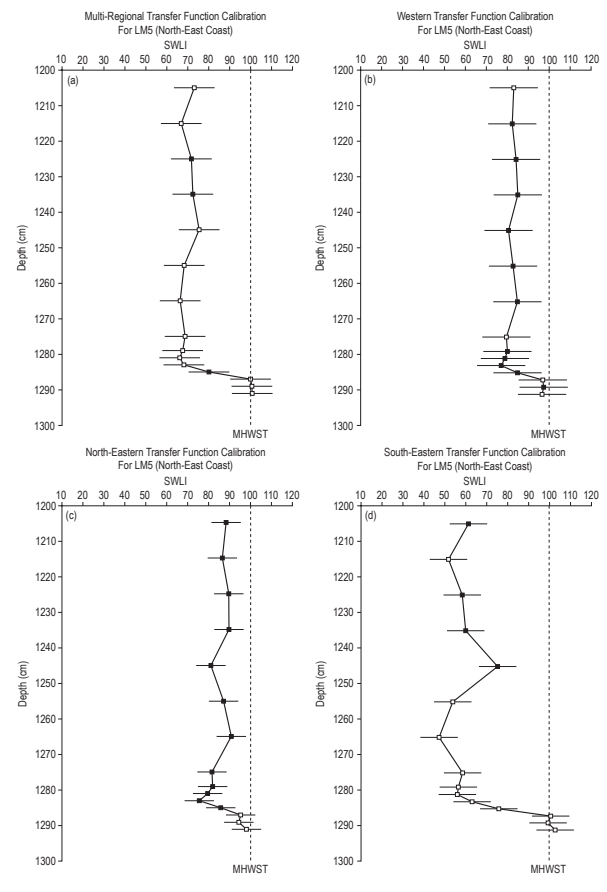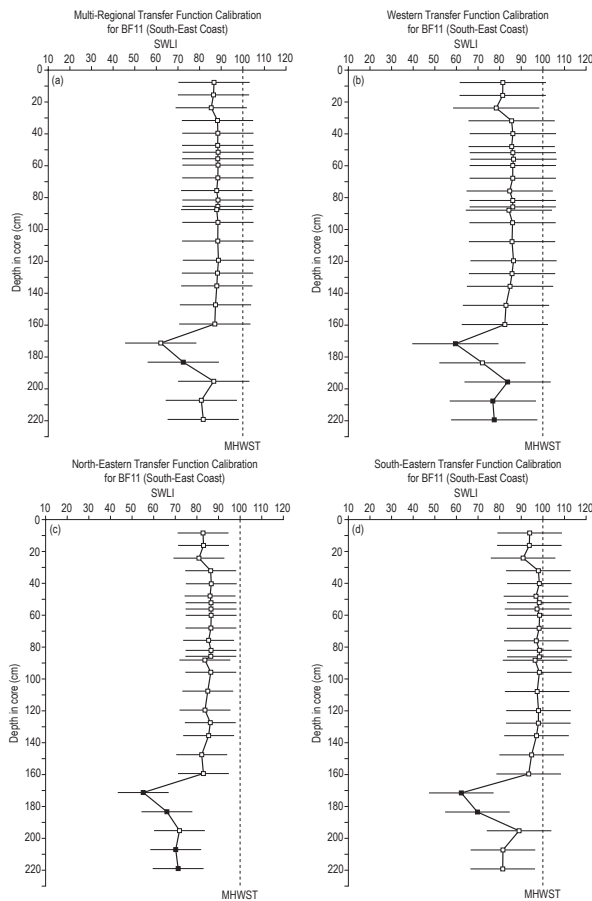

FIGURE 51. WA-PLS reconstruction for Southampton Water, core BF11 using (a) multi-regional, (b) western, (c) north-eastern and (d) south-eastern transfer functions. Samples with 'no modern analogues' are plotted as black squares.

the very low species diversity and abundance associated with the sedimentary sequence at Bury Farm. Similar sequences are recorded in neighboring Poole Harbour where considerable decalcification of the assemblages appears to have occurred, removing the calcareous component and producing an agglutinated 'dissolution' assemblage (Edwards, 1998; Edwards and Horton, 2000). In contrast to Poole Harbour and the study of Alve and Murray (1995), where lower abundance agglutinated foraminifera ensure paleoecological information is retained within the fossil assemblage, the Bury Farm core is dominated by *J. macrescens* to the virtual exclusion of all else. As a consequence, all elevation information is lost and the resulting reconstructions are of little practical value in inferring depositional environment.

3.6 POST-DEPOSITIONAL MODIFICATION

The transformation of living populations into the dead assemblages that are ultimately incorporated into sedimentary sequences is poorly understood and largely unquantified. A number of recent studies analyzing foraminiferal time series (e.g. Murray, 2003; Horton and Murray, 2006) and the preservation of modern foraminifera in fossil salt-marsh deposits (e.g. Goldstein and Watkins, 1999; Culver and Horton, 2005; Tobin and others, 2005) have investigated this area, but at present, the quantity of data specific to salt-marsh systems is insufficient to draw any firm conclusions. Whilst dead assemblages exhibit less spatial and temporal variability than live populations, comparison of live and dead

specimens from single sampling stations reveals that not all living forms are retained within a death assemblage, and certain dead species are never found among the living populations (e.g. Murray, 2003). Clearly, post-depositional modification in the form of test addition and removal takes place during the transformation of living to dead assemblages.

Since modern analogues are compiled from surface death assemblages, these changes will not influence the calibration of fossil material. However, if similar changes are associated with the transformation from surface to sub-surface assemblages, alterations in the relative abundance of key taxa may result in erroneous water level reconstructions. In the context of sea-level research, the dissolution of calcareous taxa has received most attention (e.g. Scott, 1976; Scott and Medioli, 1980b; Jonasson and Patterson, 1992; Murray and Alve, 1999). Dissolution is most problematic in low pH environments and tends to be associated with organic-rich sediments and intertidal areas receiving acidic runoff from adjoining land surfaces. Dissolution is likely to be most significant in middle to low marsh settings where the organic content of sediments is relatively high and acidic runoff may be locally important.

Edwards and Horton (2000) observed significant destruction of calcareous tests in core material from Poole Harbour, southern England, and attributed this to post-depositional dissolution. Fossil assemblages were enriched in agglutinated taxa that typically formed minor contributions of lower elevation assemblages and resulted in poor transfer function performance due to the lack of modern analogues. The presence of test-linings preserved within the fine-grained sediments was used as a calcareous 'fingerprint', and enabled the application of an agglutinated foraminifera-based transfer function. Edwards and Horton (2000) note that the use of MAT is important to highlight samples that have potentially suffered from the influence of dissolution.

Agglutinated species are not immune to post-depositional destruction and certain studies from North American salt-marshes have identified fragile species such as *Pseudothurammina limnetis* and *Polysaccammina ipohalina* that are commonly found in surface sediments but rarely preserved in fossil sequences (e.g. de Rijk and Troelstra, 1999). Fortunately, these species rarely contribute more than 5% of a sample in temperate or tropical environments and so are routinely screened out of modern training sets. Nevertheless, more common foraminiferal species such as *M. fusca* may also be prone to test destruction (Goldstein and Watkins, 1999; Culver

and Horton, 2005). Scott and others (2001) and Edwards and others (2004b) draw attention to the possible destruction of fragile agglutinated tests if sediment samples are dried, highlighting the importance of sample processing and analysis methods (see Section 2.2.1).

The erosion, transport and re-deposition of tests will become increasingly significant as energy regime increases and will therefore be broadly associated with increasing grain size and decreasing elevation. The introduction of 'exotic species' onto the marsh platform has already been discussed in Section 3.2.2. This process is unlikely to have a significant influence on the fossil record however, since the dominant calcareous taxa introduced in this way will be rapidly dissolved after death. A degree of sediment mobility is to be expected in lower elevation contexts and is reflected in broader vertical ranges occupied by foraminiferal species and assemblages. These lower elevation samples will contain both allochthonous and autochthonous components and, providing the former component is minor or consistent in composition, can still be used to provide elevation estimates. An important question, therefore, is the extent to which low marsh to tidal flat assemblages are time-invariant and the point at which transport destroys any relationship with elevation.

3.6.1 An Investigation into the Consistency of Low Elevation Salt-marsh Assemblages

We investigate the issue of transport and mixing by comparing the results of repeat surface foraminiferal surveys from the salt-marshes at Brancaster, Thornham and Welwick. Four surveys were taken at each site over the period of one year in accordance with the results of Horton and Edwards (2003) (see Section 2.3). These assemblages are calibrated via the 'multi-regional' transfer function to produce estimates of elevation that may be compared with the true (observed) elevation at which the sample was collected.

These data are used as a simple first assessment of the extent to which variable transport and mixing may influence the predicted elevations from different parts of the marsh. The residuals (observed minus predicted) are calculated for each sample. The mean residual for each station, compiled from the four surveys over the course of a year, is shown in Figure 52 plotted against observed SWLI. These data illustrate the general presence of 'edge effects' which result in underestimation of species optima at the top of the environmental gradient (samples plot low), and the over-estimation of species optima at
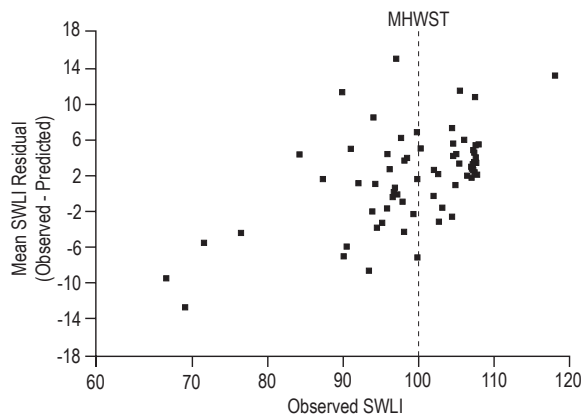
FIGURE 52. Mean residual of observed SWLI versus predicted SWLI using the multi-regional transfer functions from seasonal assemblages from Welwick, Thornham and Brancaster marshes.
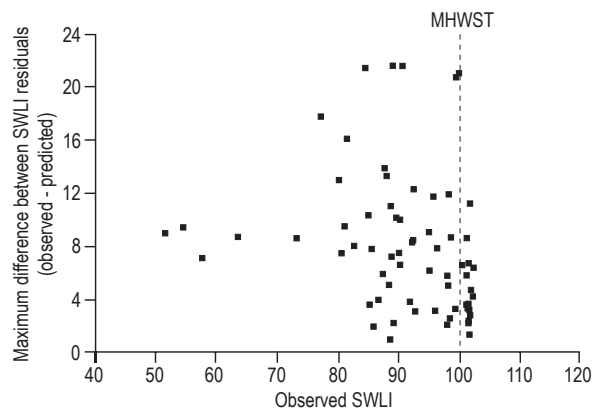
FIGURE 53. Maximum difference in residuals of observed SWLI versus predicted SWLI using the transfer functions from seasonal assemblages from Welwick, Thornham and Brancaster marshes.

the bottom of the environmental gradient (samples plot high). This is a common phenomenon in analyses that consider averages, or incorporate species with unimodal distributions. At the top of the environmental gradient, for example, the peak in *J. macrescens* abundance occurs around HAT. Whilst *J. macrescens* is also found at a range of elevations below HAT, no other foraminifera are found above this, with the result that the estimated optimal elevation of *J. macrescens* is lowered and 100% *J. macrescens* sample elevations are consistently underestimated.

Between approximately MLWNT and MHWST, samples are found to plot both above and below the observed values. In terms of the utility of lower elevation samples, the data from Brancaster, Thornham and Welwick indicate that lower marsh samples down to approximately MTL are not associated with larger errors than those from other parts of the salt-marsh system, although the smaller number of samples from these contexts should be noted.

As a second simple test, the maximum difference (highest residual minus lowest residual) for each sample estimate is also plotted against SWLI (Fig. 53). If significant temporal variations in dead assemblage are present, such as would arise by variable erosion, transport, deposition and sediment mixing, larger maximum differences in estimates would be expected. Inspection of Figure 53 also indicates, within the limitations of the available data, that lower elevation samples are not associated with greater temporal variability than those from the middle marsh. The least variability is associated with the 100% *J. macrescens* assemblage at the upper

limit of marine influence.

These results suggest, for the surveyed salt-marshes at least, that foraminiferal assemblages down to approximately MTL appear to retain a consistent elevation signature and may therefore be reliably used to reconstruct RSL changes. They also serve to illustrate how edge effects inherent in the transfer function approach tend to dampen reconstructed variations in elevation when considering switches from highest to lowest marsh environments. The implications of this for RSL reconstructions are discussed in Section 4.

3.7 SUMMARY AND CONCLUSIONS

The reconstructed values of SWLI produced by the various transfer functions and transfer function methods show differing degrees of agreement when applied to the west, north-east and south-east core material. There appears to be no simple relationship between transfer function precision and sample size. The west coast transfer function (the smallest sample size) has the largest standard errors of prediction, whilst the multi-regional transfer function (largest sample size) has the second largest standard errors of prediction. From this, it can be inferred that precision also appears unrelated to the spatial scale over which data are collected.

Whilst the reconstructions for core DBM50 are comparable between transfer functions, the pattern of change is quite different for core LM5. The west and north-east transfer functions appear to be less sensitive to changes above 1280 cm depth in core than the multi-regional and south-east data, probably due to a lack of

suitable low elevation modern analogues. These results support the conclusion of Horton and Edwards (2005) and indicate that the multi-regional transfer function offers improved performance in terms of available modern analogues in comparison to the use of locally-derived variants. In general, the local transfer functions do not perform significantly better when calibrating the local core material in comparison with the cores collected from the other 'regions'. For example, the north-east coast transfer function, which performs least well in all regions, is most successful (in terms of modern analogues) in calibrating material from the west coast, whilst the west coast transfer function shows comparable performance in calibrating both west and south-east coast cores. These data provide no evidence that local, modern surface assemblages are more representative of sub-surface foraminiferal assemblages than those from other regions.

The results of the calibrations from core BF11, whilst consistent between transfer functions and generally associated with low occurrences of no modern analogue samples, are inconsistent with the lithostratigraphic changes evident in the host core. These results highlight two important points that must be considered when undertaking sea-level research using transfer functions. In the first instance, it is essential to have a firm understanding of the taphonomic processes operating within the study area and influencing the modern and fossil data used in the reconstruction process (Hippensteel and others, 2002; Martin and others, 2003; Duchemin and others, 2005). The simple reliance on statistical performance measures such as MAT cannot replace an intimate familiarity with the nature and composition of foraminiferal assemblages in a study region. The transfer function approach is a tool to assist in the analysis of foraminiferal data and offers a number of powerful advantages over simple visual interpretation. However, it should not be employed as a 'black-box' procedure to produce quick 'answers' from available data.

In addition, the selection of appropriate core material, coupled with a strong lithostratigraphic context, is also essential to the success of a reconstruction program. A detailed lithostratigraphic investigation must always precede a biostratigraphic one, and close attention to the nature of the sediments must be given to ensure that the reconstructions are environmentally reasonable on both lithostratigraphic and biostratigraphic grounds. The application of the foraminiferal transfer function approach to sea-level reconstruction is considered in detail in the following section.

4. RECONSTRUCTING RELATIVE SEA-LEVEL CHANGE USING FORAMINIFERAL TRANSFER FUNCTIONS

A range of methodologies are employed to reconstruct sea-level changes and a considerable body of literature is devoted to assessing their relative applicability and effectiveness, as well as the errors and limitations associated with them (e.g. van de Plassche, 1986; Horton and others, 2000; Shennan and Horton, 2002). These methodologies can be sub-divided into two general approaches, each of which considers changes in RSL in slightly different ways.

The first approach examines vertical movements of RSL, measured relative to a geodetic datum (e.g. Godwin and others, 1958; Fairbridge, 1961, 1992; Jelgersma, 1961; Bloom and Stuiver, 1963; Shephard, 1963; Mörner, 1969; Kidson and Heyworth, 1973, 1978; Tooley, 1974, 1978, 1982; Chappell, 1974; Kidson, 1977; Clark and others, 1978; Preuss, 1979; Peltier, 1980; van de Plassche, 1982, 1986; Shennan, 1982; Shennan and others, 1983; 2000a, 2000b, 2002; Long and Shennan, 1993; Lambeck, 1995; Pirazzoli, 1996; Peltier and others, 2002; Shennan and Horton 2002; Horton and others, 2004, in press). This is commonly referred to as age-altitude analysis, and in Great Britain it has been pursued via the use of sea-level index points (SLIs) surveyed relative to Ordnance Datum (mean sea level Newlyn, Great Britain). A SLI possesses information on location, age, altitude, and indicative meaning (the vertical relationship of the sample to a defined contemporaneous tide level). In combination, these fix the former position of RSL at one instant in time. These data do not supply information on the nature of sea-level change between points or of the way that these changes are expressed in the coastal environment.

The second approach examines lateral movements in coastal sub-environments which are expressed as increases or decreases in marine influence at a sampling location (e.g. Curray, 1964; Geyh, 1971; Roeleveld; 1974; Morrison, 1976; Griede, 1978; Shennan, and others, 1983; 2000a). These shifts in depositional environment reflect changes in the balance between sea level and sediment accumulation and consequently record a composite signal of coastal change. In Great Britain, researchers have attempted to identify periods of time where increases or decreases in marine influence (referred to as positive and negative sea-level tendencies

respectively) are witnessed throughout a region (e.g. Tooley, 1978, 1982; Long, 1991, 1992; Long and Shennan, 1993) The rationale then dictates that regional changes are most reasonably explained as responding to a regional forcing (which, in the absence of other obvious controls, is equated to RSL change). A similar approach has been used in the salt-marshes of North America, where relative marsh elevation diagrams are constructed from chemical and/or biostratigraphic data (e.g. Thomas and Varekamp, 1991; Varekamp and others, 1992). These diagrams (also referred to as marsh paleoenvironmental curves) plot phases of marsh submergence and emergence which are used to infer changes in the rate of RSL rise. Whilst these types of data have a clear spatial relationship to observed coastal changes, they are indirectly linked to sea level, and cannot be used to reconstruct former altitudes of RSL.

These two principal approaches, and derivatives of them, can be applied in concert to strengthen the power and reliability of reconstruction techniques (e.g. Edwards, 2001). In this section, we outline the application of the transfer function to both these methodologies, and discuss how the use of transfer functions can facilitate their synergistic combination.

4.1 VALIDATION OF SEA-LEVEL INDEX POINTS

Sea-level index points are the mainstay of British sea-level studies. They have been used to produce local records of Holocene RSL change (e.g. Tooley 1982; Shennan, 1982, 1989; Long, 1991, 1992; Shennan and others, 2000b; Shennan and Horton, 2002; Horton and others, 2004, in press), and have been combined with geophysical models to reconstruct regional patterns of RSL change (e.g. Lambeck 1993a, b, 1995; Peltier, 1998; Shennan and others, 2000a, 2002; Peltier and others, 2002; Gehrels and others, 2004; Horton and others, in press). The establishment of SLIs is usually associated with lithostratigraphic transitions between organic-rich freshwater or salt-marsh peats, and minerogenic intertidal or sub-tidal sands, silts and clays. Biostratigraphic data, such as foraminifera or diatoms, can be used to pinpoint the onset or removal of marine conditions, but prior to the development of transfer functions, it was common practice to assign the indicative meaning on the basis of the lithostratigraphic sequence as it related to the source of dated material (see Shennan, 1982, 1986).

The transfer function approach can assist in the establishment of SLIs by expanding the range of depositional environments that can be assigned an indicative meaning (e.g. Edwards and Horton, 2000; Boomer and Horton, 2006; Edwards and Horton, in press; Horton and others, 2005b). Prior to transfer functions, SLIs could be established only at certain lithostratigraphic contacts, with the result that only restricted sub-environments could be used to provide sea-level data. In contrast, a foraminiferal transfer function can calibrate sediments from a range of intertidal environments and, providing these can be dated, can expand the availability of sea-level data. For example, Edwards and Horton (2000) combined foraminiferal data with two pollen chronohorizons to establish SLIs from within a single lithostratigraphic unit, whilst Horton and others (2000) used intertidal foraminifera to provide both age and elevation data via direct AMS radiocarbon dating of foraminiferal tests and transfer function calibration.

In a study of fifty-two SLIs from the North Sea coastline, Horton and others (2000) compared the reconstructed elevations produced by the traditional lithological approach with the results of calibration by foraminiferal transfer function. They demonstrated that the traditional approach commonly underestimates the vertical error associated with an index point due to an inability to account for differences in tidal range. In addition, foraminiferal assemblages appear to respond more rapidly and consistently to RSL change than gross lithological variations, permitting more reliable estimation of marsh surface elevation and indicative meaning (Allen, 1995; Horton and others, 2000).

Whilst the transfer function approach offers a number of advantages over the use of lithological-based techniques, the highest precision reconstructions will still be provided by the identification of the first occurrence of marine conditions at a site in the form of a basal peat deposit devoid of foraminifera and the onset of highest salt-marsh conditions associated with a 100% *J. macrescens* assemblage. At present, the transfer function methodology is not ideally suited to the calibration of this particular assemblage due to the edge effects outlined in Section 3.6.1, coupled with the singular, low vertical range of this distinctive assemblage.

4.2 RELATIVE MARSH ELEVATION DIAGRAMS

When a fossil foraminiferal assemblage is calibrated by the transfer function, an estimate of the former elevation of the host sediment sample is generated. Multiple samples collected from a sediment core will

produce a sequence of paleomarsh-surface elevation change. The resulting diagram, plotting elevation against depth, shows changes in the balance between sediment accumulation and RSL. In Connecticut, USA, Thomas and Varekamp (1991) and Varekamp and others (1992) identified similar sequences of paleomarsh-surface elevation change in multiple cores from Hammock River marsh. The authors used these apparently marsh-wide phases of submergence and emergence to infer accelerations and decelerations in the rate of RSL rise. In Great Britain, despite the complex relationships among sediment supply, elevation and accumulation rate, Edwards (2001) demonstrated that similar sequences of paleomarsh-surface elevation change could also be recorded in multiple cores from salt marshes in Poole Harbour. In contrast to the sequences in Connecticut, however, changing sedimentation rates exerted a strong influence on the paleomarsh-surface elevation diagrams, with some phases of emergence being driven by the infilling of accommodation space. As a consequence, a composite approach was employed that used phases of paleomarsh-surface elevation change in conjunction with SLIs to outline a framework chronology of RSL change for the area.

Clearly, the use of paleomarsh-surface elevation changes to infer variations in RSL is strongly dependent on the nature of the sedimentary environment under investigation and requires the collection of data from multiple cores. Inferences drawn from a single core, whilst potentially representative of local to regional scale changes, will always be subject to doubt due to the possibility that local sedimentary conditions have influenced the record. A reliable record of RSL change can only be extracted when variations in sedimentation are accounted for, and these changes are placed in a firm chronological framework (Gehrels and others, 2005). The first step in this process is to consider the altitude of each sediment sample and, using these data in conjunction with the estimates of elevation change, reconstruct the altitude of former RSL. In this way, a relative measure (elevation) is converted into an absolute measure (altitude).

4.2.1 Converting Elevation to Altitude – an Example

To illustrate this, we present three hypothetical sedimentary sequences, all of which have accumulated under the same RSL rise of 1.0 mm/yr for a period of 1000 years (Fig. 54). The accumulation of each core is driven by a different sedimentary regime resulting in contrasting balances between the rates of sedimentation and RSL rise. Core 1 comprises high marsh sediments that have accumulated in balance with the rate of rising RSL. The resulting plot of paleomarsh surface elevation shows no variation, and the reconstructed position of MTL is simply derived by subtracting sample elevation from sample altitude.

Core 2 shows a typical sedimentary sequence driven by the infilling of accommodation space. The core commences in a tidal flat environment with a comparatively high sedimentation rate (7 mm/yr). This increases the elevation of the sediment surface and changes the depositional environment from tidal flat through low and middle marsh to a high marsh deposit. With each change in sub-environment, sedimentation rates decrease and this is reflected by differing rates of change of marsh surface elevation. Overall, the sequence shows a decrease in marine influence (a negative sea-level tendency). The altitude of MTL is reconstructed in the same way as core one and, importantly, produces the same record of change despite the contrasting patterns of marsh surface elevation.

Core 3 shows a sequence in which sediment supply has been limited to 0.5 mm/yr (slower than the rate of RSL rise). The resulting transgressive sequence shows the change from terrestrial sedimentation (no foraminifera and no MTL reconstruction) through high to middle marsh deposition. The graph of marsh surface elevation shows an increase in marine influence (positive sea-level tendency), but once again, the record of MTL change is the same with the exception that the earliest portion of the sequence, equating to freshwater conditions with no indicative meaning, produces no record.

This simple example demonstrates a potentially powerful advantage of RSL records derived from foraminiferal transfer functions over those constructed from lithostratigraphic data: the same record of MTL change is produced irrespective of sedimentary regime. Hence, whilst the elevation (SWLI) will vary from borehole to borehole, reflecting the accumulation history at that location on the marsh, given continuity of the sequence, the reconstructed altitude of MTL should be the same irrespective of borehole location and intertidal environment. This direct measurement of former MTL altitude means that, in theory, rises or falls in RSL can be detected irrespective of the sea-level tendencies expressed by the sedimentary sequence.

4.2.2 Spatial Representativity

Variations in sedimentation rate across a marsh surface can change both the availability of age-altitude data collected from transgressive and regressive peat / silt-clay contacts and the sea-level tendencies associated with them. As a consequence, the ability of traditional sea-level techniques to discern variability is intimately linked with, and dependent upon, the nature of sedimentation at the sampling location. In contrast, Figure 54 demonstrates that the foraminiferal approach is capable of producing the same record of MTL change from sediment cores encompassing a range of altitudes, sedimentation rates and depositional environments, as long as these sediments have accumulated in a context for which the modern training set of foraminiferal distributions possesses reliable faunal-elevation data. Comparable records of change are reproduced irrespective of local
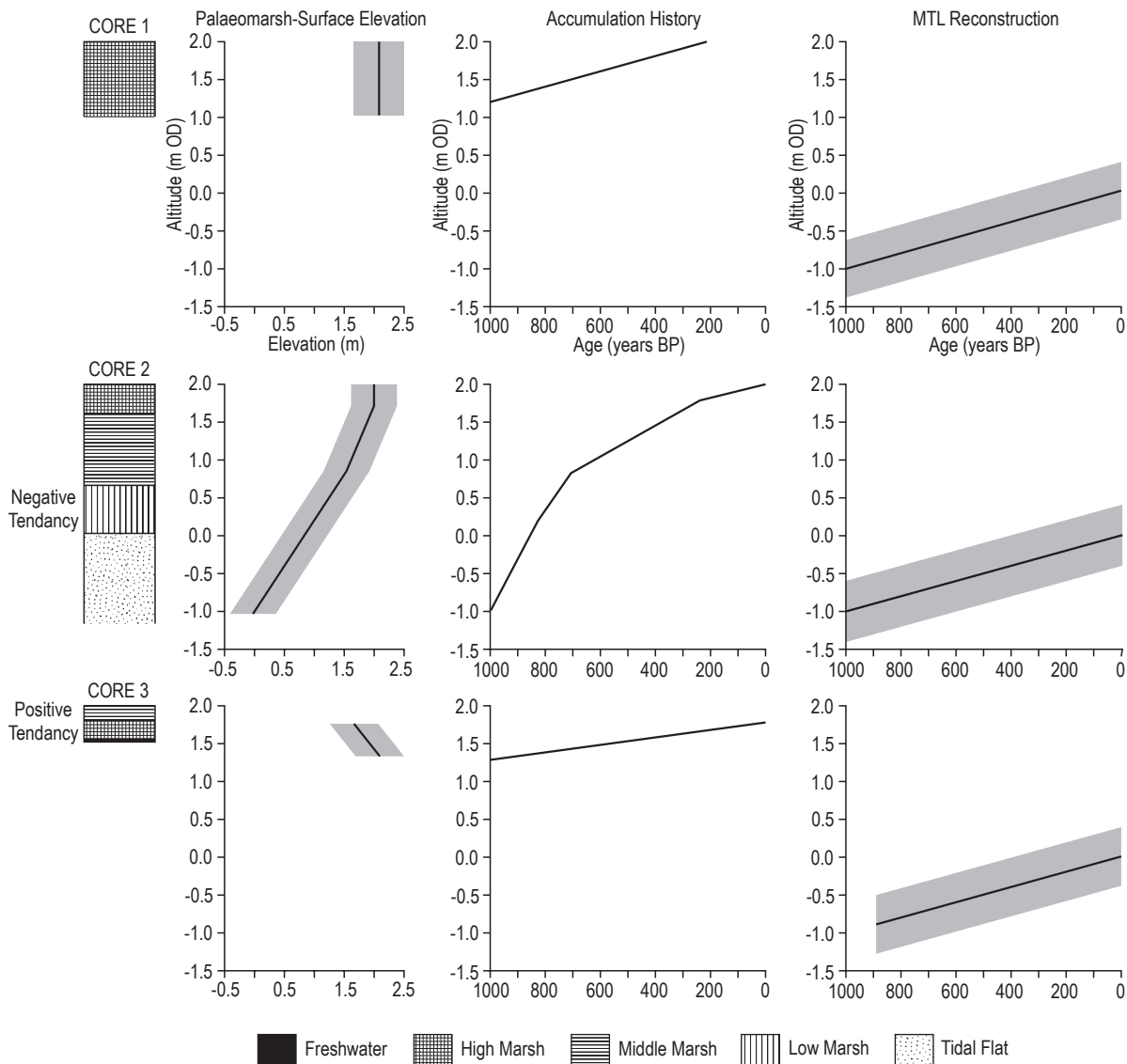
FIGURE 54. Hypothetical sedimentary sequences formed under a RSL rise of 1mm/yr for a period of 1000 years. Core 1 comprises high marsh sediments that have accumulated in balance with the rate of rising RSL. Core 2 shows a typical sedimentary sequence (tidal flat, low, middle and high marsh environments) driven by the infilling of accommodation space. Core 3 shows a sedimentary sequence (tidal flat, low, middle and high marsh, and terrestrial environments) in which sediment supply has been limited to 0.5 mm/yr.

sea-level tendency and data are extracted from the full range of sediments, including those sequences that exhibit no change in lithostratigraphy. Consequently, in the absence of complicating factors, the foraminiferal transfer function approach is less strongly coupled to local sedimentary processes and has the potential to provide representative reconstructions of MTL from a single borehole, irrespective of its location on the salt-marsh.

In reality, a number of complicating factors may arise, which mean that this basic premise of spatial consistency is associated with a number of important caveats. Principal among these is the influence of differential sediment autocompaction, which will serve to lower the altitude of a sediment sample and, by extension, produce an anomalously low reconstruction of MTL.

4.2.3 Introducing Altitude Errors - Autocompaction

The problem of sediment autocompaction is by no means unique to the foraminiferal transfer function approach. The majority of sediments (and therefore data derived from them) employed in sea-level studies have been subject to post-depositional changes in altitude, largely associated with autocompaction (e.g. Jelgersma, 1961; Kaye and Barghoorn, 1964; Tooley, 1978; Haslett and others, 1998; Allen, 1999, 2000; Edwards, in press). Shennan and others (2000a) and Shennan and Horton (2002) have reviewed some of the literature on this topic and stressed that consolidation of deposits with a high sand fraction is very low, whilst compaction of peat may be as high as 90 % by volume. In the absence of a suitable technique for quantitative assessment, most sea-level studies are forced to acknowledge its existence as an arbitrary, unquantified error term (Shennan and others, 2000a; Shennan and Horton, 2002). An

alternative approach to reduce the problem of sediment autocompaction is to date sequences of basal peats (van Straaten, 1954; Jelgersma, 1961; van de Plassche 1979, 1980, 1991, 1995; Denys and Baeteman, 1995; Kiden, 1995; Haslett and others, 1998; Törnqvist, and others, 1998, 2004; Gehrels, 1999; Donnelly and others, 2004). The basal peats are thought to be compaction-free because the underlying consolidated Pleistocene deposits are practically unaffected by compaction (Jelgersma, 1961). However, samples from the top of basal peats are themselves subject to some autocompaction. Furthermore, there are criticisms surrounding the interpretation and indicative meaning of samples from the base of basal peats. For example, van de Plassche (1979) noted that groundwater gradients may influence the initiation of peat growth. Consequently, before these deposits can be reliably used to reconstruct sea level, knowledge of the underlying Pleistocene topography is required. Hence, employing only compaction-free data would severely limit the availability of sea-level information.

Similarly, autocompaction remains an unquantified source of error in transfer function reconstructions and precludes the definitive reconstruction of past MTL altitude. When assessing the record, however, it is important to remember that the influence of autocompaction is uni-directional, acting to lower the apparent altitude of RSL and therefore increase the magnitude of any apparent rises in tide level. Consequently, this process cannot be invoked as a mechanism for producing oscillations and falls in RSL.

4.2.4 Gaps in the Sedimentary Record

A second important proviso regarding the extent to which a record from a single borehole can be considered spatially representative, is the presence of hiatuses in the sedimentary sequence, resulting either from periods of

Tidal Characteristics (m OD)					
HAT	MHWST	MHWNT	MTL	MLWNT	MLWST
2.25	2	1	0	-1	-2
Sedimentation Model (rate mm/yr)					
Freshwater (>HAT)	High Marsh (HAT to MHWST)	Mid Marsh (MHWST to 1.5 m)	Low Marsh (1.5 m to MHWNT)	Mudflat (MHWNT to MLWST)	Sub-tidal (<MLWST)
0.5	1.0	2.0	5.0	7.0	10.0

TABLE 10. Tidal characteristics and sedimentation model for cores 4 and 5 presented in Sections 4.2.4 and 4.3.

erosion or non-deposition. Since the accumulation of sediment records a history of environmental change, a break (hiatus) in the sequence constitutes missing time and a gap in the record. This will have consequences for dating sequences and the palaeoenvironmental interpretations derived from them (Cearetta and Murray, 2000).

Each hiatal plane has two dates: the age of the top of the sequence below the plane; and the age of the base of the sequence above the plane. Consequently, on an age-depth graph, a hiatus plots as two separate points, and can introduce complications in establishing reliable accumulation histories when interpolating between dated deposits. To illustrate this we generate two sedimentary sequences (cores 4 and 5) that are forced by the same

oscillating rise in RSL (linear term of 2mm/yr; oscillation 1m in amplitude and 1400 year period). Sedimentation is driven by a simple, stepped model that broadly equates to the asymptotic relationship between accumulation and elevation described by Allen (1995, 1999, 2000, 2003). Details of the model are summarized in Table 10.

In Figure 55, core 4 is plotted along with the oscillating RSL term and the associated change in marsh surface elevation produced by the sedimentation model. We 'sampled' this hypothetical core to simulate a biostratigraphic investigation and produce a series of elevation 'estimates'. Sampling was conducted at 8 cm intervals except across transgressive or regressive contacts that would be used to provide dateable material, where samples were taken every 2 cm. The

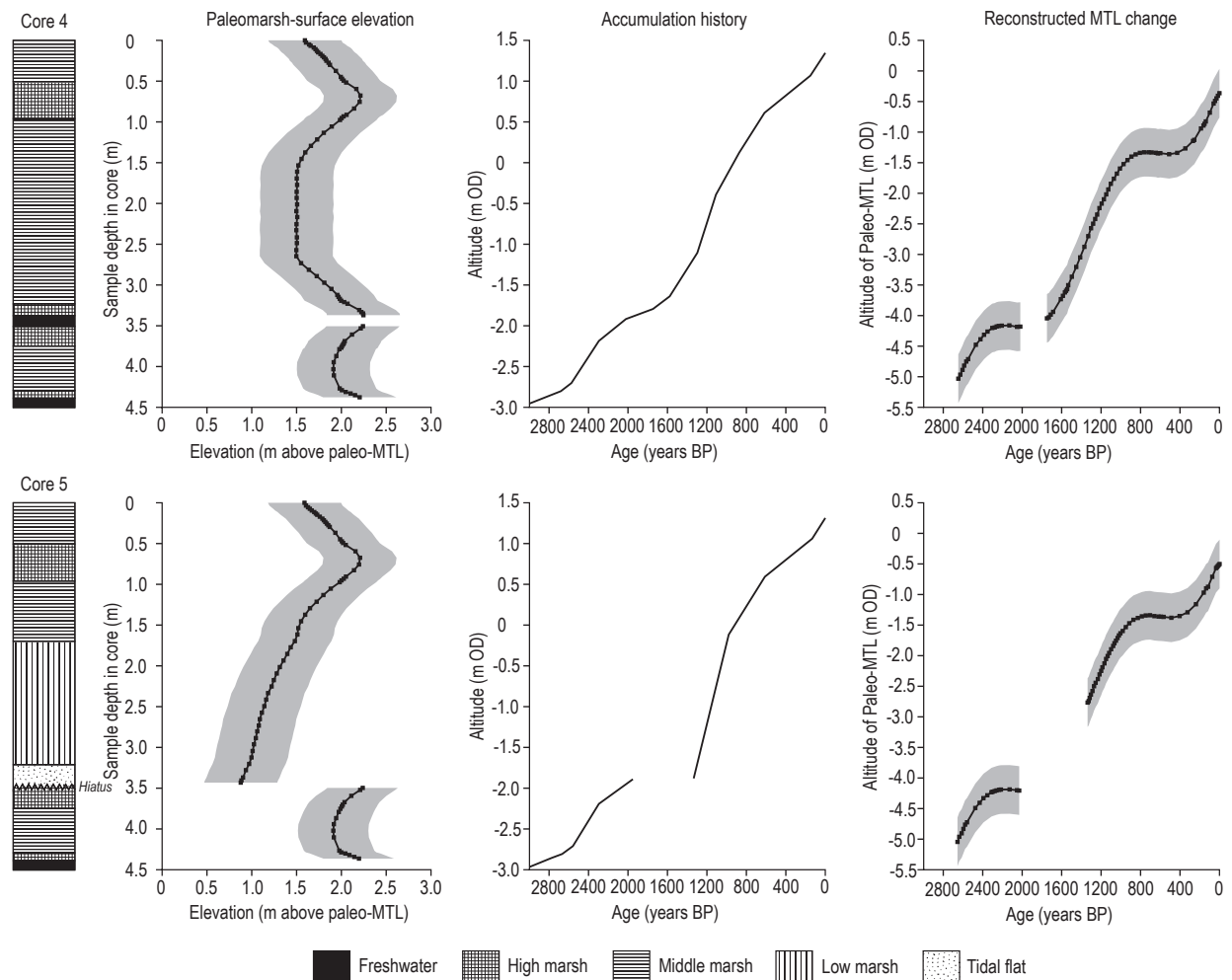FIGURE 55. Hypothetical sedimentary sequences formed under an oscillating RSL (linear term of 2 mm/yr; oscillation 1m in amplitude and 1400 year period) and driven by a simple stepped model of sedimentation (see Table 10 for details). Core 4 shows a complete sedimentary sequence whilst core 5 is associated with an episode of erosion, producing a gap in the record. The accumulation history and reconstructed MTL are shown.

'reconstruction' shown in Figure 55 assumes that the transfer function reliably estimates the elevation of all samples containing foraminifera and is associated with a typical error term of ± 10 SWLI (which for this site equates to around 40 cm).

A second sediment core (core 5) is generated in the same manner but this time an erosive phase is associated with the inundation of the second peat layer, erosively truncating the upper contact and removing 10 cm of freshwater deposit. Conditions conducive to deposition and preservation did not recommence until the rate of RSL rise began to slow once more around 1400 BP. At this point, sediments began to accumulate in a tidal flat environment. This second core is 'sampled' in the same way as the first, and the resulting record of elevation change and MTL rise is presented in Figure 55.

Inspection of cores 4 and 5 (Fig. 55) show some of the complications that may arise from gaps in the accumulation of marine sediments, either through erosion or associated with sediments forming above the limit of marine influence. Erosion of intertidal sediments introduces 'missing time' into a sequence that, in the case of core 5, equates to almost 600 years. This results in the removal of a portion of the record and the anachronistic juxtaposition of separate MTL phases. Since the foraminifera contained within a sediment sample relate to its elevation at the time of deposition, hiatuses do not influence the reconstructed altitude of MTL given good chronological control (Fig. 55). In fact, clues to the existence of breaks in sedimentation may be evident as abrupt changes in SWLI occurring between successive samples. This is why rapid excursions in MTL based on single data points should be treated with caution, especially in the absence of a precise chronology of sediment accumulation (Cearreta and Murray, 2000).

4.3 CONSTRUCTING CHRONOLOGIES

Establishing a reliable age-depth relationship is another essential component of producing an accurate picture of RSL change (Gehrels and others, 2005). A detailed consideration of chronology construction is beyond the scope of this review, but an overview of some key issues relating to the reconstruction of sea-level change from salt-marsh deposits is provided in Edwards (2004). Instead, we limit discussion to the implications of changing sedimentation rates and hiatuses for chronology construction as they pertain to transfer function application.

The extraction of a history of sea-level change from fossil samples rests upon the construction of unique age-depth relationships charting the course of sediment accumulation through time. In an ideal record, each sample used to provide information on the former altitude of RSL would also be independently dated forming, in effect, a sequence of SLIs. In reality, this is unlikely to be possible given current limitations in dating techniques, particularly when considering largely minerogenic sequences from the late Holocene (Edwards, 2004). As a consequence it is necessary to interpolate between dated horizons and the quality of the resulting chronology will depend upon the number and distribution of age estimates, the sedimentation rate variability and the method of interpolation employed.

To illustrate this, we 'date' samples from the hypothetical sedimentary sequences of cores 4 and 5 (Fig. 56). Samples are taken at classic transgressive and regressive contacts between terrestrial and marine sediments, and from within salt-marsh sequences where sufficient organic material is still present for AMS radiocarbon dating. Furthermore, samples are taken from the top 30 cm to simulate the range of sediments that may be dated using ^{210}Pb analysis. Composite chronologies employing ^{14}C and ^{210}Pb are thus developed for both cores in a similar fashion to that presented in Gehrels and others (2002). For clarity we do not consider age uncertainties that are inherent in both these radiometric methods and assume the age of the sediment is correctly represented by the dating process.

Fig. 56 shows a comparison of the reconstructed accumulation curves (derived from linear interpolation of dated horizons) plotted against the actual accumulation histories of the sediment sequences. The reconstructed MTL changes for both cores, derived from the combination of the interpolated accumulation curves and paleomarsh-surface elevation data, are also plotted alongside the actual pattern of MTL change. The diagrams for core 4 illustrate the fact that reconstructed changes are most accurate in the vicinity of dated horizons and remain reliable between dated points providing very large changes in sedimentation rate do not occur. In contrast, the hiatus in core 5 removes one of the radiocarbon-dated points (due to erosion of the upper freshwater peat contact), reducing the availability of age information and necessitating interpolation over larger portions of the sedimentary record. As interpolation distance increases, so does the possibility that a number of short period variations in sedimentation rate will have occurred between the measured age horizons and that these are masked within the longer-term interpolation. These rate

changes will distort the age-depth relationship and serve to shift the reconstructed RSL changes in time. Whilst the resulting MTL curve will be displaced along the time axis, the sequence of events will be unchanged and the reconstructed altitudes of MTL will be unaffected. The introduction of a hiatus breaks the sequential nature of sediment accumulation and has the result of stretching the chronology along the time axis, 'ageing' sediments immediately post-dating the break in sedimentation: this results in gross distortion of the MTL record (Fig. 56).

Hence, whilst a foraminiferal transfer function-based reconstruction from a single borehole is less susceptible to local processes such as sediment infilling in terms of altitude reconstruction, problems surrounding the

reliable dating of the sequence mean that multiple cores are, at present, an important means of assessing the reliability of inferred water level changes. In particular, comparison of reconstructed MTL altitudes in the vicinity of dated contacts has the potential to act as tie points for the correlation of separate cores which may throw further light on the presence of hiatuses, rapid changes in sedimentation rate or the influence of compaction (Edwards and Horton, in press). Additional AMS radiocarbon dating of calcareous foraminiferal assemblages may further help to constrain the accumulation history of inorganic portions of the sedimentary sequence (Horton and others, 2000).
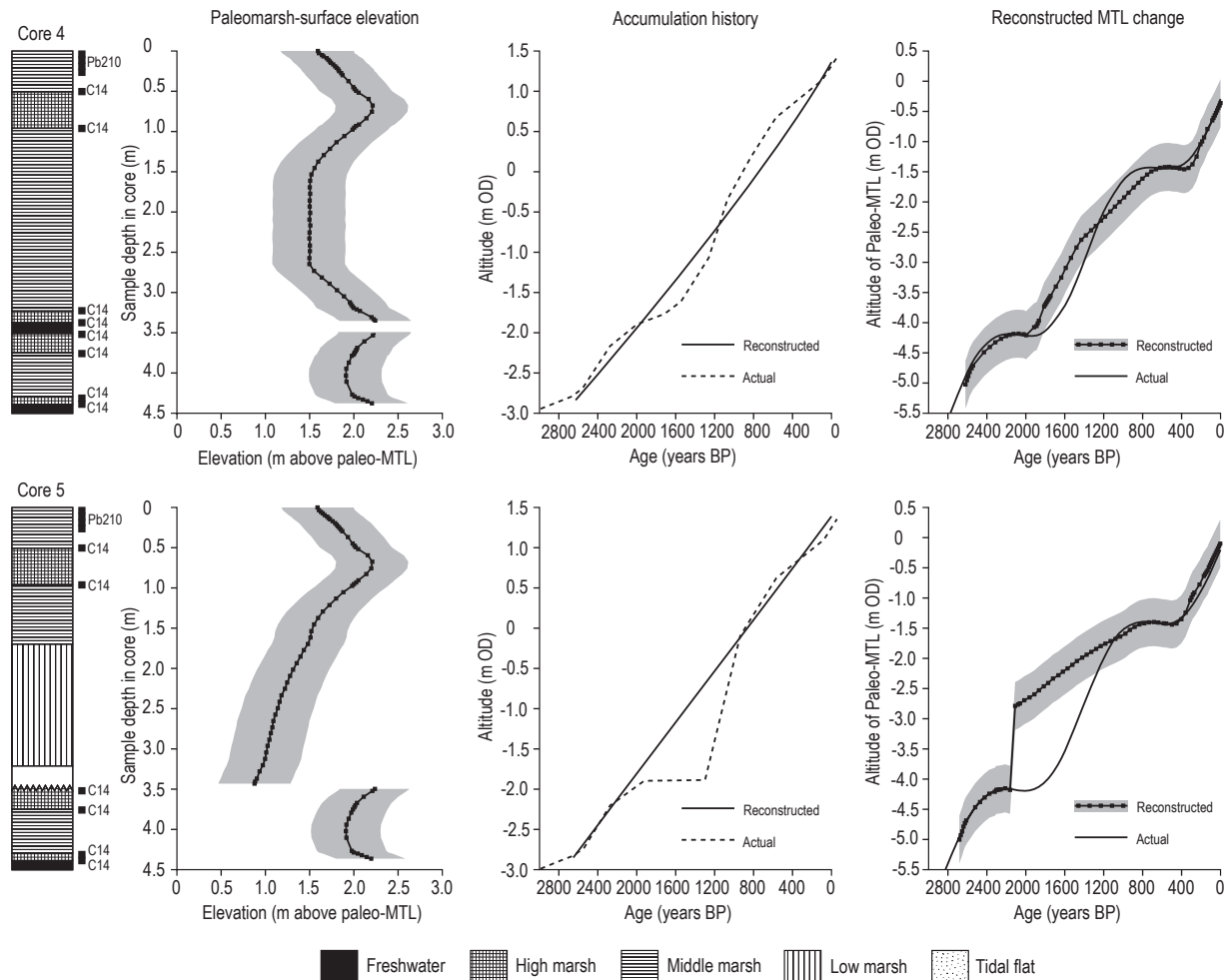
FIGURE 56. Hypothetical sedimentary sequences formed under an oscillating RSL (linear term of 2 mm/yr; oscillation 1m in amplitude and 1400 year period) and driven by a simple stepped model of sedimentation (see Table 10 for details). Core 4 shows a complete sedimentary sequence whilst core 5 is associated with an episode of erosion, producing a gap in the record. The age of a series of points have been selected to simulate radiocarbon and lead-210 dating of the sedimentary sequences. The resulting reconstructed accumulation histories and MTL records are shown alongside the actual records.

4.4 RECONSTRUCTION OF HOLOCENE SEA LEVELS: AN ILLUSTRATION FROM NORTH NORFOLK, ENGLAND

We use the multi-regional transfer function to construct a new RSL curve from fossil assemblages within sediment core NNC17 from Holkham, North Norfolk, Great Britain (Fig. 5). The fossil sequence of Holkham is characteristic of many British coastal paleoenvironments. It begins with a glacial diamicton, overlain by a thin, well-humified basal peat, in this instance found at an elevation of -6.70 m to -6.36 m OD (Horton and Edwards, 2001, 2005). The peat is in turn overlain by an olive-grey silty clay, containing dispersed organic remains and numerous bivalve fragments. Foraminiferal tests are absent in the diamicton (Fig. 57). Agglutinated species (e.g. *J. macrescens* and *T. inflata*) dominate the peat samples, indicative of a salt-marsh environment. In the overlying

silty clay, percentage frequencies of agglutinated species fall, to be replaced by calcareous taxa such as *Ammonia* species, *H. germanica* and *Elphidium* species, which are indicative of estuarine or tidal flat environments. Towards the top of core NNC17 an increase in relative abundance of agglutinated taxa suggests a return to salt-marsh conditions.

The reconstructed water levels reflect these changes in foraminiferal assemblage (Fig 58; Table 11). The maximum water level (102.14 ± 8.94, -6.32 m OD) occurs within the peat, associated with the agglutinated, salt-marsh foraminifera, at the radiocarbon-dated sedimentary horizon (7050-6500 cal. yrs. BP) and is indicative of deposition above MHWST. The water level curve crosses a threshold at the transgressive contact and rapidly declines within the silty clay to reach a minimum at -2.08m OD (72.81 ± 9.82) between the infrared stimulated luminescence (IRSL) and ^{14}C assays of 5050-
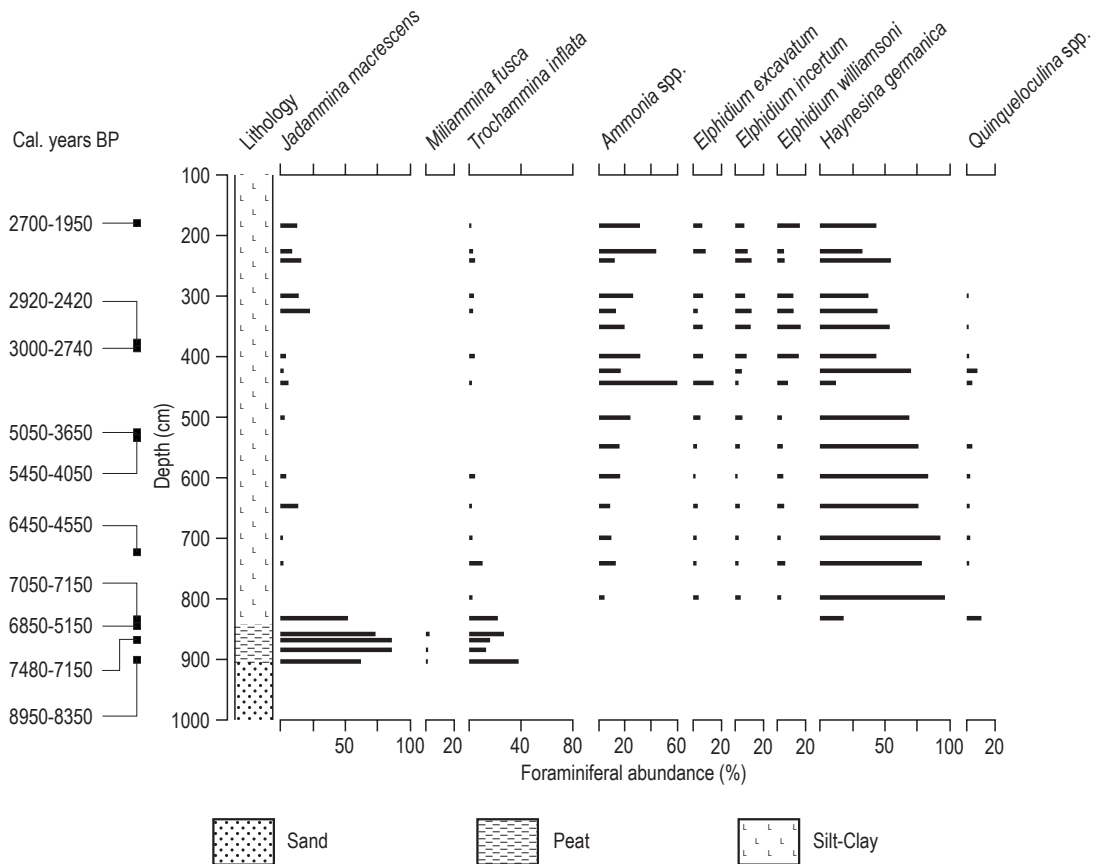
FIGURE 57. Holkham core, NNC 17. Foraminiferal abundance is calculated as the percentage of dead foraminiferal tests (only species comprising greater than 10 % of the assemblage are shown). Radiocarbon (expressed in calibrated years BP using the 95% confidence limits for the probability option) and IRSL ages are shown adjacent to the lithological log (see Andrews and others, 2000).

Altitude (m OD)	SWLI	SWLI error	Elevation (m)	MTL (m)
0.57	80.24	8.98	1.83	-1.26 ± 0.58
0.12	75.90	9.29	1.54	-1.42 ± 0.60
-0.03	82.20	8.94	1.95	-1.98 ± 0.58
-0.63	79.77	9.02	1.80	-2.43 ± 0.59
-0.88	83.60	8.92	2.04	-2.92 ± 0.58
-1.13	77.48	8.97	1.65	-2.78 ± 0.58
-1.63	77.71	9.02	1.66	-3.29 ± 0.59
-1.88	82.00	8.98	1.94	-3.82 ± 0.58
-2.08	72.81	9.82	1.34	-3.42 ± 0.64
-2.63	81.80	9.05	1.93	-4.56 ± 0.59
-3.03	82.14	8.99	1.95	-4.98 ± 0.58
-3.63	85.26	9.00	2.15	-5.78 ± 0.58
-4.13	87.40	8.98	2.29	-6.42 ± 0.58
-4.23	86.07	9.03	2.20	-6.43 ± 0.59
-5.06	86.33	8.99	2.22	-7.28 ± 0.58
-5.63	86.45	9.05	2.23	-7.86 ± 0.59
-5.98	97.51	8.90	2.95	-8.93 ± 0.58
-6.24	101.51	8.92	3.21	-9.45 ± 0.58
-6.28	101.98	8.93	3.24	-9.52 ± 0.58
-6.30	102.02	8.93	3.24	-9.54 ± 0.58
-6.32	102.14	8.94	3.25	-9.57 ± 0.58
-6.34	100.89	8.92	3.17	-9.51 ± 0.58
-6.88	85.02	8.98	2.14	-9.02 ± 0.58

TABLE 11. Summary of the standardized water level index (SWLI) and elevation (m relative to mean tide level) predictions generated by multi-regional foraminifera-based transfer function for samples from the Holkham core NNC17. Mean tide level (MTL) is calculated by subtracting sample elevation from sample altitude.

Altitude (m OD)	Laboratory Code/ Sample Reference	Age Max	Age Mean	Age Min	Method	^{14}C age ± 1σ	Oxcal Results Max	Oxcal Results Min	Age BP Max	Age BP Mid	Age BP Min	Rate
2.37			0									
0.54	NNC-17-3	2500	2300	2100	IRSL		750	0	2700	2325	1950	0.00
-1.44	NNC-17-2	3000	2800	2600	IRSL		970	470	2920	2670	2420	0.01
-1.61	AA22707	2672	2360	2271	^{14}C	2715±70$^{\#}$	1050	790	3000	2870	2740	0.00
-2.94	NNC-17-5	5100	4700	4300	IRSL		3100	1700	5050	4350	3650	0.00
-3.00	NNC-17-6	4900	4500	4100	IRSL		3500	2100	5450	4750	4050	0.00
-4.88	NNC-17-4	6400	5700	500	IRSL		4500	2600	6450	5500	4550	0.00
-6.10	NNC-17-1	6500	5900	5300	IRSL		4900	3200	6850	6000	5150	0.00
-6.36	AA22681	7006	6750	6494	^{14}C	5930±100	5100	4550	7050	6775	6500	0.00
-6.53	AA23465	7384	7240	7173	^{14}C	6375±60	5530	5200	7480	7315	7150	0.00
-6.70	AA22682	8943	8490	8346	^{14}C	7760±95	7000	6400	8950	8650	8350	0.00

TABLE 12. Chronology for Holkham NNC17 (modified from Andrews and others, 2000). All mean 14C ± 1σ dates are calibrated (# marine reservoir effect included) using the Intcal98 calibration curve (Stuiver and others, 1998) and combined with the IRSL ages and associated stratigraphic information employing OxCal (ver 3.5: Bronk Ramsey, 1995, 1998). We use the 95% confidence limits for the probability option.

3650 yrs BP (-2.94 m OD) and 3000-2740 cal yrs BP (-1.61 m OD), respectively. Each sample produces an estimate of past mean tide level altitude by subtracting the reconstructed elevation from sample altitude (Section 4.2.1).

The chronological framework for the core is provided by four radiocarbon dates and five infrared stimulated luminescence ages (Andrews and others, 2000; Horton and Edwards, 2005). Radiocarbon data are calibrated using the Intcal98 calibration curve (Stuiver and others, 1998) and combined with the IRSL ages and associated stratigraphic information using OxCal (ver 3.5: Bronk Ramsey, 1995, 1998). The resulting sequence of ages is interpolated to produce the general accumulation history used to temporally constrain the variations in mean tide level identified from the foraminiferal data (Table 12).

Figure 59 illustrates that the general pattern of mean tide level change indicated by the transfer function is consistent with existing geologically-based sea-level data (Shennan and Horton, 2002), and the results of geophysical modeling studies (ICE 4G model, Peltier

and others, 2002). In common with other ice-marginal regions, the general pattern of RSL change is of an initially rapid rise during the early Holocene, followed by a mid-Holocene slow-down (Shennan and Horton, 2002). The foraminifera-based curve exhibits greater variation than the ICE4G glacial isostatic adjustment model predictions (Peltier and others, 2002) but this is to be expected given the inability of the latter to capture such short period (sub-millennial) variability. Furthermore, the transfer function reconstructions run through the centre of the scattered SLIs. The scatter apparent in the sea-level index points is typical of most age-elevation data from Great Britain and illustrates the difficulties associated with resolving sub-millennial scale variability. The scatter includes the total influence of local-scale processes and also any differential isostatic movements. Local scale processes operating within the North Norfolk area may include variable sedimentation rates, changes in hydrographic characteristics and post-depositional sediment consolidation (see Section 4.2.3; Shennan and Horton, 2002).
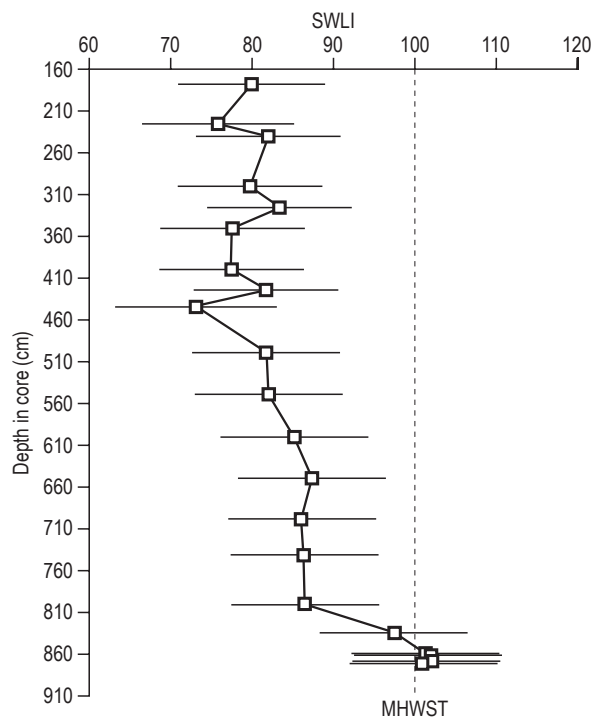
FIGURE 58. WA-PLS reconstruction of SWLI (elevation) for Holkham core, NNC 17 using the multi-regional transfer function. The position of local mean high water spring tides is shown for reference.
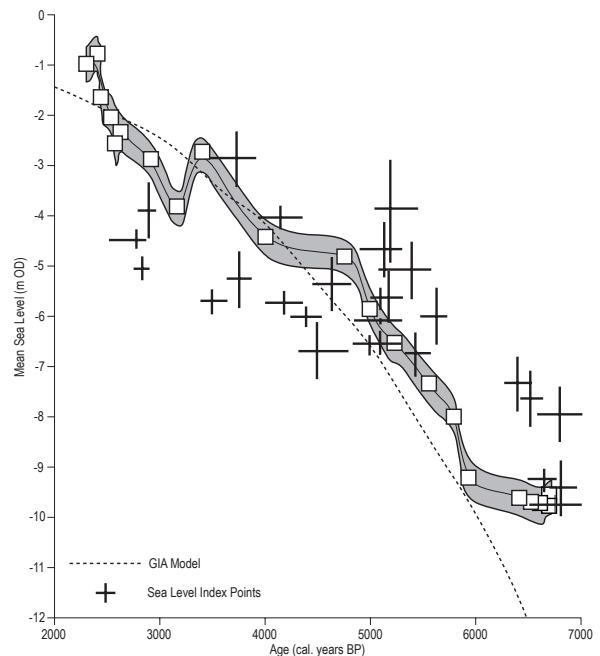
FIGURE 59. Reconstruction of Holocene mean tide levels for Holkham core NNC 17 using the foraminifera-based transfer function (multi-regional). The transfer function and associated error are plotted as open boxes and grey shaded area, respectively. Existing sea-level index points for North Norfolk are plotted as crosses (see Shennan and Horton, 2002). The modeled mean sea level produced by the Glacial Isostatic Adjustment (GIA) model ICE4G (Peltier and others, 2002) is shown as a dashed line.

5. CONCLUDING REMARKS

More than a quarter of a century after salt-marsh foraminifera were presented as high-resolution indicators of sea-level change, they remain at the centre of new developments seeking to improve our understanding of how sea level changes, how these variations influence coastal evolution, and how this is recorded within coastal sedimentary sequences. The combination of intertidal foraminiferal data and the transfer function approach to paleoenvironmental reconstruction offers a number of distinct advantages over the use of vertical foraminiferal assemblage zones and lithostratigraphically-based age-altitude analysis. These can be summarized as follows:

•Expanded range of 'useful' intertidal sediments;

•Reconstructions with quantified error terms;

•Replicable methodology and improved record comparability;

•Reduced influence of sedimentary regime (greater representativity).

It is also clear from the examples presented here that development of the foraminiferal transfer function approach to sea-level reconstruction remains a work in progress. Ample scope exists for improving the reliability, accuracy and precision of the reconstructions. This may come through the development of new statistical tools or the novel combination of foraminiferal data with other quantitative environmental proxies. In addition, a number of outstanding issues relating to the use of foraminiferal transfer functions also warrant further investigation. In terms of modern training sets, these include questions such as: is there an optimum sample size; what constitutes a geographic 'region'; and at what elevation does the vertical relationship between foraminifera and the tidal frame break down? In terms of application to fossil material, important questions still surround the nature and extent of the various taphonomic processes that act to alter the composition of sub-surface foraminiferal assemblages, as well as ways to assess the integrity of a sedimentary sequence and its accumulation history. Finally, the application of a refined and updated taxonomy, as outlined in Appendix 1, may assist in identifying particular sub-species that have diagnostic distributions (Hayward and others, 2004b). This will enhance our ability to extract elevation information from foraminiferal assemblages, and may enable transfer functions to be tailored to account for changes in other variables such as salinity.

The data and examples presented here are all taken from the British Isles and are most readily applicable to similar salt-marsh systems in other parts of northwest Europe. Foraminiferal transfer functions have also been developed and applied in temperate (Horton and others, 1999b; Edwards and Horton, 2000; Gehrels, 2000; Gehrels and others, 2001, 2002, 2005; Horton and Edwards, 2003, 2005; Edwards and others, 2004b; Patterson and others, 2004, 2005; Sawai and others, 2004a, b) and tropical (Horton and others, 2003; Woodroffe and others, 2005) regions from around the world. The differing sedimentology, geochemistry and morphostratigraphy of these systems may well significantly alter both the presence and behavior of foraminiferal species. In particular, the significance of infaunal activity and the preservation potential of different taxa are likely to vary between environments as contrasting as an Indonesian mangrove and a salt-marsh from north-east England.

Many other issues arising here will be of more universal applicability and interest, however. The general principles and techniques associated with the development and application of foraminiferal transfer functions should be equally valid irrespective of geographical setting. Perhaps the most important lesson from the British Isles is that, whilst the transfer function approach provides a useful addition to the range of existing techniques employed to study sea-level change, it has, like them, important limitations that preclude its use as a simple 'black box' application. A firm understanding of the ecology and taphonomy of salt-marsh foraminifera must remain central to the development and application of these transfer functions.

Furthermore, the quality and reliability of resulting reconstructions is dependent upon a firm understanding of the geological and geomorphological context of the sampling location, and the processes operating within it. Central to this is the accurate determination of sediment accumulation history, since errors in chronology can result in erroneous patterns of reconstructed RSL change. Developments in foraminiferal transfer functions will need to be supported by improvements in the dating of sediments and the methods used to interpolate between dated horizons (van de Plassche and others, 2001; Edwards, 2004; Gehrels and others, 2005; Boomer and Horton, 2006; Horton and others, 2005b).

The union of foraminiferal transfer function data with SLIs and other paleoenvironmental information gives the modern researcher an unprecedented opportunity to probe coastal archives of environmental change (e.g. van de Plassche and others, 1998, 2003; Gehrels and others, 2005; Horton and others, in press). As the application

of the transfer function approach becomes more widespread, and an increasing body of data becomes available, important new information will be provided, not only on RSL change, but also on the strengths and limitations of the approach itself. The development of new records of RSL change must therefore proceed in conjunction with continued development and testing of the transfer function approach itself.

ACKNOWLEDGEMENTS

APPENDIX 1

Glossary

Allochthonous Foraminifera, sediments etc., found in a place other than where they and their constituents were formed.

Altitude Vertical position measured in metres relative to a national vertical datum. In the UK, this is Ordnance Datum (OD) Newlyn, which is the mean sea level recorded at Newlyn, Cornwall, between 1915 and 1921. In Ireland it is Ordnance Datum Malin Head, which is the mean sea level recorded at the Malin Head tide gauge, County Donegal, between 1960 and 1969.

Autochthonous Foraminifera, sediments etc., found where they and their constituents were formed.

Bootstrapping A computer-intensive method to obtain confidence intervals or to estimate parameters. The bootstrap is considered a "resampling method", and is allied to Jack-knifing.

CCA Canonical Correspondence Analysis: a widely used method for direct gradient analysis, best developed by C.J.F. ter Braak. CCA assumes that species have unimodal distributions along environmental gradients.

Cluster analysis A multivariate numerical tool used to quantify the relationship between species and samples and develop assemblage models.

Coefficient of determination (r^2) Denotes the percentage of variation in the dependent variable accounted for by the independent predictor variables. It varies between 0 and 1.

Coefficient of variance (V_c) The degree to which a set of data points varies. It is often called the relative standard deviation, since it takes into account the mean.

DC Dissimilarity coefficient.

DCA Detrended Correspondence Analysis: an ordination technique used to represent samples as points in a multi-dimensional space. Similar samples are located together and dissimilar samples apart.

DCCA Detrended Canonical Correspondence Analysis: the detrended form of Canonical Correspondence Analysis.

Elevation Height in metres measured relative to local mean tide level.

HAT Highest Astronomical Tide: the highest level which can be predicted to occur under average meteorological conditions and under any combination of astronomical conditions.

HHW Higher High Water: the highest of the high

waters reached on a specified tidal day (related to declination of moon and sun).

Indicative meaning The indicative meaning of a coastal sample is the relationship of the local environment in which it accumulated to a contemporaneous reference tide level.

Indicative range The vertical range within which a given sea-level indicator may be found.

IRSL Infrared stimulated luminescence dating is based on the measurement of the amount of light that is released upon infrared stimulation, by minerals such as quartz and feldspar. The light signal is a measure of the radiation dose that has accumulated in these minerals through time.

Jack-knifing A computer-intensive method to estimate parameters, and/or to gauge uncertainty in these estimates. The name is derived from the method that each observation is removed (i.e., cut with the knife) one at a time in order to get a feeling for the spread of data.

LAT Lowest Astronomical Tide: the lowest level which can be predicted to occur under average meteorological conditions and under any combination of astronomical conditions.

Macrotidal A tidal environment with a tidal range > 4 m.

MAT Modern Analogue Technique: compares numerically, using an appropriate dissimilarity or similarity measure, the biological assemblage in a fossil sample with the biological assemblages in all available modern samples that have associated environmental data. Analogue matching is an important means of evaluating the likely reliability of transfer function reconstructions.

ML Maximum Likelihood: a transfer function technique that is suitable for species which respond unimodally to an environmental variable. It is referred to as a 'classical approach' (see Birks, 1995)

Mesotidal A tidal environment with a tidal range 2 - 4 m.

MHWST Mean High Water Spring Tide: a tidal datum that equates to the average spring tide water level, determined over a specified period of time.

MHWNT Mean High Water Neap Tide: a tidal datum that equates to the average neap tide water level, determined over a specified period of time.

Microtidal A tidal environment with a tidal range < 2 m.

MLWNT Mean Low Water Neap Tide: a tidal datum that equates to the average neap tide low water level, determined over a specified period of time.

MLWST Mean Low Water Spring Tide: a tidal datum that equates to the average spring tide low water level, determined over a specified period of time.

MSL Mean Sea Level: the average level of the sea surface over a long period, preferably 18.6 years, or the average level that would occur in the absence of tides.

MTL Mean Tide Level: calculated by averaging MHWST, MLWST, MLWNT and MLWST.

Pearson's correlation coefficient (*r*) Pearson's correlation coefficient measures the strength of the linear relationship between two variables and can take on the values from -1.0 to 1.0. Where -1.0 is a perfect negative (inverse) correlation, 0.0 is no correlation, and 1.0 is a perfect positive correlation.

RSL Relative sea level: the height of the sea measured relative to a tide gauge on land. Changes in RSL will be a combination of ocean and land level changes.

RMSE Root mean square error: determined by calculating the deviations of points from their true position, summing up the measurements, and then taking the square root of the sum.

RMSEP Root means square error of prediction.

RPD Redox Potential Discontinuity.

SE Standard error

Sea-level indicator A sample/organism/feature that has a quantified, consistent vertical relationship to a component of the tidal frame and may be used to infer past sea level.

Sea-level tendency An increase (positive) or decrease (negative) in the proximity of marine conditions, commonly recorded as a change in water level or salinity. Tendencies refer to trends in the lateral position of coastal subenvironments and are not synonymous with rises or falls in sea level.

SLI Sea-level index point: a sample of known age from a known geographical position (horizontally and vertically) that possesses an indicative meaning. SLIs collected from an area can be used to fix the former altitude of relative sea-level in that locality.

SWLI Standardized water level index: a conversion of the elevation of each sample to take into account sites with differing tidal ranges:

$$\text{SWLI} = \left[\frac{\text{Alt}_{ab} - \text{MLWS}}{\text{MHWST}_b - \text{MLWST}_b} \right] \times 100$$

where Alt_{ab} is the altitude of samples *a* at site *b* (m OD); MLWST_b is the mean low water spring tide level at site *b* (m OD); and MHWST_b is the mean high water spring tide at site b (m OD).

Training set The fundamental data used to develop a set of equations for the transfer functions. In this

paper, the training set comprises measurements of the environmental parameter (elevation in the form of the standardized water level index) and the associated relative abundances of foraminifera.

Transfer function A transfer function expresses the value of an environmental variable (e.g., standardized water level index) as a function of biological data (e.g., foraminiferal assemblages) or environmental proxy data (e.g., salinity, vegetation cover, etc.).

WA Weighted averaging: a transfer function technique that is suitable for species that respond unimodally to an environmental variable and is quite robust when samples are not entirely evenly distributed along the environmental gradient.

WA-PLS Weighted averaging partial least squares: a modification of WA. It uses the structure in the WA residuals to improve predictions and is suitable for less noisy data.

Appendix 2

Taxonomy

In this appendix we describe and illustrate the dominant agglutinated and calcareous foraminifera encountered in surface and sub-surface sediments from our study sites in the British Isles. The agglutinated forms characterize the vegetated marsh surface, whilst the calcareous species dominate the intertidal sand and mudflats (see Section 2.5.4).

As noted in Section 2.1.2, a conservative approach to taxonomic sub-division was adopted in the development of our transfer functions. This was necessary to ensure consistency and data quality when combining results produced by different analysts over a number of years. Phenotypic variation within species, together with superficially similar species (notably within the calcareous genera *Ammonia*, *Elphidium* and the agglutinating foraminifera in general), has resulted in an often confusing nomenclature. The following taxonomy, which presents a more detailed sub-division than we have employed to date, is intended to facilitate more refined studies in the future.

In addition to noting diagnostic features and summary distributions, we provide a brief systematic treatment for each species, comprising the original reference, junior synonyms and any important revisionary text. Where appropriate, we highlight comparisons with similar species, making reference to type material from

the collections held in The Natural History Museum, London, UK. This is particularly important as most of the species presented herein have their type localities in NW Europe, yet are of truly worldwide distribution.

Suites of representative material are deposited in the United States National Museum of Natural History (Smithsonian Institution), Washington D.C., and in The Natural History Museum, London, UK.

Suborder Textulariina

Balticammina pseudomacrescens **Brönnimann,**

Lutze and Whittaker, 1989

Plate I, Figure 1a-d.

Balticammina pseudomacrescens Brönnimann, Lutze and Whittaker, 1989, p. 169, pl. 1, figs. 1-5, pl. 2, figs. 1-9, pl. 3, figs. 1–4.

Description. Tests brown in color, agglutinated and composed of extremely fine detrital grains with abundant organic cement. Trochospirally coiled but compressed with a wide, shallow umbilicus. Has both a primary interiomarginal aperture and secondary umbilical apertures.

Remarks. *Balticammina pseudomacrescens* has been much confused in the past with *Jadammina macrescens* (Brady) and *Trochammina inflata* (Montagu). Both *B. pseudomacrescens* and *J. macrescens* have a very low trochospiral test with a primary interiomarginal apertural slit. However, *B. pseudomacrescens* has supplementary apertures opening within the wide umbilicus, whereas *J. macrescens* has a shallow umbilicus and secondary areal pores on the apertural face (it is also much prone to chamber collapse as illustrated in Plate I, Fig. 4d). *T. inflata* has a somewhat higher and more robust trochospiral test, with globular chambers. Moreover, it has only one primary interiomarginal aperture, with a pronounced lip (see Plate II, Figs. 8a and 8c). For further remarks concerning the confusion between these species, especially in the North American literature, see de Rijk (1995a) and Gehrels and van de Plassche (1999).

Death Distribution. *Balticammina pseudomacrescens* is recorded at Alnmouth and Welwick marshes, Arne Peninsula, Bury Farm and Newton Bay, where it is restricted to the landward edge of the saltmarsh

habitats.

Eggerelloides scaber **(Williamson, 1858)**

Plate I, Figure 2a.

Bulimina scabra Williamson, 1858, p. 65, pl. 5, figs. 136, 137.
Eggerelloides scabrum [sic] (Williamson). Haynes, 1973, p. 44, pl. 2, figs. 7, 8, pl. 19, figs. 10, 11, text-figs. 8.1-4.

Description. Tests agglutinated, consisting of variable sizes of detrital grains held together in organic cement, with a white to pale brown color. Initial part of the test is trochospiral but the adult section is triserial. Chambers increase rapidly in size so that the last whorl usually forms half the length of the test. Aperture is high-arched or loop shaped.

Death Distribution. Eggerelloides scaber is restricted to Keyhaven Marsh where it is found in high relative abundance (greater than 30% at one sample station) in the marsh habitats. Although *E. scaber is* essentially a marine, inner shelf species it is known to penetrate into estuary mouths and onto marsh surfaces (Murray, 1979). It is recorded in the fossil sequences from a number of sites.

Haplophragmoides **spp.**

Plate I, Figure 3a-d.

Description. Tests agglutinated, composed of fine silt grains held together by organic cement; pale brown in color with a smooth finish. Planispirally coiled with an interiomarginal aperture.

Remarks. Haplophragmoides manilaensis and *H. wilberti* (both described in the same paper by Andersen, 1953) are difficult to differentiate and subsequently are grouped here as *Haplophragmoides* spp. Likewise, de Rijk (1995a) stated that there are strong similarities between the two forms because of interspecific variability.

PLATE I

1. Balticammina pseudomacrescens **Brönnimann Lutze & Whittaker, 1989**.
1a) oblique-umbilical view, showing primary interiomarginal and secondary umbilical apertures (x 100); 1b) spiral view (x 100); 1c) edge view (x 100); 1d) close-up of broad umbilicus showing apertures (x 200).
Specimen BH2/13-1. Contemporary sample, Alnmouth, North Sea coast, northeastern England.
2. Eggerelloides scaber **(Williamson, 1858).**
2a) oblique side view (x 100).
Specimen BH2/7-2. Contemporary sample, Keyhaven, The Solent, southern England.
3. Haplophragmoides **species.**
3a) side view (x 100); 3b) edge view (x 100); 3c) side view of smaller specimen (x 100); 3d) edge view of same specimen (x 100).
Specimen BH2/2 (3a,b). Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
Specimen RJE 15 (3c,d). Fossil sample, Arne Peninsula, Poole Harbour, southern England.
4. Jadammina macrescens **(Brady, 1870).**
4a) spiral view (x 100); 4b) umbilical view (x 100); 4c) oblique spiral view showing primary aperture and secondary areal apertures (x 100); 4d) spiral view of specimen with collapsed chambers (x 100).
Specimen BH2/3-2 (4a-c). Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
Specimen BH2/3-3 (4d). Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
5. Miliammina fusca **(Brady, 1870).**
5a) side view (x 100); 5b) end view showing aperture (x 100).
Syntype 2 - Natural History Museum London, UK.
6. Reophax moniliformis **Siddall, 1886.**
6a) side view (x 100); 6b) oblique end view showing the terminal aperture (x 100); 6c) side view of abnormal 'branched' specimen (x 100).
Specimen RJE 9 (6a,b). Fossil sample, Arne Peninsula, Poole Harbour, southern England.
Specimen RJE 10 (6c). Fossil sample, Arne Peninsula, Poole Harbour, southern England.
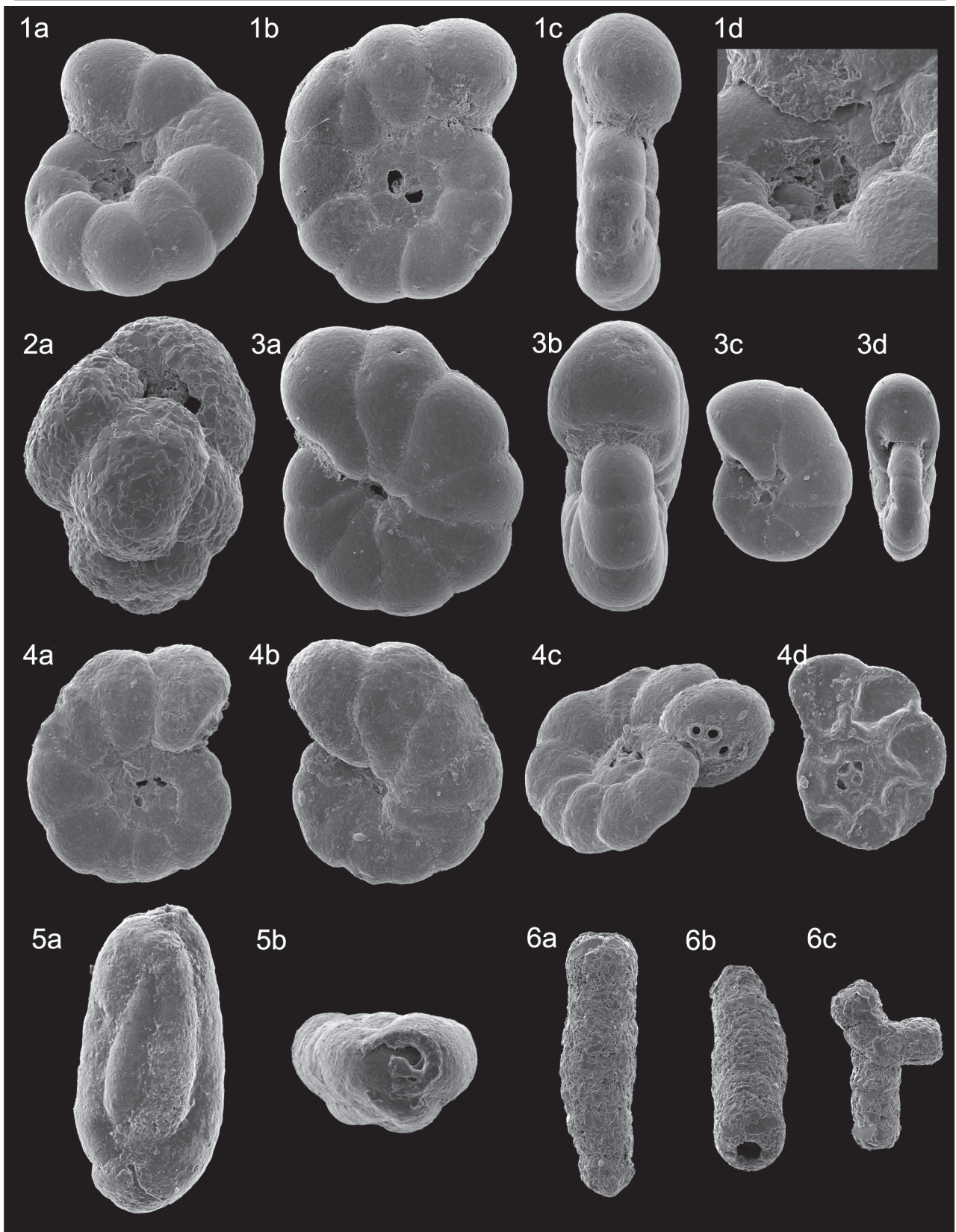
Moroever, under the optical microscope it is difficult to separate *Cribrostomoides jeffreysii* (Williamson, 1858) (with an areal slit, just above the base of the apertural face) from true *Haplophragmoides* (see Haynes, 1973, p. 27-31).

Death Distribution. Haplophragmoides spp. are present at most study areas; the exceptions are Alnmouth and Welwick marshes and Rusheen Bay transects 1 and 2. *Haplophragmoides* spp. usually make a minor contribution to the death assemblage, but are locally abundant, with relative frequencies of greater than 20% at stations in Bury Farm and Roudsea Marsh. It is found in all marsh habitats but the abundance decreases in areas below MHWST.

Jadammina macrescens (Brady, 1870)

Plate I, Figure 4a-d.

Trochammina inflata (Montagu) var. *macrescens* Brady, 1870, p. 290, pl. 11, figs. 5a-c.
Jadammina polystoma Bartenstein and Brand, 1938, p. 381, text-figs. 1-3.
Jadammina macrescens (Brady). Brönnimann and Whittaker, 1984a, p. 303-309, figs. 1-21 (lectotype erected).

Description. Tests agglutinated, composed of extremely fine detrital grains with abundant organic cement; brown in color. Very low trochospiral coil and compressed with a shallow umbilicus. Walls thin and flexible when wet and chambers commonly collapse when dried (Plate I, Fig. 4d). Interiomarginal primary aperture and one or more large areal pores on the face of the last chamber.

Remarks. Jadammina is distinguished from *Trochammina* by apertural characteristics (Murray, 1971; Brönnimann and Whittaker, 1984a; de Rijk, 1995a). The former has a multiple aperture consisting of a single interiomarginal slit at the base of the apertural face with scattered supplementary areal pores. The latter has a single interiomarginal slit-like umbilical aperture with a lip, between the coiling and the periphery.

Death Distribution. Jadammina macrescens is the most abundant species (agglutinated or calcareous) occurring at all study sites. The highest abundances are found in the high marsh above MHWST. These habitats are characterized by a low diversity, agglutinated assemblage, which is remarkably consistent among study areas. Alnmouth, Cowpen and Thornham marshes, Arne Peninsula and Nith Estuary exhibit monospecific

assemblages of *J. macrescens* at the landward limit of the high marsh.

Miliammina fusca (Brady, 1870)

Plate I, Figure 5a, b.

Quinqueloculina fusca Brady, 1870, p. 286, pl. 11, figs. 2a-c.
Miliammina fusca Brady. Murray, 1971, p. 21, pl. 3, figs. 1-6.

Description. Tests agglutinated, composed of detrital grains in an organic cement; pale brown in color. Morphology varies slightly with grain size (sand or silt). Tests elongate and rounded in section. Chambers coiled on a milioline plan. Aperture terminal with a tooth.

Death Distribution. Miliammina fusca is found at most British study areas, although it is not reported at Rusheen Bay. It is abundant in all marsh habitats, reaching percentages greater than 50% at sampling stations in Arne Peninsula, Bury Farm, Keyhaven Marsh, Tramaig Bay and Nith Estuary. At Cowpen and Roudsea marshes, and Bury Farm, *M. fusca* is restricted to a narrow elevation zone within the middle to low marsh, around or below MHWST.

Reophax moniliformis Siddall, 1886

Plate I, Fig. 6a-c.

Reophax moniliforme [sic] Siddall, 1886, p. 54, pl.1, fig. 2.
Reophax moniliforme [sic] Siddall. Haynes, 1973, p. 24, pl. 3, fig. 17, pl. 6, fig. 8.

Description. Tests agglutinated, composed of detrital grains in an organic cement; pale brown in color. Cylindrical, consisting of a column of chambers (uniseral) with a terminal aperture.

Remarks. Reophax (a masculine genus, see MacFadyen and Kenney, 1934) is used here in the broad sense. At present, it is thought that the test is comprised of a proloculus followed by exclusively uniserial chambers (although the initial portion has never been sectioned). It does not, however, possess the asymmetrical chambers of the type-species, *R. scorpiurus* (see Brönnimann and Whittaker, 1980). It is widely reported in British waters (Heron-Allen and Earland, 1913) but not elsewhere, probably due to the obscurity of the original reference.

Plate I, Fig. 6c shows an abnormal "branched" specimen. A similar species widely reported from American salt marshes is *Polysacammina ipohalina* Scott (1976), which has a fragile, irregularly formed uniseral test with a small restricted aperture. The genus *Polysaccamina* is (mainly) diagnosed on its inner organic lining, but all agglutinating foraminifera with organic cement have an inner organic lining (Bender, 1995), and this is not, therefore, a diagnostic generic feature.

Death Distribution. Reophax moniliformis is found at Alnmouth Marsh, Arne Peninsula, Bury Farm and Nith Estuary. It is restricted to tidal flat and low marsh environments with a maximum abundance of 6% at a sample station of Bury Farm.

Tiphotrocha comprimata

(Cushman and Brönnimann, 1948)

Plate II, Figure 7a-e.

Trochammina comprimata Cushman and Brönnimann, 1948, p. 41, pl. 8, figs 1-3.

Description. Tests agglutinated, composed of extremely fine detrital grains with abundant organic cement; brown in color. Compressed, trochospirally coiled with depressed, curved sutures. Test has characteristic umbilical lobe on the final chamber, and other chambers with secondary openings.

Remarks. Adults (Plate II, Fig. 7a-c) and juveniles (Plate II, Fig. 7d,e) are illustrated. The adults, in particular can readily be distinguished from *J. macrescens* and *T. inflata* by the T-shaped final chamber on the ventral side, the more irregular outline of the chambers and the apertural characteristics.

Death Distribution. Tiphotrocha comprimata is found in marsh habitats at Arne Peninsula, Bury Farm, Newton Bay, Roudsea Marsh, Nith Estuary and Tramaig Bay. At most sites it is a minor species, however its relative abundance exceeds 9% at sample stations in Newton Bay.

Trochammina inflata (Montagu, 1808)

Plate II, Figure 8a-d.

Nautilus inflatus Montagu, 1808, p. 81, pl. 18, fig. 3.
Trochammina inflata (Montagu). Brönnimann and

Whittaker, 1984b, p. 311-315, figs. 1-11 (neotype erected).

Description. Tests agglutinated, composed of extremely fine detrital grains with an outer organic layer and abundant organic cement; brown in color. Trochospirally coiled with globular chambers. The size and globular character of the chambers varies among samples. Aperture an interiomarginal slit with a lip.

Remarks. Trochammina inflata differs from *Balticammina pseudomacrescens* in having more (and inflated) chambers in the final whorl, a higher coil, a tighter umbilicus (without supplementary apertures) and a discrete primary aperture with a lip. Plate II, Fig. 8d shows a "feeding tube" extending from the final chamber.

Death Distribution. Trochammina inflata is abundant in all study areas and relative abundances of greater than 30% are reported in sample stations from nine of the fifteen sites. It co-dominates with *J. macrescens* and *M. fusca* in high and middle marsh environments above and around MHWST.

Suborder Miliolina

Quinqueloculina spp.

Plate II, Figure 9a,b

Description. Tests porcellaneous with a translucent to opaque appearance. Chambers are coiled on a quinqueloculine plan. Aperture usually has a tooth.

Remarks. Various smooth miliolid species found in this study are difficult to differentiate and are subsequently grouped as *Quinqueloculina* spp. The specimen figured in Plate II, Fig. 9a appears to be a juvenile.

Death Distribution. Quinqueloculina spp. are present at most study areas; the exceptions are Keyhaven Marsh, Nith Estuary and Kentra Bay. Even though *Quinqueloculina* spp. have been classified as characteristic of the inner shelf (e.g., Murray, 1979) they are found in high abundances, both living (Horton, 1997) and dead in middle and low marshes, and tidal flat habitats. *Quinqueloculina* spp. exhibit abundances greater than 20% at the sampling stations of Alnmouth, Thornham, Brancaster, Roudsea marshes, Arne Peninsula and Rusheen Bay Transect 2.

Suborder Rotaliina

Ammonia spp.

Description. Tests calcitic with radially arranged crystallites and pores; glassy or translucent in appearance, sometimes brownish in color; biconvex and subcircular in outline. Chambers trochospirally coiled with six to nine chambers in the last whorl. Sutures on the spiral side are flush to depressed whereas those on the umbilical side are depressed; an umbilical boss may be present or absent.

Remarks. In this study, a number of *Ammonia* spp. are grouped together for taxonomic consistency. Previously, many workers have referred to these species as *Ammonia beccarii* (Linnaeus, 1758), but following the molecular systematics of Hayward and others (2004b) they should be recognised as separate species. In fact none of these is *A. beccarii sensu stricto*, which is restricted to the Mediterranean. For future reference, we discriminate three species of *Ammonia* that are found in our study area (see below).

Death Distribution. Ammonia spp. are present at most British and Irish study areas; the exceptions are Newton and Kentra Bays. *Ammonia* spp. are characteristic of low marsh and tidal flat environments, occasionally present in extremely high relative abundances (e.g., >75% at sampling stations in Thornham Marsh).

The following species of *Ammonia* are found in the study area:

Ammonia aberdoveyensis Haynes, 1973
Plate III, Figures 10a-c.

Ammonia aberdoveyensis Haynes, 1973, p. 184, pl.18, fig. 15, text-figs. 38, 1-7.

Description. Tests calcitic with radially arranged crystallites and pores; glassy or translucent in appearance, sometimes brownish in color. Biconvex with low conical dorsal side and rounded periphery. Commonly 8-9 chambers visible on ventral side. Pointed chambers tuberculate and project into large open umbilicus (Plate III, Fig. 10a).

Remarks. A. aberdoveyensis is similar in size to *A. batavus* but lacks the umbilical ornamentation of the latter.

Ammonia batavus (Hofker, 1951)

Plate III, Figure 11a-c
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Streblus batavus Hofker, 1951, p. 498, text-figs. 340, 341.

Ammonia batavus (Hofker). Haynes, 1973, p. 187, pl.18, figs. 5,6,14,16, text-figs. 39, 1-4.

Description. Tests calcitic with radially arranged crystallites and pores; glassy or translucent in appearance,

Plate II

7. *Tiphotrocha comprimata* (Cushman & Brönnimann, 1948).
7a) umbilical view showing the characteristic T-shaped final chamber (x 100); 7b) spiral view (x 100); 7c) edge view (x 100); 7d) umbilical view of juvenile specimen (x 100); 7e) spiral view of same specimen (x 100).
Specimen RJE 4 (7a-c). Contemporary sample, Newton Bay, Poole Harbour, southern England.
Specimen RJE1 (7d,e). Contemporary sample, Newton Bay, Poole Harbour, southern England.
8. *Trochammina inflata* (Montagu, 1808).
8a) oblique-umbilical view showing characteristic single aperture with lip (mag. x 100); 8b) spiral view (mag. x 100); edge view showing aperture (mag. x 100); 8d) umbilical view showing agglutinated 'feeding tube' (mag. x 100).
Specimen BPH2/4-1 (plates 8a, 8b & 8c). Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
Specimen RJE 30 (plate 8d). Contemporary sample, Hamble River, Southampton Water, southern England.
9. *Quinqueloculina* species.
9a) side view of large specimen (x 100); 9b) side view of small specimen (x 100).
Specimen BPH1/10-2 (9a). Contemporary sample, Southampton Water, southern England.
Specimen BPH1/10-1 (9b). Contemporary sample, Southampton Water, southern England.
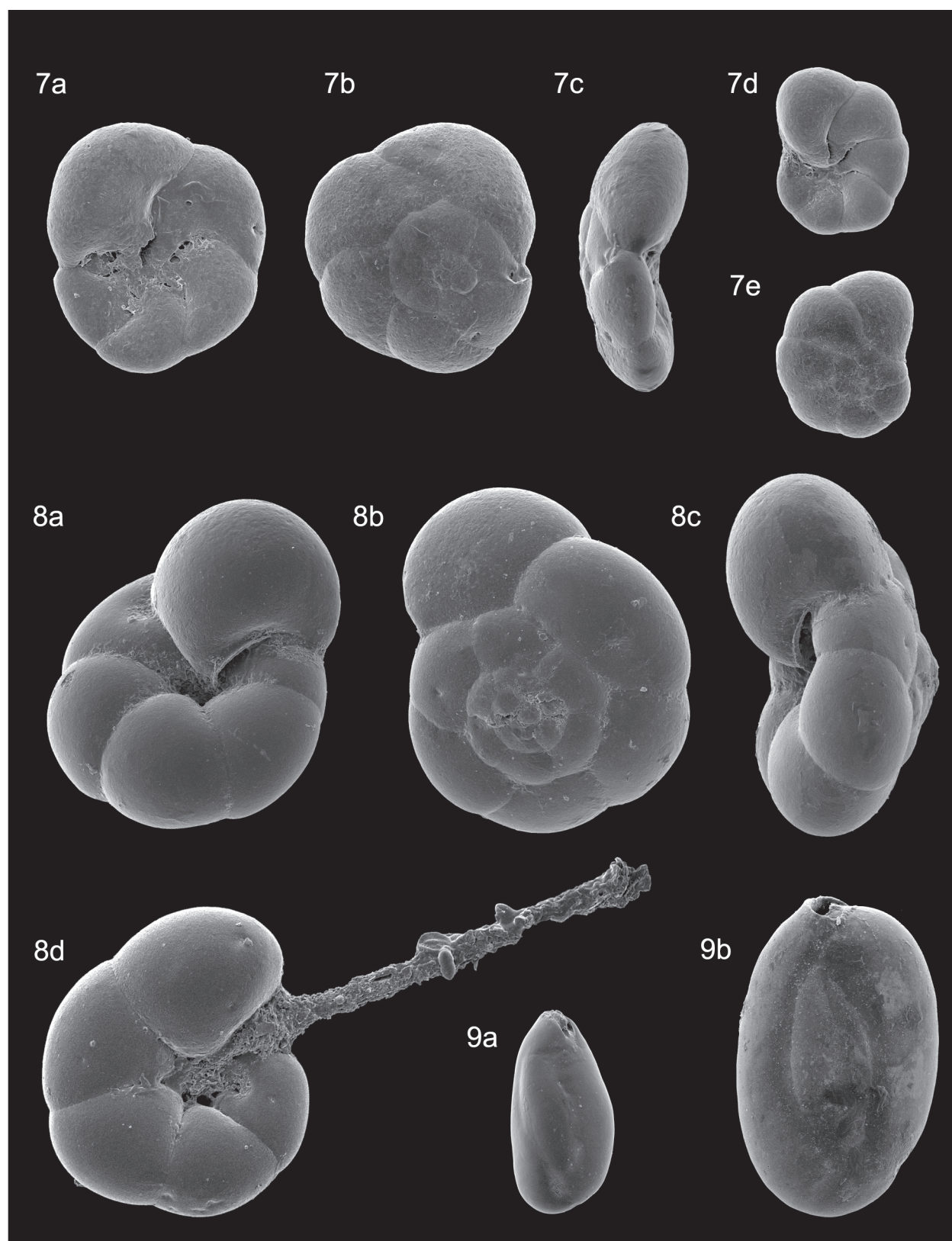
sometimes brownish in color. Biconvex with generally flattened dorsal side and subangular to subrounded periphery. Commonly 8-9 chambers visible on ventral side. Umbilicus filled with large boss which may be divided (Plate III, Fig. 11a).

Remarks. A. batavus is the most marine of the three species presented here. *Ammonia parkinsoniana* (d'Orbigny, 1839) bears a superficial resemblance to it but once again, Hayward and others (2004b) have shown that the two (respectively their molecular types T9 and T3S) are distinct. Consequently the use of *A. parkinsoniana* outside American waters should be discouraged.

Ammonia limnetes

(Todd and Brönnimann, 1957)

Plate III, Figure 12 a-c.

Streblus limnetes Todd and Brönnimann, 1957, p. 38, pl. 10, figs. 4a-c.
Ammonia limnetes (Todd and Brönnimann, 1957). Haynes, 1973, p. 189, pl. 18, figs. 7-9, pl. 19, fig. 8. pl. 30, fig. 8, text-fig. 40, 1-5.

Description. Tests calcitic with radially arranged

crystallites and pores; glassy or translucent in appearance, sometimes brownish in color. Compressed with flattened dorsal side. Commonly 6-7 chambers visible on ventral side with subangular to subrounded lobes protruding into umbilicus.

Remarks. A. limnetes has the simplest morphology of the three *Ammonia* spp. presented here, and is associated with the most brackish conditions.

Cibicides lobatulus (Walker and Jacob, 1798)

Plate III, Figure 14 a-c.

Nautilus lobatulus Walker and Jacob, 1798, p. 642, pl. 14, fig. 36.
Cibicides lobatulus (Walker and Jacob). Haynes, 1973, p. 173, pl.20, figs. 1, 2, pl. 21, figs. 3, 5, 6, pl. 33, figs. 1-7, text-figs. 35.4-10.

Description. Tests calcitic, radial and granular in nature with large pores; planoconvex, trochospirally coiled with planar spiral side and convex umbilical side. Aperture an arch and a slit, bordered by a lip which extends along the spiral suture on the spiral side. Numerous morphological variations are observed, apparently dependant on what, the foraminifer is attached to.

PLATE III

10. Ammonia aberdoveyensis **Haynes, 1973.**
10a) umbilical view showing open umbilicus and absence of umbilical boss (x100). 10b) spiral view (x 100); 10c) edge view (x 100).
Paratype 1 – Natural History Museum London, UK.
11. Ammonia batavus **(Hofker, 1951).**
11a) umbilical view showing large umbilical boss (x 100); 11b) spiral view (x 100); 11c) edge view (x 100).
Specimen BPH1/3-2. Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
12. Ammonia limnetes **(Todd & Brönnimann, 1957).**
12a) umbilical view showing star-shaped pattern of sutures (x 100); 12b) spiral view (x 100); 12c) edge view (x 100).
Paratype (12a) – Natural History Museum London, UK.
Specimen JW8 (12b,c). Contemporary sample, East Fleet, southern England.
13. Stainforthia fusiformis **(Williamson, 1858).**
13a) side view (x 100); 13b) side view showing aperture (x 100).
Specimen BH1/16-1 (13a). Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
Specimen BH1/16-2 (13b). Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
14. Cibicides lobatulus **(Walker & Jacob, 1798).**
14a) dorsal view (x 100); 14b) ventral view (x 100); 14c) edge view showing aperture (x 100).
Specimen BH1/5-2. Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
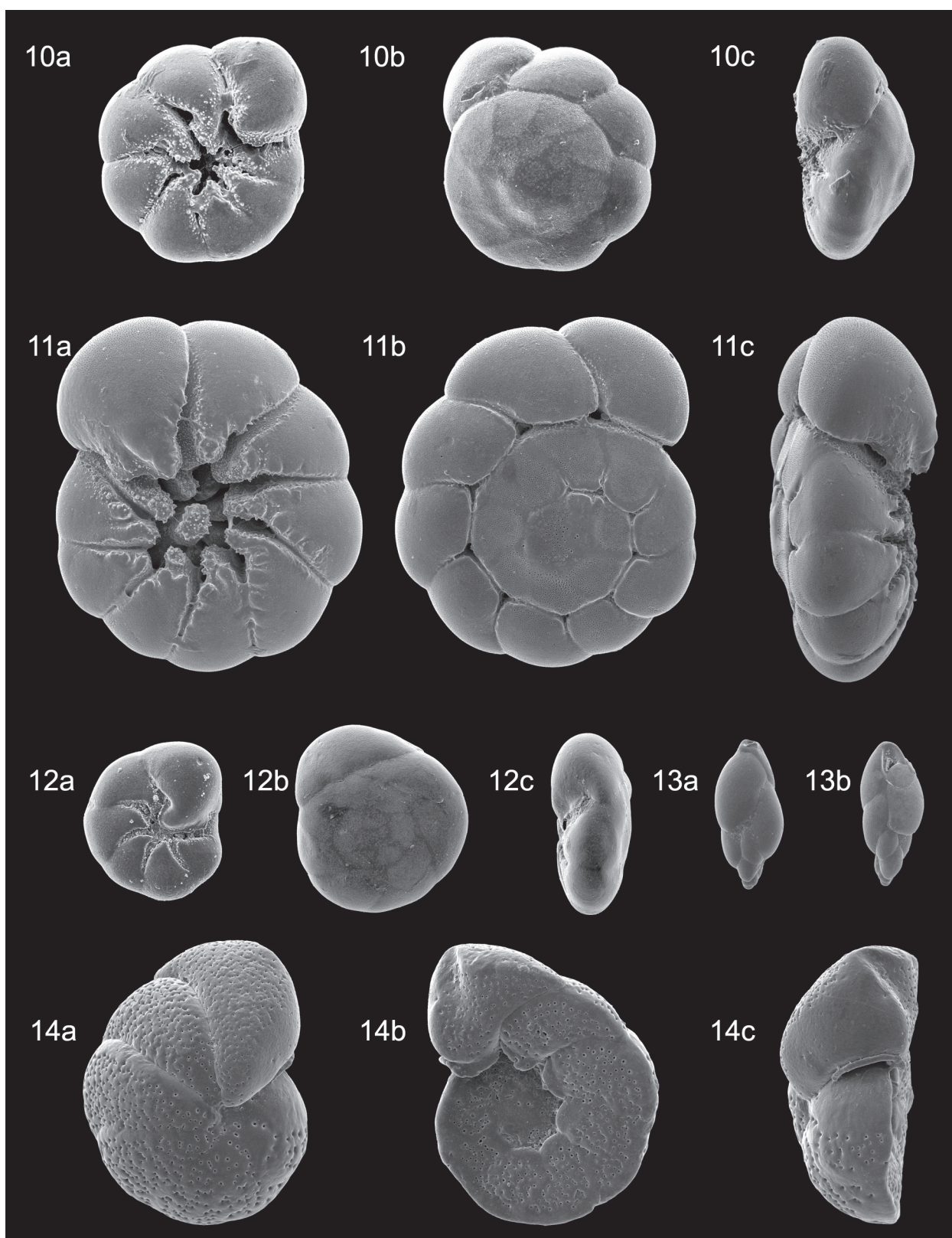
Death Distribution. Cibicides lobatulus is found at Alnmouth, Cowpen, Welwick and Roudsea marshes, Arne Peninsula, Nith Estuary and Tramaig Bay. It is commonly a minor species, although relative abundances exceed 35% at stations in Alnmouth Marsh and Tramaig Bay. Although *C. lobatulus* is a marine species, high abundances are occasionally found within the tidal flat. Live *C. lobatulus* cling to firm substrates such as seaweeds, tunicates, shells and rocks, in areas subject to disturbance, and hence dead tests may be transported into estuary mouths (Murray, 1979).

"Elphidium earlandi" sensu **Murray, 1971**

Plate IV, Figure 15 a,b.

not *Elphidium earlandi* Cushman, 1936, p. 85, pl. 15, fig. 5.

Elphidium earlandi Cushman. Murray, 1971, p.157, pl. 65, figs 1-7.

Description. Tests calcitic, involute, planispirally coiled and laterally compressed with generally 8 or 9 chambers in the final whorl. Four or five long sutural bridges between chambers. Aperture a series of irregular openings along basal suture of last chamber.

Remarks. This species is quite widely known from British waters but it is neither *E. earlandi* of Cushman (1936) nor appears not to have a valid name (J.W. Murray, pers. comm.). It will be validated elsewhere. It is superficially like *E. williamsoni* Haynes, but the latter species has a larger number of chambers and associated sutural bridges.

Death Distribution. "*Elphidium earlandi*" *sensu* Murray occurs at all east coast marshes (Alnmouth, Cowpen, Welwick, Thornham and Brancaster marshes) and Arne Peninsula, Roudsea Marsh and Tramaig Bay. It is a minor species, restricted to low marsh and tidal flat habitats with the maximum relative abundance at sampling stations in Cowpen Marsh (8%).

PLATE IV

15. Elphidium earlandi **sensu Murray, 1971.**
15a) side view (x 100); 15b) edge view (x 100).
Specimen RJE29. Fossil sample, Dibden Bay, Southampton Water, southern England.
16. Elphidium excavatum **(Terquem, 1875).**
16a) side view showing umbilicus with calcite bosses and tubercles (x 100); 16b) edge view (x 100).
Specimen BH1/18-2. Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
17. Elphidium selseyense **(Heron-Allen & Earland) Cushman, 1939.**
17a) side view showing thickened, glassy umbilicus (x 100); 17b) edge view (x 100).
Syntype 2 – Natural History Museum London, UK.
18. Elphidium incertum **(Williamson, 1858).**
18a) side view showing sutures with characteristic semicircular septal openings (x 100); 18b) edge view (x 100).
Paralectotype – Natural History Museum, London, UK.
19. Elphidium magellanicum **Heron-Allen & Earland, 1932.**
19a) side view showing broad, depressed sutures with fine tubercles (x 100); 19b) edge view (x 100).
Paratype 2 – Natural History Museum London, UK.
20. Elphidium williamsoni **Haynes, 1973.**
20a) side view showing numerous, long sutural bridges (x 100); 20b) edge view showing rotund nature of test (x 100).
Specimen RJE 27. Contemporary sample. Newton Bay, Poole Harbour, southern England.
21. Haynesina germanica **(Ehrenberg, 1840).**
21a) side view (x 100); 21b) edge view (x 100).
Specimen BH1/14-1. Contemporary sample, Cowpen Marsh, North Sea coast, northeastern England.
22. Nonion depressulus **(Walker & Jacob, 1798).**
22a) side view (x 150); edge view (x 150).
Paralectotype – Natural History Museum London, UK.

15a 15b 16a 16b

17a 17b 18a 18b

19a 19b 20a 20b

21a 21b 22a 22b
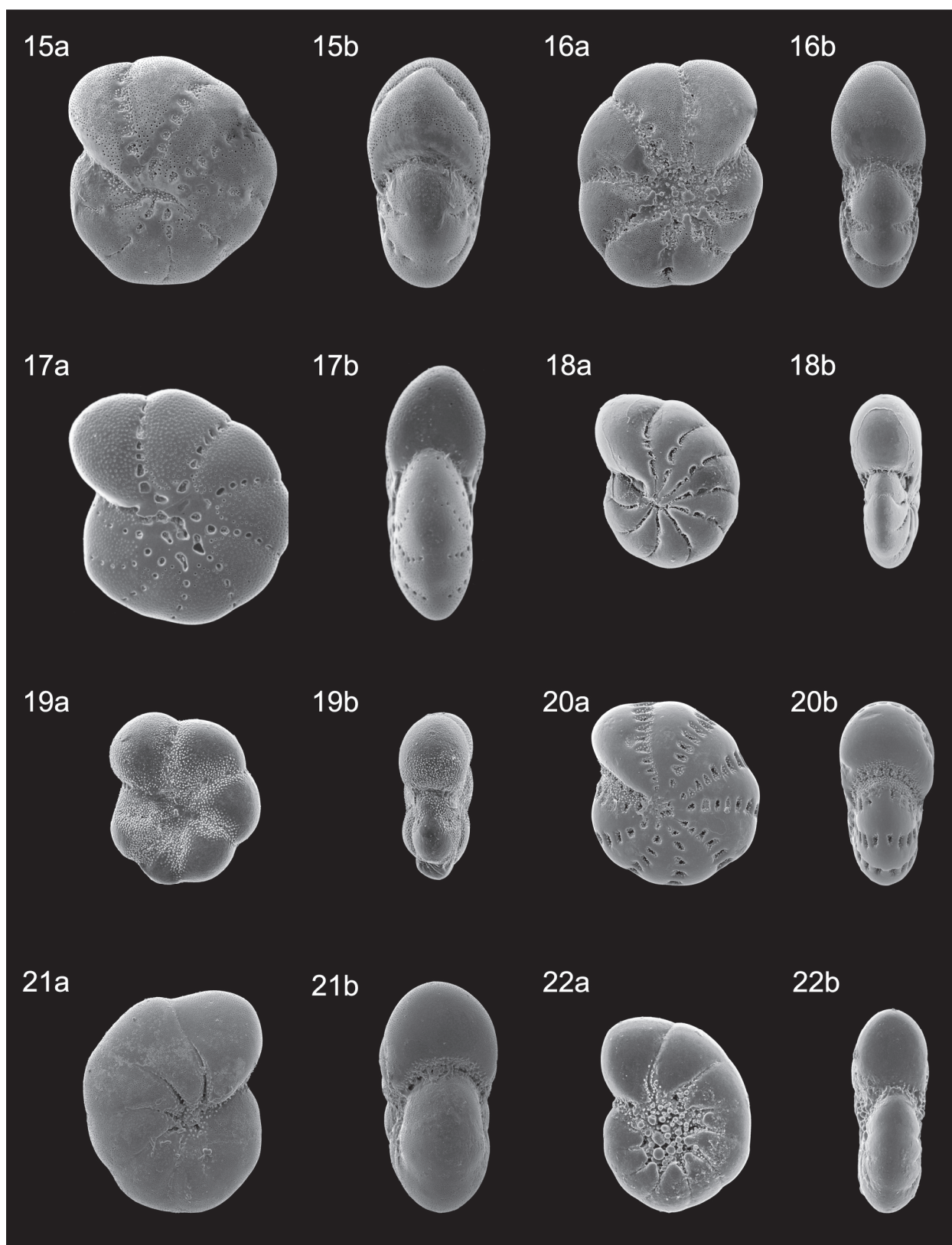
Elphidium excavatum (Terquem, 1875)

Plate IV, Figure 16 a,b.

Polystomella excavata Terquem, 1875, p. 25, pl. 2, figs. 2a-f.

Cribrononion excavatum [sic] (Terquem). Lévy and others, 1969, p. 93, pl. 1, figs 1, 2, 4.

Description. Tests calcitic, involute, planispirally coiled and laterally compressed with 8 to 9 chambers in the final whorl. Sutures deeply depressed with three to five very short sutural bridges between chambers. Aperture a series of irregular openings along basal suture of last chamber. Umbilicus possesses calcite bosses and/or tubercles.

Remarks. Levy and others (1969) redefined this species, using material collected from the type-locality of Dunkirk, northern France, and included *E. selseyense* (Heron-Allen and Earland, 1911). However, the syntypes of *E. selseyense* are characterized by the lack of any tubercular ornament and by the development of thickened, glassy umbilici, as in *E. cuvillieri* Lévy (1966), which is probably its junior synonym (see Plate IV, Figs. 17 a,b). Our material corresponds well with Murray's (1971) illustrations of *E. excavatum*.

Death Distribution. Elphidium excavatum is present in low marsh and tidal flat environments of Cowpen, Thornham, Brancaster and Roudsea marshes, Arne Peninsula, Nith Estuary and Tramaig Bay. It is commonly a minor species, although relative abundances exceed 19% at sampling stations in Thornham Marsh.

Elphidium incertum (Williamson, 1858)

Plate IV, Figure 18 a,b.

Polystomella umbilicatula var. *incerta* Williamson, 1858, p. 44, pl. 3, fig. 82a.

Description. Tests calcitic, involute, planispirally coiled and laterally compressed with flat sides, and 8 to 11 chambers in final whorl. Sutures depressed and curved in a star-shaped configuration centered on umbilicus; sutures contain distinctive septal openings. Umbilicus closed by fused ends of chambers. Aperture a series of irregular openings along basal suture of last chamber.

Remarks. Often misidentified in the literature. The specimen illustrated in Plate IV, Figs. 18 a,b, is from Williamson's syntypic series in The Natural History Museum, London.

Death Distribution. Elphidium incertum is present at all east coast marshes (Alnmouth, Cowpen, Welwick, Thornham and Brancaster marshes) as well as Keyhaven Marsh and Rusheen Bay transects 1 and 2. It occurs within the middle and low marsh, and in tidal flat environments, although the high relative abundances (greater than 30%; Keyhaven Marsh and Rusheen Bay transects 1 and 2) are restricted to tidal flat stations.

Elphidium magellanicum Heron-Allen & Earland, 1932

Plate IV, Figure 19 a,b.

Elphidium (Polystomella) magellanicum Heron-Allen and Earland, 1932, p. 440, pl. 16, figs. 26-28.

Description. Tests calcitic, involute, planispirally coiled and compressed with lobate to pentagonal periphery; 5 to 6 chambers visible. Wide umbilicus and broad, depressed sutures filled with fine tubercles. Aperture a series of irregular openings along basal suture of last chamber, usually hidden by tubercles.

Death Distribution. Elphidium magellanicum is found in low marsh and tidal flat environments of western (Roudsea Marsh, Nith Estuary and Kentra and Tramaig bays) and eastern (Alnmouth, Cowpen, Welwick, Thornham and Brancaster marshes) marshes of Great Britain. Although it is a minor species of the former marshes it is a key species of the latter with relative abundances at some sample stations exceeding 14%.

Elphidium williamsoni Haynes, 1973

Plate IV, Figure 20 a,b.

Elphidium williamsoni Haynes, 1973, p. 207, pl. 24, fig. 7, pl. 25, figs. 6, 9, pl. 27, figs. 1-3.

Description. Tests calcitic, involute, planispirally coiled, rotund with rounded periphery; 10 to 14 chambers visible. Numerous, long sutural bridges between chambers. Umbilicus filled with irregular ends of chambers. Aperture a series of irregular openings along basal suture of last chamber.

Remarks. Referred to as *E. umbilicatulum* (Williamson, 1858) by Levy and others (1969) in their revision of *E.*

excavatum (Terquem) and related forms, and thus latterly by other subsequent European workers. *E. umbilicatulum* is a junior secondary homonym of *Nonion umbilicatus* (Walker and Jacob, 1798) (Haynes, 1973).

Death Distribution. Elphidium williamsoni is the most abundant species of *Elphidium*. It is found at all study areas. It is a key species which is restricted to middle and low marshes and tidal flat habitats. Kentra Bay has a monospecific assemblage of *E. williamsoni* at the seaward edge of the transect. However, we believe other calcareous species are not preserved in the dead assemblage because the intertidal environment is subject to acidic runoff from a raised bog which enhances the dissolution of calcareous foraminifera.

Haynesina germanica **(Ehrenberg, 1840)**

Plate IV, Figure 21 a,b.

Nonionina germanica Ehrenberg, 1840a, p. 23 [figured in Ehrenberg, 1840b, pl. 2, figs. 1a-g].
Protelphidium anglicum Murray, 1965, p.149-150, pl. 25, figs. 1-5, pl. 26, figs. 1-6.
Haynesina germanica Banner and Culver, 1978, p. 191, pl. 4, figs. 1-6, pl. 5, figs. 1-8, pl. 6, figs. 1-7, pl. 7, figs. 1-6, pl. 8, figs.1-10, pl. 9, figs. 1-11, 15, 18.

Description. Test calcitic with radially arranged crystallites, finely perforate and glassy in appearance; rotund, planispirally coiled with five to eleven chambers in the last whorl. Sutures slightly depressed over the periphery but deeply depressed close to the umbilicus. Aperture a row of pores at the base of the last chamber.

Remarks. This common marsh species differs from the more marine *Nonion depressulus* (Walker and Jacob, 1798) in having a radial wall. It is also much less compressed and generally has less depressed sutures. *Nonion depressulus* is not a major species reported in our study area, but is illustrated (Plate IV, Figs. 22a,b) for comparative purposes.

Death Distribution. Haynesina germanica is the most abundant calcareous species. It is present at all sites apart from Keyhaven Marsh and Kentra Bay. Although it is found in middle and low marshes, the highest relative abundance is found in stations within tidal flat habitats. For example, eight of the study sites have relative abundances greater than 35%.

Stainforthia fusiformis **(Williamson, 1858)**

Plate III, Figure 13 a,b.

Bulimina pupoides var. *fusiformis* Williamson, 1858. p. 63, figs. 129, 130.

Description. Test walls calcitic and composed of radially arranged crystallites with very fine pores. Tests elongate and fusiform; chambers have a twisted biserial arrangement and are inflated, reaching a maximum size in the mid section of the test. Aperture either terminal or comma shaped with a toothplate.

Remarks. The change in apertural position from comma-shaped to terminal is part of the ontogenetic development and is well seen within Williamson's original syntypic material in The Natural History Museum, London. The wall of this species is radial and it is therefore placed in *Stainforthia*, rather than *Fursenkoina*. See Haynes (1973, p. 125) for further discussion.

Death Distribution. Stainforthia fusiformis is found at all east coast marshes (Alnmouth, Cowpen, Welwick, Thornham and Brancaster marshes) and Arne Peninsula, Roudsea Marsh, Nith Estuary and Tramaig Bay. *S. fusiformis* is commonly a minor species, although relative abundances exceed 23% at stations in Alnmouth Marsh. Whilst *S. fusiformis* is a marine species, it is found within middle and low marshes, and tidal flat environments.

Appendix 3

Foraminiferal Dataset

This appendix presents the relative abundance (%) of each species and the total number of dead foraminifera counted from each station at fifteen study sites located on the east, south and west coasts of Great Britain, and west coast of Ireland. Cowpen Marsh was sampled at approximately two-weekly intervals for a twelve-month period. Welwick, Thornham and Brancaster marshes were sampled four times during a twelve-month period (once in each season). The remaining study areas were sampled once around the time of spring tide. The seasonal measurements are expressed as annual averages and combined with the single measurements to produce the modern foraminiferal dataset. In addition the appendix shows the environmental data (where available) for each site. The species are listed in alphabetical order.

Alnmouth Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Ammonia spp.	1.5	1.5	2.0	0.9	2.0	0.3	0.2	1.9	0.6	0.5	4.0	1.8	1.9							
Balticammina pseudomacrescens																		0.3		
Brizalina pseudopunctata							2.9	0.8	1.8	2.9	0.9		0.9	0.6						
Bulimina marginata				0.5		0.3	1.2	0.4				0.4		0.3						
Cibicides lobatulus	71.2	61.5	66.5	57.9	69.6	18.9	14.6	24.2	12.7	4.9	5.5	20.2	5.2	0.3	0.3		0.8			
Cyclogyra involvens						0.2														
Elphidium "earlandi"						0.6	1.2	0.4	0.9	0.5	0.6	0.4	1.9	1.0		0.4				
Elphidium incertum	1.0	0.5		1.0	0.9			0.4	0.3					0.3	0.3					
Elphidium magellanicum						0.6	1.7	4.5	2.7	3.9	0.9		0.5							
Elphidium williamsoni	5.4	2.5	3.0	6.5	3.9	13.9	14.1	11.3	2.6	24.0	38.0	32.5	22.6	10.6	7.2	10.6	5.4	0.3		
Fissurina lucida												0.4		0.3	2.1	0.4				
Fissurina marginata											0.3	1.3	2.8							
Gavelinopsis praegeri										0.3										
Globigerina quinqueloba											1.0	0.3	0.4	1.4	0.6	0.6				
Haynesina germanica	2.9	3.5		5.1	6.9	40.8	28.6	37.0	47.5	35.9	37.4	16.2	20.8	19.3	33.0	5.9	0.8			
Jadammina macrescens						1.8	0.2	2.6	0.6	0.5	0.6	6.6	6.6	13.5	4.2	37.3	52.6	65.6	70.5	98.1
Lagena semistriata								0.4	0.3	0.8	0.9									
Lagena sulcata						0.3	1.0	0.4	0.9		0.6		0.5	0.3						
Miliammina fusca								1.1	0.3									1.3		
Pateoris hauerinoides	5.9	6.5	6.4	7.4	2.9	3.0	4.5		1.8	1.3	0.9		0.5	0.3						
Planorbulina mediterranensis		1.0		1.0		2.7	1.4	0.4		0.3	0.3									
Quinqueloculina spp.	12.2	23.0	19.7	17.6	11.8	1.5	2.6	1.1	1.8	0.3	0.6	3.1	4.7	26.4	34.8	32.2	19.3	0.3		
Reophax scottii						1.2	0.5			0.5		0.4			0.3	0.3	0.8			
Rosalina williamsoni			2.5	3.7	1.0	0.6	1.7	0.4	0.3	1.3		0.4								
Spirillina vivipara						1.5	0.2					0.4	1.9	7.1	8.4	6.7	1.0			
Spiroloculina excavata						1.5														
Spiroloculina rotunda				0.5																
Stainforthia fusiformis						9.5	22.7	12.8	7.7	20.6	6.1	13.6	23.6	13.8	8.4	3.9				
Trochammina inflata						0.3	0.2				0.6	0.4	2.8	1.9		1.6	18.6	33.0	29.5	1.9
Trochammina ochracea										0.5	1.2	1.3	1.4	2.9	0.3	0.4	0.3	0.6		
Trochammina squamata							0.2													
Total dead foraminifera (per 10cm³)	547	800	541	576	816	2704	3352	2120	2712	3072	2608	1824	848	2488	2664	2040	3104	2864	1736	422
Elevation (m OD)	2.6	2.3	2.2	2.0	1.9	1.7	1.6	1.6	1.4	1.3	1.1	0.9	0.8	0.5	0.4	0.6	0.5	0.3	0.1	0.0
pH	6.8	6.8	6.9	7.2	7.4	7.5	7.4	7.5	7.7	7.9	7.9	7.8	7.8	7.8	7.8	7.9	7.9	7.9	7.7	7.6
LOI (%)	75.7	75.6	74.3	61.8	52.4	59.3	58.7	43.6	38.8	34.6	31.9	33.5	40.2	39.6	40.7	24.6	24.1	25.2	26.2	24.6
Porewater Salinity	39.0	53.0	47.0	58.0	41.0	40.0	41.0	26.0	31.0	27.0	27.0	27.0	28.0	28.0	7.0	21.0	20.0	19.0	17.0	16.0
Clay (%)	11.5	17.5	11.8	13.9	13.3	11.8	11.7	9.2	6.4	4.6	4.3	4.3	4.8	5.4	4.9	1.1	0.6	1.0	0.9	0.9
Silt (%)	69.2	75.5	63.7	75.2	74.1	68.8	69.8	54.4	40.4	27.3	25.2	25.4	30.7	33.2	32.3	2.8	1.4	1.9	1.6	2.2
Sand (%)	19.3	7.0	24.5	10.9	12.6	19.4	18.5	36.4	53.2	68.1	70.5	70.4	64.5	61.4	62.8	96.1	98.0	97.2	97.5	96.9
Distance (m)	0	20	40	70	105	150	190	225	260	290	310	330	345	355	362	366	369	372	377	380

Arne Peninsula	1	2	3	4	5	6	7	8	9	10	11	12
Ammobaculites balkwilli										0.7		0.4
Ammonia spp.					3.9	24.0		9.9	27.9	15.6	28.8	23.6
Ammoscalaria runiana					2.2		3.5	35.8			1.5	1.8
Ammotium salsum					1.1							
Balticammina pseudomacrescens		0.5	0.7	1.3	0.6			1.2				
Cyclogyra involvens						1.0				0.7		
Elphidium "earlandi"										1.4		0.9
Elphidium excavatum										0.7	3.0	11.6
Elphidium gerthi									0.7	1.4		1.3
Elphidium incertum												4.4
Elphidium spp.						1.0			0.7	2.1		
Elphidium williamsoni					18.0	6.3	0.7	2.5	16.3	7.8		0.9
Haplophragmoides spp.			2.7	6.7				2.8	1.2			0.4
Haynesina germanica						2.1			38.1	30.5	33.3	36.9
Jadammina macrescens	100.0	70.2	73.2	41.4	36.5	43.8	77.8	34.6	4.1	12.8	7.6	5.8
Miliammina fusca		26.3	21.4	50.0	11.8					2.1	6.1	3.6
Nonion depressulus										16.3	7.6	1.8
Quinqueloculina spp.					23.0	19.3	3.5	2.5	10.2	3.5	4.5	3.6
Reophax sp.												0.4
Stainforthia fusiformis												0.4
Textularia earlandi												0.4
Tiphotrocha comprimata		0.5		0.2			1.4	2.5				
Trochammina inflata		2.4	2.0	0.5	2.8	2.6	10.4	4.9	0.7	0.7	3.0	0.4
Trochammina squamata								4.9	1.4	3.5	4.5	1.3
Total dead foraminifera (per 10cm³)	20	205	598	616	178	192	144	81	147	141	66	225
Elevation (m OD)	0.85	0.80	0.75	0.70	0.60	0.55	0.49	0.33	0.25	0.05	-0.05	-0.16
Distance (m)	0	3	4	6	18	103	108	113	115	118	119	121

Brancaster Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Ammonia spp.	0.4	1.9	0.6	8.2	0.6	0.3	0.4		1.2	0.4	1.3	1.8	3.9	7.6	3.5	0.5	0.5	5.6	7.5	13.8	6.0	3.2	
Brizalina inflata																		1.2	1.9	0.8	2.0		
Brizalina variabilis																0.5					0.9		
Buliminella elegantissima																0.5							
Cassidulina obtusa																		0.6					
Cyclogyra involvens		1.3	2.3	1.4										0.3	2.0	2.7	2.7	1.6			0.5		
Elphidium "earlandi"	1.1	0.3	1.0	1.3	0.4	0.3	0.3	1.1	3.7					0.2	1.2		0.7	2.8		2.1	0.4		
Elphidium excavatum				0.7													1.2		1.4		1.5		
Elphidium incertum																	1.8	1.9	4.7	3.8	3.9		
Elphidium magellanicum														0.5	0.8	1.4	2.9	6.7	2.4	4.3			
Elphidium spp.																	0.3			0.5			
Elphidium williamsoni	3.2	3.8	3.1	4.9	0.8	1.6	0.6	2.5	3.5	2.6	2.0	2.4	1.4	0.8	6.2	16.2	6.9	4.4	1.9	11.0	7.4	4.1	2.0
Glabratella millettii																			1.5				
Globigerina quinqueloba																		0.4	2.2		1.6		
Haplophragmoides spp.	6.4	2.6	2.4	0.6	0.3	4.3	1.8	1.1	0.2	0.5	0.4	1.3	0.2		0.4								
Haynesina germanica	1.4	2.8	3.2	6.8	1.1	1.4	1.9	1.6		5.3	1.3	4.3	1.8		1.4	4.1	4.5	14.9	14.3	34.3	41.2	52.7	73.4
Jadammina macrescens	44.7	37.5	35.5	27.9	40.4	33.8	45.8	39.4	39.7	44.6	30.2	38.3	39.0	49.5	43.6	22.5	44.4	46.6	56.3	21.6	12.9	17.5	5.9
Miliammina fusca	19.8	17.1	20.2	13.6	24.9	25.5	16.5	27.4	16.3	14.4	16.9	13.6	6.0	8.4	7.0	4.1	1.7		0.4				
Quinqueloculina spp.	4.8	7.8	8.1	21.2	3.0	1.4	0.2	1.1		0.8	2.0	2.6	2.0		11.5	22.6	14.4	4.6	2.3	11.8	9.1	4.8	
Rosalina spp.																						0.5	
Spirillina vivipara				0.3																			
Stainforthia fusiformis															0.8		0.4	1.1					
Trochammina inflata	17.8	24.2	23.5	12.9	26.2	30.7	32.0	24.9	36.1	30.6	46.8	36.2	47.9	36.2	21.8	23.0	22.0	24.0	9.6	2.3	0.5	0.6	0.7
Trochammina ochracea																						0.7	
Total dead foraminifera (per 10cm³)	1116	846	692	740	780	814	832	708	636	834	620	766	612	606	1328	1166	538	642	634	226	318	378	478
Elevation (m OD)	3.27	3.21	3.24	3.23	3.21	3.22	3.22	3.23	3.22	3.24	3.21	3.19	3.19	3.14	3.03	2.98	3.07	3.02	3	2.48	2.31	1.88	1.85
pH	5.8	6.5	6.5	6.1	5.9	5.8	6.1	6.5	6.7	6.5	6.3	6.1	6.3	6.5	6.5	6.5	6.7	6.1	6.7	7	6.9	7	7
LOI (%)	45.0	43.3	42.0	37.0	36.4	36.8	37.1	38.0	37.0	36.4	35.7	33.4	31.6	29.7	30.0	23.6	20.8	19.9	18.6	17.9	15.7	13.4	11.9
Porewater Salinity	7.2	8.3	9.1	9.2	10.1	12.9	13.1	13.8	12.5	10.3	10.3	8.9	10.0	11.8	9.8	8.8	8.1	7.6	7.8	7.7	7.2	7.1	9.0
Clay (%)	36.0	32.5	25.2	21.2	16.6	14.6	15.3	18.5	23.7	32.5	33.1	32.9	35.7	21.6	31.0	39.1	38.7	36.6	35.2	39.0	36.9	37.2	38.4
Vegetation cover (%)	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	90	50	0	0
Distance (m)	0	3	6	9	11	13	16	19	21	28	31	36	44	53	63	69	83	87	89	90	91	92	94

Bury Farm	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Ammobaculites balkwilli									0.1		0.6					
Ammonia spp.										1.2	3.9	28.4	27.1	17.8	18.5	21.0
Ammoscalaria runiana										0.2	0.4		0.7	0.4	3.1	
Ammotium salsum										0.1	0.6	0.7		0.4		0.6
Balticammina pseudomacrescens		1.6	2.2	1.2												
Elphidium excavatum										0.3		0.7	2.1	0.7		0.6
Elphidium gerthi								0.1		0.3		2.7		0.4		
Elphidium incertum												1.4	0.3			
Elphidium spp.													0.3	1.1		
Elphidium williamsoni								0.4	0.1	0.6	0.3	2.0	3.1	2.2		1.7
Haplophragmoides spp.		12.1	2.2	16.5	24.6	0.6	6.0	9.1	3.4	6.2	1.0		0.3	0.4		2.3
Haynesina germanica										1.5	0.7	18.9	21.3	11.6	15.4	13.6
Jadammina macrescens	93.8	83.5	77.2	52.4	30.1	58.1	50.6	38.4	24.5	27.6	17.2	24.3	26.8	42.5	44.6	33.5
Miliammina fusca		2.2	5.6	22.3	24.6	20.6	30.0	35.7	57.8	39.4	65.7	16.2	7.6	7.3	6.2	9.7
Nonion depressulus										0.2						
Quinqueloculina spp.								0.9	0.3	0.6	0.2					
Reophax spp.							4.6	3.5	6.0	0.7	0.2	0.7	0.3		3.1	0.6
Stainforthia fusiformis																
Textularia earlandi								0.1	0.1							
Tiphotrocha comprimata						0.6							0.3	2.5		
Trochammina inflata	6.3	0.5	12.7	7.5	20.7	20.0	8.8	11.7	7.5	21.0	9.2	4.1	9.6	12.7	9.2	16.5
Total dead foraminifera (per 10cm³)	16	182	268	412	386	155	777	691	702	890	991	148	291	275	65	176

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Elevation (m OD)	2.18	2.08	1.99	1.88	1.73	1.64	1.53	1.43	1.23	1.04	0.83	0.43	0.23	-0.16	-0.57	-1.762
Distance (m)	3	7	8	9	14	22	82	86	92	97	117	132	146	158	169	190

Cowpen Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Ammonia spp.							0.3								0.4	0.1	2.4	0.1	0.7	0.7	3.9	3.8	4.0	5.5	3.7	3.2	3.5	4.7	4.1	6.0	7.7
Brizalina inflata																						1.0	0.9	0.2	1.0	0.6	1.1	1.3	0.3	0.5	
Brizalina pseudopunctata																														0.5	
Brizalina variabilis																0.9			0.4	0.5	0.9	1.9	1.4	1.5	0.3	1.4	2.7	2.3	1.5	1.6	0.7
Bulimina marginata																						0.1	0.1	0.1	0.1	0.1			1.5	0.3	
Buliminella elegantissima																				0.6	0.4	0.9	1.2	0.6	0.4	0.8	0.4	0.4	0.6		0.7
Cibicides lobatulus														0.2	0.6		0.6	1.4	2.8	1.9	5.7	4.7	1.9	4.3	3.5	5.5	6.0	7.8	7.5	6.6	6.3
Elphidium "earlandi"						0.1					1.5	1.0	0.5	0.9	1.2	2.6	6.8	6.6	5.0	8.3	5.1	2.6	2.8	4.6	4.2	6.1	2.9	3.9	5.2	3.4	2.9
Elphidium excavatum											0.2					0.2		0.3	0.6	0.5	2.1	1.6	2.3	2.7	1.3	2.8	1.8	1.6	2.4	2.1	2.1
Elphidium incertum																	1.3		0.3	2.7	4.6	6.0	3.8	3.7	7.4	6.2	6.2	7.3	7.5	4.2	2.0
Elphidium magellanicum																	0.3	0.6	1.4	2.5	1.5	5.4	4.1	5.7	3.4	2.7	2.5	1.5	5.6	11.3	12.5
Elphidium margaritaceum																							0.0	0.1			0.1				
Elphidium williamsoni		0.5		1.1		0.1		0.1	1.0	0.3	1.2	2.6	0.5	2.6	5.3	8.9	23.5	19.1	10.7	15.0	7.6	10.6	10.9	7.2	6.3	10.6	4.6	7.3	9.1	1.3	2.1
Globigerina quinqueloba																	0.5			1.8	0.6	0.5	1.5	0.2	0.6	1.2	1.0	1.0	0.8	0.7	
Haplophragmoides spp.			0.5	1.6	1.5	2.0	1.2	2.5	3.3	2.8	2.3	1.5	3.3	2.3	1.3	0.9	0.5	0.7										0.1			
Haynesina germanica							0.2		0.2	0.5	0.3	1.2	2.2	4.8	11.6	25.7	35.9	42.9	41.5	36.9	45.7	46.9	51.0	41.3	49.4	44.2	52.8	44.3	39.5	42.6	36.0
Jadammina macrescens	100.0	76.3	66.0	62.8	69.3	70.7	76.5	72.9	69.5	71.4	63.9	52.8	44.1	49.0	52.0	42.0	12.6	7.2	9.8	11.9	1.3	1.8	1.6	2.1	5.9	2.8	3.5	6.0	7.2	4.9	5.0
Lagena elongata																							0.0	0.3				0.1		0.5	
Lagena sulcata																		0.2		2.3	2.1	0.4	0.5	0.8	0.6	1.0	0.3	1.3	0.2	2.2	0.7
Miliammina fusca		7.5	4.1	2.3	2.3	3.6	7.0	5.3	3.4	10.4	26.4	32.8	32.8	35.7	24.2	10.9	8.3	9.5	3.5	0.4				0.2	0.2	0.0	0.3	0.3	0.6	0.5	
Miliolinella subrotunda																											0.5			0.6	1.3	2.1
Patellina corrugata																						0.1									
Quinqueloculina spp.		0.1	0.6	0.4	0.8			0.2	0.9		0.4	0.2		0.2	0.2	5.3	4.5	10.0	15.7	5.6	8.3	0.2	1.3	0.9	0.4	1.6	1.0	1.0	1.8	7.5	11.4
Rosalina spp.																							0.2	0.6							
Spirillina vivipara																											0.1	0.1	0.1		
Stainforthia fusiformis																	0.7		1.7	8.3	3.8	7.1	6.7	7.5	6.1	6.3	3.9	3.9	4.4	4.2	2.9
Trochammina inflata		15.1	28.1	31.8	26.1	23.0	14.8	19.0	21.8	14.6	3.8	7.9	15.3	4.3	2.9	1.9	2.1	1.2	4.2		0.5	0.5			0.1						
Trochammina ochracea						0.6																0.1							0.9		
Total dead foraminifera (per 10cm³)	47	334	686	616	659	908	661	621	699	732	446	305	236	307	276	323	176	234	237	148	272	532	636	491	506	401	457	446	310	341	256

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Elevation (m OD)	3.24	2.86	2.81	2.57	2.47	2.42	2.38	2.33	2.27	2.22	2.18	2.22	2.17	2.14	2.09	2.04	1.99	1.94	1.88	1.74	1.52	1.32	1.13	0.93	0.72	0.54	0.36	0.17	-0.04	-0.22	-0.35
pH	5.4	6.0	6.0	6.1	6.1	6.1	6.1	6.1	6.8	6.8	6.9	6.9	6.7	6.7	6.6	6.6	6.9	6.9	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.8	6.9	6.9	6.8
LOI (%)	56.1	42.8	31.7	29.4	27.4	27.4	26.5	26.5	23.3	23.3	20.4	20.4	19.9	19.9	19.5	19.5	17.5	17.5	14.6	14.6	14.0	14.0	14.3	14.3	12.4	12.4	13.2	13.2	16.3	17.3	18.0
Porewater Salinity	8.6	15.5	15.2	15.3	21.0	21.0	18.7	18.7	23.0	23.0	20.8	20.8	23.6	23.6	18.0	18.0	15.8	15.8	14.5	14.5	13.6	13.6	11.5	11.5	12.3	12.3	12.3	12.3	13.4	13.5	13.7
Clay (%)	44.5	53.5	34.5	30.3	34.4	34.4	30.9	30.9	29.4	29.4	27.3	27.3	31.0	31.0	21.9	21.9	25.5	25.5	21.7	21.7	27.0	27.0	15.4	15.4	16.1	16.1	18.8	18.8	22.2	22.2	22.2
Vegetation cover (%)	96	96	96	89	83	70	67	58	49	58	54	51	28	26	26	23	5	5	1	0	0	0	0	0	0	0	0	0	0	0	0
Distance (m)	0	4	42	115	150	155	156	158	159	162	168	174	180	183	186	188	189	189	190	192	196	197	198	200	201	202	202	203	203	204	204

Kentra Bay	1	2	3	4	5	6	7	8
Elphidium williamsoni				6.3	53.3	100.0	100.0	100.0
Jadammina macrescens	98.2	75.0	98.4	59.4	12.0			
Miliammina fusca		12.1	0.3	15.6	24.0			
Trochammina inflata	1.8	12.9	1.3	18.8	10.7			
Total dead foraminifera (per 10cm³)	109	116	304	64	75	148	310	70
Elevation (m OD)	2.7	2.3	1.9	1.6	1.5	1.3	1.2	1.0
Distance (m)	0	20	50	82	100	120	138	160

Keyhaven Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13
Ammonia spp.			1.6		2.8	1.2	0.8	0.4			11.6	39.2	34.8
Eggerelloides scaber	0.4		0.8		0.8	0.4			11.2	3.2	29.4	39.6	15.2
Elphidium incertum	0.4					0.8						11.2	36.4
Elphidium williamsoni					1.6	7.2	1.6					3.6	8.8
Jadammina macrescens	60.4	30.0	34.8	46.8	37.6	41.6	9.2	35.2	40.8	17.2	18.1	2.0	2.0
Miliammina fusca	33.6	52.0	39.6	18.8	36.8	26.4	82.4	39.2	41.6	47.6	30.3	4.4	2.8
Quinqueloculina spp.	0.4				0.4	0.4							
Trochammina inflata	4.8	18.0	24.8	31.2	19.6	22.0	6.0	25.2	6.4	32.0	10.6		
Total dead foraminifera (per 10cm³)	222	250	341	543	765	897	1111	137	1431	1250	247	4444	5012
Elevation (m OD)	1.2	1.1	1.1	1.1	1.1	1.1	1.0	1.1	1.2	1.1	0.8	0.2	0.1
pH	7.5	7.5	7.5	7.3	7.3	7.5	7.6	7.3	7.5	7.4	7.2	6.8	6.5
LOI (%)	11.8	11.8	11.8	11.4	13.3	15.1	13.5	11.9	14.6	17.0	8.4	6.9	5.5
Porewater Salinity	36.9	38.7	40.5	36.8	37.6	37.4	37.1	36.9	38.5	39.6	36.4	36.0	35.8
Clay (%)	21.0	21.2	21.6	23.6	21.6	20.0	21.5	22.9	20.0	16.5	20.1	16.3	12.5
Vegetation cover (%)	50	100	90	90	60	75	80	100	100	80	25	0	0
Distance (m)	0	10	20	70	80	95	110	130	175	180	185	188	190

Newton Bay	1	2	3	4	5	6
Balticammina pseudomacrescens	1.4	1.2				
Elphidium williamsoni		0.7	2.2	1.3		1.9
Haplophragmoides spp.	12.1	3.3	4.9	5.3		
Haynesina germanica						3.8
Jadammina macrescens	33.6	43.7	50.9	46.5	39.2	64.2
Miliammina fusca	13.5	14.4	11.9	13.2	39.2	24.5
Quinqueloculina spp.	1.2	0.3	0.9	1.6	6.2	
Tiphotrocha comprimata	9.2	7.8	1.3		2.1	
Trochammina inflata	29.0	28.6	27.9	32.1	13.4	5.7
Total dead foraminifera (per 10cm³)	414	668	226	318	97	53
Elevation (m OD)	0.75	0.71	0.66	0.61	0.56	0.51
Distance (m)	0	10	12	15	22	34

Nith Estuary	1	2	3	4	5	6	7	8	9	10	11	12	13
Ammonia spp.					0.4	7.6	3.4	8.3	0.7	2.9	10.2	3.5	6.4
Brizalina pseudoplicata													1.2
Brizalina spathulata													4.6
Brizalina variabilis											3.1	7.0	5.5
Buccella frigida												1.7	5.5
Bulimina elongata													3.0
Bulimina gibba												1.7	
Bulimina marginata											2.0		1.5
Buliminella elegantissima									0.4			0.9	0.6
Cassidulina spp.												0.9	1.2
Cibicides lobatulus													4.9
Cibicides spp.												1.7	
Elphidium excavatum												2.6	5.8
Elphidium gerthi													1.5
Elphidium magellanicum													0.6
Elphidium margaritaceum													1.5
Elphidium spp.										0.4		3.5	1.2
Elphidium williamsoni							0.4		13.0	1.7		1.7	1.2
Glabratella millettii													2.4
Globigerina quinqueloba													1.8
Haplophragmoides spp.	8.2		1.8	6.4	5.8	2.9	3.8	1.4	17.0	8.6		2.6	
Haynesina germanica						1.0	0.4		2.2	4.6	12.2	32.2	34.5
Jadammina macrescens	91.8	97.5	95.5	78.9	71.2	51.4	27.0	37.3	26.4	57.1	66.3	28.7	5.5
Miliammina fusca		12.5	2.8	14.7	22.6	37.1	63.5	48.8	33.6	24.0	3.1	3.5	4.3
Neogloboquadrina pachyderma												0.9	
Nonion depressulus													3.0
Nonionella spp.													0.3
Oolina spp.													0.3
Oolina williamsoni													0.3
Planorbulina mediterranensis													0.3
Reophax moniliformis							1.1					0.9	
Rosalina anomala												2.6	0.3
Stainforthia fusiformis												0.9	
Tiphotrocha comprimata									0.4				
Trifarina spp.												0.9	
Trochammina inflata							0.4	3.7	6.0	1.1	3.1	1.7	0.6
Trochammina ochracea								0.5					
Total dead foraminifera (per 10cm³)	49	64	436	816	452	105	526	868	2212	700	393	230	328
Elevation (m OD)	5.4	5.3	5.2	5.1	4.9	4.7	4.7	4.7	4.7	4.7	4.6	4.7	2.5
Distance (m)	0.0	0.6	1.2	2.0	3.3	5.0	6.7	8.3	10.0	12.7	19.3	25.9	34.7

Roudsea Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Ammonia spp.			1.0	1.8		3.4	1.8	2.4	3.6	4.2	5.7	7.5	12.8	14.4
Amphicoryna scalaris										0.3				
Asterigerinata mamilla														0.9
Brizalina inflata													0.3	
Brizalina pseudoplicata								0.7						
Brizalina pseudopunctata											1.5	2.1		0.9
Brizalina spathulata								1.2	0.7	3.6	3.6	2.4	0.9	2.1
Brizalina variabilis			0.8	0.9		0.2	1.4	3.2	3.3	7.9	3.6	2.1	2.0	3.3
Buccella frigida			0.5	0.7		0.4	0.2	4.6	11.9	9.7	10.0	9.0	10.5	11.4
Bulimina elongata			0.3	0.2				1.2	1.0	1.5	1.8	2.4	2.3	3.3
Bulimina marginata				0.2				0.2	1.3		1.2	0.9	1.2	1.5
Buliminella elegantissima							0.2	0.5		0.9	0.3		0.3	
Cancris spp.														0.3
Cassidulina obtusa											0.6	1.5	0.6	0.3
Cassidulina spp.														
Cibicides lobatulus						0.2		0.5	3.0	3.6	3.6	3.9	9.0	12.6
Clavulina obscura												0.3		
Elphidium "earlandi"									0.3					
Elphidium excavatum						0.4	3.2	1.2	4.6	5.8	4.0	5.4	7.9	10.5
Elphidium gerthi				0.5					1.0	1.8	4.9	5.1	4.7	4.2
Elphidium macellum														0.6
Elphidium magellanicum			0.3	0.9	0.5				5.6	4.6	4.3	5.4	2.3	1.5
Elphidium margaritaceum			0.3	0.7				0.5	4.3	2.4	2.7	1.2	2.0	2.1
Elphidium spp.										1.5	1.5		0.9	2.1
Elphidium williamsoni			1.8	5.0	22.1	3.2	5.8	11.0	7.0	5.5	6.1	1.8	2.3	0.6
Fissurina elliptica											0.3			
Fissurina lucida			0.3	0.2			0.2	0.2	1.3	0.9	0.3	0.9	0.3	0.6
Fissurina marginata														
Glabratella millettii				0.2				2.4	2.0	1.5	4.0	7.5	3.2	6.6
Globigerina quinqueloba										0.6	0.3	0.3	1.5	1.2
Haplophragmoides spp.	15.9	24.3	11.1	0.2		1.1								
Haynesina germanica			7.3	5.2	4.4	8.4	19.8	27.6	31.5	23.4	28.6	28.1	19.5	4.8
Islandiella islandica												0.3		0.6
Jadammina macrescens	80.4	70.3	55.7	10.0	16.3	31.6	12.2	32.8	0.7	11.9	0.3	0.3		
Lagena clavata									0.3	0.3		0.3		
Massilina secans									1.3					
Miliammina fusca	3.7	5.4	16.7	45.7	28.2	34.4	47.5	7.8	3.0		0.3			
Miliolinella subrotunda													0.3	
Nonion depressulus						0.2		0.5	8.3	2.4	6.7	6.3	9.9	10.2
Nonionella spp.												0.3	0.3	
Nonionella turgida										1.2				
Oolina williamsoni										0.3	0.3	0.3	0.6	0.3
Patellina corrugata									0.3			0.3		
Planorbulina mediterranensis												0.9	0.3	0.3
Quinqueloculina spp.			3.3	22.5	23.8	14.1	7.4	0.7	1.7		1.8	3.0	1.8	0.9
Rosalina anomala													1.5	0.6
Rosalina spp.										3.6	1.2			
Spirillina vivipara			0.3	4.5	4.1									
Stainforthia fusiformis			0.3	0.2			0.2	0.5	1.0	0.3		0.3		
Tiphotrocha comprimata			0.3								0.3			
Trifarina angulosa									0.7			0.3	0.9	1.2
Trochammina inflata					0.7	2.3			0.3					
Trochammina squamata				0.2										
Total dead foraminifera (per 10cm³)	107	74	395	440	412	474	434	409	302	329	329	335	343	333
Elevation (m OD)	5.63	5.36	5.07	4.86	4.86	4.86	4.86	4.92	4.48	4.44	4.17	4.11	3.68	3.40
Distance (m)	0	4	11	17	19	21	23	28	35	37	41	43	65	92

Rusheen Bay I	1	2	3	4	5	6	7	8	9
Ammonia spp.			2.5	2.5	1.0	3.0	6.5	0.5	4.5
Elphidium incertum			30.8	17.6	27.4	23.0	16.5		16.9
Elphidium spp.			2.5	20.4	17.0	4.5	2.0	3.0
Elphidium williamsoni			22.4	15.7	1.0	6.0	15.0	14.3	11.9
Glabratella millettii			2.0						
Haynesina germanica			35.8	61.8	50.2	51.0	57.0	83.3	61.2
Jadammina macrescens	88.6	64.0	3.5				0.5		1.0
Quinqueloculina spp.									0.5
Trochammina inflata	10.9	35.5	3.0						1.0
Trochammina ochracea	0.5	0.5							
Total dead foraminifera (per 10cm³)	201	203	201	204	201	200	200	203	201
Elevation (m OD)	2.44	1.44	0.44	0.34	0.06	0.31	-0.11	-0.56	-0.16
Distance (m)	0	7	9	18	40	69	96	118	128

Rusheen Bay II	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Ammonia spp.								0.9	1.8	6.5	5.9	5.4	4.7	2.4	10.4	5.2	12.5	7.5	6.2	7.0
Elphidium incertum								5.3	74.3	79.1	81.0	76.7	77.4	79.7	71.1	69.7	59.0	66.8	72.7	51.2
Elphidium spp.									2.3		2.3		5.7	4.8	1.0	4.7	1.0	3.3	2.4	2.9
Elphidium williamsoni					1.0		1.5	2.2	11.7	5.0	6.8	10.4	7.5	7.7	11.9	19.0	21.5	19.5	11.5	17.6
Glabratella millettii								2.2	5.0	4.0	2.7	5.0	2.8	3.4	3.5		4.0	1.7	1.9	2.9
Haynesina germanica								0.4	1.8		1.4								2.9	17.2
Jadammina macrescens	69.3	62.7	40.8	73.3	74.1	88.7	41.5	19.6					0.5							
Lagena sulcata								0.4	1.8	1.5		1.0	0.5	1.9	0.5	0.5		1.2	1.0	0.8
Quinqueloculina spp.	5.8	1.5		3.0	3.4	1.5	28.5	53.8	1.4	4.0		1.5	0.9		1.5	0.5	2.0		1.4	0.4
Trochammina inflata	24.1	35.8	59.2	23.8	21.5	9.8	28.5	15.1							0.5					
Trochammina ochracea	0.7																			
Total dead foraminifera (per 10cm³)	137	204	201	202	205	204	200	225	222	201	221	202	212	207	201	211	200	241	209	244
Elevation (m OD)	2.64	2.49	2.34	2.19	2.04	1.89	1.44	1.29	1.14	0.94	0.84	0.69	0.84	0.69	0.54	0.39	0.24	0.19	0.34	0.49
Distance (m)	0	1	2	6	8	9	11	13	15	17	21	25	39	41	43	44	46	48	54	56

Thornham Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Ammonia spp.			0.6	0.4		0.4	1.5	1.3	1.5	5.5	10.1	16.6	28.9		6.6	8.9	14.5	25.3	22.2	27.3	21.7	50.9	38.7	70.9
Brizalina variabilis												0.2												
Cassidulina obtusa										0.4		0.6					2.0	0.8	0.6					
Cibicides lobatulus										0.7	0.7	1.8	6.0	2.4	4.1	0.7	8.8	2.9	1.3	4.2	2.2	5.8	3.7	0.3
Cyclogyra involvens			6.6	4.3		0.7	1.7		2.3	9.9	1.0	5.5												
Elphidium "earlandi"			0.5	0.3	0.2	2.0			0.2	1.8	1.9	3.7	1.2		1.5		1.5	2.4	2.1	3.5	2.1	1.0	1.9	2.1
Elphidium excavatum										0.3	5.2	4.5	6.6	1.2	6.3	3.2	12.3	17.9	9.5	10.9	19.2	7.2	6.6	
Elphidium gerthi									1.9	0.7	1.7	2.3	1.8		1.7		1.5	5.4		1.5	1.2	3.3	1.2	
Elphidium incertum								0.2	0.9	0.9	2.2	3.0	1.2		1.5	2.5	2.2	3.7	4.9	8.1	6.0	4.7	5.3	0.5
Elphidium magellanicum								0.5			2.2	1.9								0.8	0.6			
Elphidium spp.																				0.7			0.3	
Elphidium williamsoni		1.0	0.7	0.3	6.4	18.6	10.2	3.9	8.7	22.4	6.8	15.2	13.0		12.7	3.2	7.6	9.6	10.0	10.3	10.2	7.0	16.6	
Globigerina quinqueloba												0.6								1.3	0.6	0.5	0.6	
Haynesina germanica				4.4	5.8	10.0	6.4	6.2	13.6	36.5	24.8	27.8	14.2		3.7	4.3	15.2	14.1	27.3	20.6	15.3	14.7	13.1	12.5
Jadammina macrescens	100.0	77.3	34.8	47.7	35.7	28.4	42.6	40.5	34.1	15.2	14.9	11.0	11.6	72.9	46.2	65.4	22.1	10.5	8.5	9.2	5.2	2.1	3.1	
Lagena sulcata																	0.5		0.4					
Miliammina fusca		5.9	12.4	3.0	12.2	3.1	1.8		1.3			0.9												
Miliolinella subrotunda									0.3	0.6		0.2									5.5	1.0	1.4	12.5
Planorbulina mediterranensis										0.4		0.2					0.5	1.3	0.4	0.7	0.7	0.5		2.1
Quinqueloculina spp.		0.7	5.6	20.0	20.0	19.8	25.9	33.8	23.0	4.0	18.3	4.7					0.5				6.6			2.1
Rosalina spp.						1.3	0.4		0.2	0.4	0.4	1.1	4.9	1.2			2.0		1.1		0.6	0.5		
Stainforthia fusiformis											1.2													
Trochammina inflata		13.7	45.4	17.6	15.3	15.6	9.4	9.8	4.3	8.7	2.2	2.4	9.2	21.1	12.0	10.4	8.6	3.7	8.9	1.7	2.3	0.5	7.0	
Total dead foraminifera (per 10cm³)	32	716	1276	1156	1626	1506	2156	1984	1280	1720	1210	1436	464	368	276	552	608	444	736	540	848	860	1408	148
Elevation (m OD)	4.32	3.23	3.09	3.12	3.04	2.87	2.82	2.72	2.71	2.42	2.23	2.4	2.64	2.86	2.75	2.35	2.15	2.06	1.87	1.62	0.99	0.6	0.4	0.21
pH	5.3	5.8	5.8	6.1	6.2	6.5	6.5	6.5	6.5	6.5	6.7	6.1	6	5.8	6.1	6.1	6.1	6.1	6.3	6.5	6.7	7	7	7
LOI (%)	48.6	40.2	25.0	18.2	20.8	20.4	17.6	15.9	15.1	14.7	12.9	11.8	10.3	5.8	6.6	7.9	7.2	8.3	7.9	7.5	4.5	2.9	1.6	1.1
Porewater Salinity	6.9	8.4	9.1	11.5	11.1	10.6	10.4	11.9	12.6	10.5	9.7	11.9	12.1	14.4	14.2	21.1	15.4	9.2	12.5	14.0	18.3	25.8	25.1	24.6
Clay (%)	48.2	45.3	46.1	44.0	43.2	42.0	41.5	41.0	37.1	35.0	32.0	20.2	15.9	12.3	20.3	22.3	22.8	25.7	24.1	21.3	16.1	9.1	8.2	2.1
Vegetation cover (%)	100	100	100	100	100	100	100	100	100	100	90	90	90	70	20	15	15	10	10	5	1	0	0	0
Distance (m)	0	9	40	87	135	263	415	507	555	584	640	699	706	735	748	753	824	865	918	927	929	935	941	949

Tramaig Bay	1	2	3	4	5	6	7
Ammonia spp.						1.0	0.3
Brizalina spathulata						0.5	0.3
Brizalina variabilis						1.5	1.0
Buccella frigida						0.5	
Bulimina marginata							0.3
Cassidulina spp.							1.3
Cibicides lobatulus						10.1	35.3
Eggerelloides scaber					1.1		
Elphidium "earlandi"							0.3
Elphidium excavatum						3.0	1.3
Elphidium gerthi						0.5	1.0
Elphidium macellum						5.0	5.0
Elphidium magellanicum						1.0	0.7
Elphidium margaritaceum						11.6	25.3
Elphidium spp.						0.5	
Elphidium williamsoni						40.7	1.7
Fissurina lucida						0.5	
Glabratella millettii						1.5	1.0
Globigerina quinqueloba						1.0	1.0
Haplophragmoides spp.	8.9	5.8	0.3	4.8	0.5		
Haynesina germanica						4.0	3.7
Jadammina macrescens	75.9	49.5	39.0	69.8	26.2	9.0	
Miliammina fusca	5.1	16.7	11.5	15.1	67.8	2.5	
Nonion depressulus						2.0	19.0
Oolina hexagona						1.0	
Quinqueloculina spp.							0.7
Spirillina spp.						0.5	
Stainforthia fusiformis						0.5	
Textularia bockii							0.3
Textularia earlandi		0.3					
Tiphotrocha comprimata		0.6		1.6			
Trochammina inflata	1.3	26.7	49.2	4.8	3.3	1.0	
Trochammina ochracea	8.9	0.3		4.0	1.1	0.5	0.3
Total dead foraminifera (per 10cm³)	79	311	313	126	183	199	300
Elevation (m OD)	0.7	0.5	0.3	0.2	0.0	-0.4	-0.9
Distance (m)	0	10	23	58	93	148	215

Welwick Marsh	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Ammonia spp.	3.8	10.4	2.9	5.5	8.3	5.2	8.4	3.8	2.9	4.1	16.8	4.8	5.4	5.6	0.4		1.5			
Brizalina inflata	0.5		0.7			0.8		0.2		0.3		0.3	1.0	5.3	0.9	0.9	1.5	8.3		
Brizalina variabilis			0.3			3.6							0.5		0.4		2.8	1.6	4.8	
Cibicides lobatulus	0.5	0.5		0.4					0.7					0.6		0.9	1.5	1.6		
Cyclogyra involvens			0.3	0.6		1.0	0.2	0.2			1.4					0.9	2.2	1.6		
Elphidium "earlandi"		0.5						0.2			1.4	5.4					2.0			
Elphidium incertum			0.3														2.0			
Elphidium magellanicum	3.2	0.9	2.6	2.0	1.3	5.0		1.9	0.7		0.6	0.3	1.5	1.1	2.7		3.7	14.3	4.8	0.3
Elphidium williamsoni		0.9					0.3	4.8	2.1	2.6	8.4	7.2	7.4	0.3		1.6	0.7			
Globigerina quinqueloba	0.5	0.5	0.6		2.5	0.8	1.3				0.3	2.8	0.3	0.9						5.6
Haynesina germanica	83.3	84.3	88.6	90.4	72.0	83.7	78.7	88.6	87.7	89.9	69.5	78.8	69.7	48.3	59.6	65.4	42.9	10.3	14.3	11.0
Jadammina macrescens	1.9						3.6		2.1	1.1			7.8	32.2	24.6	14.8	18.1	52.1	72.2	76.7
Lagena elongata		0.5	0.3																2.4	
Lagena sulcata												0.3	0.5			1.6				
Miliammina fusca																				3.3
Miliolinella subrotunda																	1.5			
Patellina corrugata															2.5					
Quinqueloculina spp.	1.2	1.1	1.7	0.8	6.1	1.8	0.3	0.8	0.4	1.0	0.6	1.2	0.3	0.3	6.7				1.6	
Rosalina spp.													0.3		5.0					
Stainforthia fusiformis		0.5		0.2	4.4			1.1	2.0	0.8		0.6	1.0				3.0	3.2		
Trochammina inflata															3.6	2.5				
Trochammina ochracea	1.3		0.7		4.2		3.6							0.3		2.4	2.0	7.1		
Total dead foraminifera (per 10cm³)	1267	171	115	275	174	193	297	399	417	335	723	453	1253	1417	407	317	710	690	884	604
Elevation (m OD)	3.54	3.48	3.40	3.37	3.29	3.14	3.09	2.95	2.91	2.74	2.71	2.69	2.67	2.68	2.66	2.64	2.60	2.55	2.45	2.50
pH	6.1	6.5	6.3	6.1	6.55	7	6.75	6.5	6.5	6.5	6.5	6.5	6.5	6.5	6.75	7	7	7	7.15	7.3
LOI (%)	14.9	14.6	14.3	14.1	13.9	13.8	14.3	14.9	14.7	14.6	13.7	12.8	12.6	12.5	12.8	13.2	12.3	11.4	11.0	10.6
Porewater Salinity	7.8	4.9	4.0	3.0	5.1	7.2	8.2	9.1	10.6	12.1	10.2	8.2	8.2	8.2	10.4	12.5	12.0	11.6	10.5	9.4
Clay (%)	39.5	25.7	26.6	27.4	31.5	35.6	33.2	30.7	32.4	34.1	31.2	28.3	28.4	28.5	27.2	25.9	23.3	20.6	22.0	23.3
Vegetation cover (%)	100	100	100	100	90	80	70	60	55	50	40	30	23	15	10	5	5	5	3	0
Distance (m)	0	92	101	131	153	174	182	190	195	206	214	217	220	221	224	228	237	245	270	302

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