

RRH: CROATIAN COAST SALT MARSH FORAMINIFERA

LRH: SHAW AND OTHERS

RRH: SALT-MARSH FORAMINIFERA AND SEA LEVEL

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CONTEMPORARY SALT-MARSH FORAMINIFERAL DISTRIBUTION FROM THE  
ADRIATIC COAST OF CROATIA AND ITS POTENTIAL FOR SEA-LEVEL STUDIES

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## ABSTRACT

Salt-marsh foraminifera serve as proxy sea-level indicators due to a quantifiable relationship with elevation in the contemporary environment. In this paper, we document the distribution of salt-marsh foraminifera from two microtidal sites, Jadrtovac and Blace, along the Adriatic coast of Croatia and assess their suitability as proxies for elevation in transfer-function-based reconstructions of sea level, which has so far evaded the Mediterranean region. The assemblages are dominated by typical salt-marsh agglutinated taxa, *Jadammina macrescens* and *Trochammina inflata*, and the calcareous taxa *Ammonia* spp. and *Quinqueloculina* spp. Quantitative analyses revealed that the assemblages are divided into three faunal zones, which are elevation dependent, and where an assemblage dominated by *J. macrescens* and *T. inflata* extends to higher elevations in the intertidal frame. The training set was used to develop a tidal-level transfer function using linear regression due to the short environmental gradients observed. The model predicts sea level with a precision of  $\pm 0.08$  m. This study highlights the strong potential of salt-marsh foraminifera in reconstructing RSL trends for the Mediterranean region, where studies of past sea-level have previously been restricted to other indicators.

## INTRODUCTION

The application of salt-marsh sediments and microfossils (e.g., foraminifera, diatoms and testate amoebae) in reconstructing relative sea level (RSL) has extended our knowledge of sea-level change beyond the limits of direct observations (i.e., tide-gauges) that are, at best, restricted to the past ~250 years or so (Woodworth, 1999). Salt-marsh sediments and, in particular, foraminifera have proven useful in providing supplementary evidence to assess the timing of recent accelerations in sea level (Gehrels & Woodworth, 2013) and can be regarded as natural archives comparable to tide-gauge records (e.g., Barlow et al., 2013), permitting sea-level inferences as far back in time as the sediments reliably allow. In addition, proxy-based reconstructions have also helped provide an insight into the spatial and temporal variability of Late Holocene sea-level trends (Kemp et al., 2011; 2013; Barlow et al., 2014; Long et al., 2014).

The premise of using salt-marsh foraminifera as markers for former sea levels stems from an established, quantifiable relationship with tidal level in the modern environment (e.g., Scott & Medioli, 1978, 1980a, 1986), referred to as the indicative meaning (Shennan, 1982, 1986; van de Plassche, 1986). This intrinsic connection forms narrow vertical niches in which characteristic assemblages occur in abundance, allowing sub-environments to be identified based on the tolerance or preference to limiting ecological parameters, such as frequency and duration of tidal flooding, sub-aerial exposure, salinity, substrate composition and food availability (de Rijk, 1995; de Rijk & Troelstra, 1997; Berkeley et al., 2007). Despite differences in climate, tidal regime and site characteristics (e.g., vegetation and salinity), this vertical zonation is persistent

across many salt-marsh and mangrove environments where similar foraminiferal assemblages are observed (Edwards & Wright, 2015; fig. 13.1).

Typically, agglutinated foraminifera are restricted to the vegetated salt-marsh platform where the common high-marsh species, *Jadammina macrescens* and *Trochammina inflata*, are consistently found in the upper reaches of the tidal frame. Indeed, Scott & Medioli (1978) suggested that monospecific assemblages of *J. macrescens* could be used to relocate (both vertically and in time) past sea level to within  $\pm 0.05$  m when applied to fossil counterparts found in sediment cores. Along the environmental gradient towards lower intertidal and unvegetated tidal-flat environments, a transition in assemblage composition occurs, reflecting a change in indicative range (Edwards et al., 2004; Leorri et al., 2010; Kemp et al., 2012; Strachan et al., 2015). While there is much similarity in the spatial distribution of intertidal foraminiferal assemblages, variability between sample sites with respect to their position in the tidal frame is not uniform, necessitating the need for site-specific data (Horton & Edwards, 2006).

Research on the distribution of foraminifera across salt-marsh environments for the purpose of sea-level reconstruction for the Mediterranean region is lacking in the published literature (e.g., Petrucci et al., 1983). The Mediterranean, and in particular Adriatic Sea, offers ideal conditions for a study of this type due to the typically low wave-energy conditions and microtidal regime. The foremost conclusion drawn from using salt-marsh foraminifera in RSL studies is the improved accuracy when conducted under microtidal settings in reducing the vertical uncertainties involved (Horton & Edwards, 2006; Southall et al., 2006; Callard et al., 2011; Mills et al., 2013; Barlow et al., 2013). While benthic foraminifera are well documented in the Adriatic Sea (e.g., Jorissen, 1987, 1988), previous research in this region has primarily

focused on the use of intertidal foraminifera as indicators of pollution histories (e.g., Coccioni, 2000; Albani et al., 2007; Frontalini & Coccioni, 2008; Frontalini et al., 2010).

Expressing biological indicators (e.g., foraminifera) as a function of an environmental variable (e.g., tidal level), known as a transfer function (Imbrie & Kipp, 1971), first requires an understanding of the contemporary environment and how the two are related. In this paper we present the first quantified, contemporary, surface-foraminiferal distributions from two microtidal salt-marsh sites along the Adriatic coast of Croatia (Fig. 1a) and assess their suitability for reconstructing former sea level through the development of a tidal-level transfer function.

## STUDY AREA

The Croatian coastline is predominantly rocky and steep with numerous pockets of sand and gravel beaches and few alluvial zones (Baric et al., 2008). The karstic nature of the coastline makes vegetated coastal sedimentary environments a rare habitat for this region, with only one large alluvial plain along the coastline at the Neretva Delta towards the south. A limited amount of research exists on salt-marsh environments in the eastern Adriatic region, with most studies focusing on the Italian and northern shoreline, primarily from a pollution perspective (e.g., Frontalini & Coccioni, 2011). The coastal wetland environments along the Croatian coast have also become increasingly threatened by human activity, as increased tourism development has converted these habitats to beaches (Pandža et al., 2007). A review of salt-marsh vegetation by Pandža et al. (2007) for the central and south-eastern Adriatic, however, identified eight

ecologically important sites and two of the sites considered, Jadrtovac (Fig. 1b) and Blace (Fig. 1c), are the focus of this investigation.

Jadrtovac is a small coastal town situated within Morinje Bay (43°40'48"N, 15°57'24"E), approximately 3 km south of Šibenik and 50 km north of Split, central Croatia. With a surface area of 3.5 km<sup>2</sup> and a maximum water depth of 21 m, the bay can be divided into two sections, a shallow northern region and a deeper southern channel (Mihelčić et al., 2006). Communication with the open Adriatic Sea occurs through 2.5 km-long channel (150–350 m wide). A relatively high sedimentation rate of 1.0 m/ka has resulted in the accumulation of 4.5 m of organic-rich sediment, which began approximately 4.5 ka BP as the Morinje depression was inundated during the latter stages of the Holocene transgression (Bačani et al., 2004; Šparica et al., 2005). The salt-marsh is located on the eastern side of the bay (Fig. 1b) and is roughly 130 m at its widest point before thinning out to the north around the bay. No tidal-flat environment is exposed at Jadrtovac and the low salt-marsh/sea interface is characterized by a micro-cliff edge 10-20 cm high. The salt marsh displays distinct zones of vegetation with *Juncus* spp., *Halimione*, *Atriplex*, *Scirpus* spp., *Phragmites* and occasional *Suaeda* spp. colonising higher elevations in the upper salt-marsh zone, while mid- to low salt-marsh zones are dominated by *Halimione* spp., *Salicornia* spp. and again occasional *Suaeda* spp. The salt marsh is intersected in the middle by a narrow (~2 m) man-made channel (which was avoided for sampling), presumably for drainage and local fishing access to the bay. The mean daily tidal range at this site is approximately 23 cm, derived from values obtained at the nearby Split tide-gauge (Table 1; Hydrographic Institute, 1956-2000).

Blace is a similarly small coastal town bordering the Adriatic Sea (43°00'15"N, 17°28'27"E) approximately 120 km south of Jadrtovac. This site comprises a remote small

pocket salt-marsh just north of the town, approximately 3 km south of the Neretva River delta, the largest outflow along the Croatian coastline with a large, 12,000 hectare alluvial plain, representing an important ecological and agricultural site (Romić et al., 2008) and recognized under the Ramsar Convention since 1993. The studied salt marsh is roughly 40 m wide and located within a sheltered embayment from the open Adriatic Sea. Distinct zones of vegetation are again apparent, with *Juncus* spp. and members of the Chenopodiaceae family (e.g., *Halimione* spp.) dominating high- to mid-salt-marsh zones; *Limonium* spp. and *Salicornia* spp. dominate the mid- to low salt marsh. The mean daily tidal range at this site is almost identical to Jadrtovac at 23 cm, as taken from values from the nearby Ploče tide-gauge (Hydrographic Institute, 1956-2000).

## METHODOLOGY

### FIELD SAMPLING

To quantify the relationship between elevation and foraminiferal assemblages, modern surface samples were collected to develop a training set suitable for use in constructing a tidal-level transfer function. At both sites, sample stations were established across two separate transects running perpendicular to the coast, incorporating all sub-environments from the high salt marsh to the low salt marsh/sea interface, following Scott & Medioli (1980a). While sampling frequency varied between sample sites, it was focused around areas of topographical and/or floral community change. To reduce the potential effects of seasonality on surface

foraminiferal distributions, as discussed by Horton & Edwards (2003, 2006), field work was conducted during winter months (January 2010).

Sediment samples of a standardised volume (10 cm<sup>3</sup>) were collected from the upper 1 cm of the salt-marsh surface for foraminiferal analyses. Specific details regarding the sampling procedure are provided in Edwards & Wright (2015) and follows the commonly adopted sampling depth of 1 cm for studies analyzing modern foraminiferal distributions from salt-marsh environments (e.g., Scott & Medioli, 1980a; Horton et al., 1999a; Gehrels et al., 2001; Edwards et al., 2004; Kemp et al., 2009a, 2012). This assumes the foraminiferal assemblages used are primarily epifaunal. Some studies, however, have highlighted the importance of infaunal populations and their potential implications for sea-level reconstructions (i.e., mixing of live foraminifera with fossil assemblages) (Tobin et al., 2005). Indeed this has shown to be evident from studies of North American salt marshes where infaunal populations can be significant (Ozarko et al., 1997; Hippensteel et al., 2002; Duchemin et al., 2005; Tobin et al., 2005). In contrast, studies from European saltmarshes have found infaunal populations to be less significant (Horton, 1997; Alve & Murray, 2001; Horton & Edwards, 2006). While the population of infaunal foraminifera may be variable and site specific, differences in these observations may in part reflect the organic nature of northern American salt-marsh environments compared to their more minerogenic European counterparts, which restrict the penetration of subsurface foraminifera (Horton, 1999). Nonetheless, using a sampling depth interval incorporating the upper 1 cm of the salt-marsh sediment surface provides an adequate model from which palaeoenvironmental reconstructions can be based (Culver & Horton, 2005; Horton & Edwards, 2006). To establish absolute altitudes, sample stations were surveyed relative to Croatian national geodetic benchmarks (m HVRS71) using Real Time Kinetic (RTK) satellite



navigation in conjunction with Leica Na820 optical levelling apparatus referenced to local benchmarks.

## FORAMINIFERAL ANALYSES

While in the field, samples were immersed using the protein stain, rose Bengal (Walton, 1952), to differentiate ‘living’ foraminifera at the time of collection; samples were stored in buffered ethanol (Edwards & Wright, 2015). Despite some contention (e.g., Bernhard, 2000; Bernhard et al., 2006), this technique is widely adopted amongst the research community and represents an effective way of staining live foraminifera (Murray & Bowser, 2000; Figueira et al., 2012). Sample preparation followed that outlined by Horton & Edwards (2006), i.e., wet sieving sediment to isolate the 63  $\mu\text{m}$  to 500  $\mu\text{m}$  fraction before transferring into a wet splitter (Scott & Hermelin, 1993), dividing the sample into eight equal aliquots. The >500  $\mu\text{m}$  fraction and supernatant were checked periodically for foraminiferal tests before being discarded. Foraminifera were counted wet under a stereo microscope at 63x magnification until a minimum of 100 (dead) specimens was reached. The precise number required to produce reliable statistical results is proportional to the relative abundance of taxa observed and the accuracy required specific to the study (Patterson & Fishbein, 1989; Fatela & Taborda, 2002). Counts of ~100, however, are statistically robust given the low diversity assemblages typical of salt-marsh environments (Edwards & Wright, 2015), and this threshold was easily surpassed in most samples (Appendix B). Relatively few living (stained) foraminiferal tests were found in the samples at the time of collection. Our statistical analysis and interpretation is therefore based on the relative abundance (%) of dead foraminiferal assemblages only (following Gehrels et al.,

2001; Horton & Edwards, 2003; Leorri et al., 2010; Rossi et al., 2011; Kemp et al., 2013), which are less susceptible to seasonal (Murray, 1991) and/or post-depositional changes (Horton & Edwards, 2006). Foraminiferal assemblages can suffer from test destruction through dissolution in intertidal environments (e.g., Murray, 1989; Berkeley et al., 2007) caused by acidic conditions often associated with salt-marsh sediments (Scott & Medioli, 1980a). However, we observed no obvious sign of this taphonomic process in the samples analyzed.

Foraminiferal taxonomy was confirmed through comparison with type specimens logged at the Smithsonian Institution, Washington, DC, and Scanning Electron Microscope (SEM) images of salt-marsh foraminifera from the published literature (e.g., Horton & Edwards, 2006; Appendix A). Figure 2 provides SEM images of the main foraminiferal taxa encountered in this study, which were captured using a Hitachi TM3000 Tabletop microscope. The various calcareous species of *Ammonia*, *Elphidium* and *Quinqueloculina* are grouped together at genus level following Horton & Edwards (2006) and Kemp et al. (2012). Raw counts of both ‘living’ and ‘dead’ foraminifera are provided in Appendix B.

## STATISTICAL ANALYSES

To identify faunal zones (clusters) based on similarities in the foraminiferal assemblages, unconstrained cluster analysis using unweighted Euclidean distance was performed using output from CONISS total sum of squares within *Tilia View* (Grimm, 2004). Elevation-dependent faunal zones were created for transects J-J<sub>1</sub> and B-B<sub>1</sub>, represented through box plots of cluster order (faunal zone) by height relative to vertical datum (m HVR571). Three surface samples (16,

17 and 18), taken from very similar locations and altitudes to sample stations 1 to 4 from transect B-B<sub>1</sub>, were also included in the analysis for Blace (Appendix B).

Surface data from additional transects at each site were included in developing a transfer function to maximize the full range of sub-environments studied, reduce the potential influence of spatial autocorrelation (Telford & Birks, 2005; Edwards & Wright, 2015) and improve reliability by increasing training set size (n=60) (Barlow et al., 2013; Kemp & Telford, 2015). The spatial scale from which training sets are derived can have important consequences for transfer-function performance in RSL studies (e.g., Watcham et al., 2013). While transfer functions based on local training sets may offer an increase in vertical precision, combining regional data provides a greater number of modern analogues and improvements in predictive power when applied to fossil counterparts (Horton & Edwards, 2005).

The utility of foraminiferal assemblages from salt-marsh environments as sea-level indicators is founded on their relationship with tidal level. Inter-correlation with other environmental parameters, however, can influence distribution patterns in explaining variance in modern training sets (e.g., Horton & Culver, 2008). While it is beyond the scope of this paper to document these in detail, Shaw (2013) studied the influence of elevation amongst other environmental variables (e.g., pH, salinity, organic matter and grain size) to confirm the suitability of salt-marsh foraminifera in transfer-function reconstructions. Within the observed inter-correlations between the variables, elevation within the tidal frame was statistically significant in explaining variance in the foraminiferal distributions from the sample sites presented. Following this, the combined training set was used to develop a transfer function quantifying the relationship between dead foraminiferal assemblages and tidal elevation.

Understanding species response, to thus derive ecological response functions (Horton & Edwards, 2006), first allows the selection of the most appropriate regression model based on the linear or unimodal distribution of training sets (Birks, 1995). Detrended canonical correspondence analysis (DCCA) was performed to determine the appropriate method (Birks, 1995; Leps & Smilauer, 2005) using CANOCO v4.5 (ter Braak & Šmilauer, 2002) and gradient lengths assessed in standard deviation units. Prior to analysis, low counts and insignificant species were removed, following Fatela & Taborda (2002). Usually, those species, which do not contribute more than 5% of the total dataset, are removed, however due to the low diversity of the studied salt-marsh environments this was amended to 2% (following Horton et al., 2003; Edwards et al., 2004). Species removed included *Balticammina pseudomacrescens*, *Haplophragmoides wilberti*, *Scherochorella moniliformis*, *Siphotrochammina lobata* and *Textularia earlandi*. A transfer function using linear-based partial least-squares (PLS) regression was developed using C<sup>2</sup> v1.7 (Juggins, 2003) due to the short gradient lengths observed (<2 SD units). The coefficient of determination ( $r^2$ ) and root mean-square error of prediction (RMSEP) were used to assess the strength of relationship and prediction error of the transfer function. As  $r^2$  and RMSEP can overestimate and underestimate the performance of the transfer function when applied to the whole dataset alone (Birks, 1995), cross-validation procedures through jack-knifing the data (ter Braak & Juggins, 1993) were also performed, providing a more robust and reliable assessment of the training sets predictive ability and error (Gehrels, 2000). Component selection followed the ‘principle of parsimony’ (Horton et al., 2003) in which the lowest component displaying low RMSEP under cross-validation and high  $r^2$  values was chosen (Birks, 1995). The influence of other environmental variables (e.g., salinity), may inevitably cause some samples within the dataset to show a weaker relationship with elevation, displaying a high

residual distance from the first ordination axis constrained by the environmental variable of interest (Birks, 1995). Outliers in the training set were therefore screened to remove surface samples with an absolute residual greater than the standard deviation (SD) of the environmental gradient, following Horton & Edwards (2006).

## RESULTS

### FORAMINIFERAL DISTRIBUTIONS

Thirteen foraminifera species were identified in the dead assemblages across a transect spanning 122 m, covering an altitudinal range of 0.44 m at Jadrtovac (Fig. 3). With a mean and maximum abundance of 2917 and 8820 individuals per 5 cm<sup>3</sup>, the total concentration of dead tests increased in the mid-low salt-marsh environment. The assemblages (living and dead) were dominated by agglutinated species, *J. macrescens* and *T. inflata*, and calcareous species, *Ammonia* spp. and *Quinqueloculina* spp. Increased sampling frequency was focused in the high salt-marsh environment from sample station 1 to 10, where an elevation change from 0.485 m to 0.095 m HVRs71 occurs over 13 m. A small altitudinal range is then observed across the remainder of the transect. The uppermost two samples were beyond the clearly identifiable limits of tidal inundation (HAT; 0.284 m HVRs71) and were devoid of statistically sufficient counts, with sample station 1 (0.48 m) containing no foraminiferal tests while sample station 2 (0.44 m) contained < 10. From station 3, 2 m along the transect, *J. macrescens* and *T. inflata* were present in every sample covering all of the sampled altitudinal range.

In the high salt-marsh environment, *T. inflata* dominated the assemblages between stations 3 and 9, exceeding 73% of the total count at station 9. Its relative abundance then rapidly decreased at sample station 10 (7%) and remained relatively low across the transect as *J. macrescens* became increasingly common, peaking at sample station 14 to 78% of the total count at 53 m. While relatively low counts of *Miliammina fusca* were observed, its presence was limited to the upper 40 m between high and mid salt-marsh environments, reaching 14% of the total count in station 6 at an altitude of 0.185 m. The reappearance of calcareous taxa (principally *Quinqueloculina* spp. and *Ammonia* spp.) in the mid-low salt-marsh environment, at sample stations 16 and 17, coincided with a significant decrease in the relative abundance of *J. macrescens* at 83 m along the transect.

Relatively few living foraminifera were present at the time of collection at Jadrtovac. A minimum count of 100 stained tests was achieved at only five sample stations (sample stations 10, 16, 17, 20 and 22). Only ten sample stations contained  $\geq 50$  foraminiferal specimens, (Appendix B). Species diversity was also limited in the living assemblage and dominated by *J. macrescens*, *T. inflata* and *Quinqueloculina* spp. Minor occurrences of other taxa (e.g., *M. fusca* and *Spirillina vivipara*) were observed.

Eleven species were identified across a transect spanning 29.2 m, with an elevation change of 0.35 m at Blace (Fig. 4). Again *J. macrescens*, *T. inflata* and *M. fusca* dominated the assemblages, together with *Quinqueloculina* spp., *Ammonia* spp., *Elphidium* spp., and *Haynesina germanica*. Tests were abundant, with a maximum concentration of 8210 individuals per 5 cm<sup>3</sup> occurring at sample station 11. In contrast to Jadrtovac, the abundance of dead tests decreased in the lower salt-marsh environment. With the exception of *Quinqueloculina* spp. in the upper 3 samples (up to 43% at 0 m), a clearer zonation between the foraminiferal assemblages was

observed at Blace. The transition to lower salt-marsh environment corresponded with an increase in the relative abundance of calcareous taxa and reduction of agglutinated forms. At 65% of the total count, *J. macrescens* peaked 2.5 m along the transect in the high salt-marsh, then gradually decreasing as the relative abundance of *T. inflata* increased to 66% at 12.5 m along the transect. Reaching 13% of the total count at 3.5 m along the transect, *M. fusca* was confined to the upper reaches of the salt-marsh environment (0.29 m HVR571). Moving into the mid-low salt-marsh, the above taxa were replaced by a more diverse calcareous assemblage, as *Ammonia* spp., *Elphidium* spp., *Quinqueloculina* spp. and *Spirillina vivipara* increased in abundance. The maximum occurrence of *Quinqueloculina* spp. occurred 22.5 m along the transect, peaking at 68% of the overall count at sample station 11. The lowermost sample stations were dominated by *Ammonia* spp., rising to 66% of the total count at sample station 14 (29.1 m along transect).

Live foraminifera were also uncommon at Blace compared to dead tests. Across all environments of the salt-marsh, the analyzed samples contained <100 living individuals each (Appendix B). Species diversity was similarly restricted, primarily comprising *J. macrescens*, *T. inflata* and *Quinqueloculina* spp.

#### DEVELOPMENT OF A TRANSFER FUNCTION

Unconstrained cluster analysis identifies three faunal zones at Jadrtovac (Fig. 5a). Zone JD-A is characterized by an exclusively agglutinated-dominated assemblage, dominated by *J. macrescens* (up to 77%) and *T. inflata* (up to 47%), with minor occurrences of *M. fusca* (up to 6%). This zone has a vertical range of 0.12 m, extending from 0.08 m to 0.20 m HVR571 (Fig. 5b). A decrease in the relative abundance of *J. macrescens* and the increase in *T. inflata* (up to

78%) characterizes zone JD-B; while the occurrence of calcareous taxa, *Elphidium* spp. and *Quinqueloculina* spp., and peaks of *M. fusca* are also notable. The occurrence of *Elphidium* spp. at higher elevations in sample stations 3 and 4 creates a larger vertical range for this zone (0.23 m) between 0.04 m and 0.27 m HVRs71. Comprising four samples, zone JD-C, is characterized by an increase in calcareous taxa (*Ammonia* spp. and *Quinqueloculina* spp.) and occupies elevations below MTL between 0.06 m and 0.11 m.

Similar faunal zones are identified at Blace (Fig. 5c). Zone BL-A is dominated by *J. macrescens* (up to 65%) and *T. inflata* (up to 65%) and covers an altitudinal range above MHWST of 0.28–0.40 m HVRs71 (Fig. 5d). Zone BL-B is characterized by a more diverse assemblage of agglutinated and calcareous taxa. *Quinqueloculina* spp. typically dominates (up to 68%), while *Ammonia* spp. (< 21%) are common, as are *Spirillina vivipara*, *J. macrescens* and *T. inflata*, reflecting the vertical range between 0.17 m and 0.37 m HVRs71. An overlap with faunal zone BL-A is due to the inclusion of sample stations 1 and 18, where relatively high abundances of *Quinqueloculina* spp. occur at higher elevations (>0.29 m HVRs71). The occurrence of *Quinqueloculina* spp. in these samples is similar to that observed from sample stations 2, 3 and 17 from faunal zone BL-A. Sample stations 14 and 15 in zone BL-C have vertical range below MTL between -0.01 m and 0.05 m HVRs71 and are dominated by calcareous species *Ammonia* spp. (up to 56%), *Elphidium* spp. (up to 16%), *Haynesina germanica* and *Quinqueloculina* spp. (up to 22%).

Results from DCCA revealed short gradient lengths for axis one (1.5 SD units; Table 2) indicating a linear species response in relation to elevation in the tidal frame. To improve predictive ability and remove sample outliers in the contemporary training set, surface samples with an absolute residual (observed minus predicted) greater than the standard deviation for



elevation (0.141 m) were removed. A statistical summary for the five components produced by an unscreened and screened PLS transfer function is provided in Table 3. Component 2 was chosen, which revealed an improvement in the strength of relationship ( $r^2_{\text{jack}} = 0.55$ ) and suggested precise reconstructions of former sea-level were possible ( $\text{RMSEP}_{\text{jack}} = \pm 0.08 \text{ m}$ ). Modelled elevations versus surveyed elevations illustrate this relationship and a bias in the training set towards the upper part of the elevational gradient, where the model both underestimates and overestimates the elevation of a number of samples (Fig. 6).

## DISCUSSION

### SALT-MARSH FORAMINIFERAL DISTRIBUTIONS

The distributions of salt-marsh foraminifera from two microtidal sites along the coast of Croatia were investigated to develop a potential proxy for tidal level in a transfer-function-based reconstruction of past sea level. Similarities in assemblage composition and their position in the tidal frame with previous studies of salt-marsh foraminifera imply that RSL studies adopting this approach are well suited to sites in microtidal settings. The foraminiferal assemblages at Jadrtovac and Blace were broadly similar throughout, where cluster analysis identified three faunal zones (Fig. 5). The main foraminiferal taxa observed included agglutinated species *J. macrescens*, *T. inflata*, *M. fusca*, and calcareous species *Ammonia* spp., *Elphidium* spp., *Haynesina germanica* and *Quinqueloculina* spp. Differences in the elevation extent of the faunal zones between each site, however, reflect the inter-site variability often observed in salt-marsh foraminiferal studies (e.g., Edwards et al., 2004; Edwards & Wright, 2015). Despite this, a

consistent overall pattern of intertidal vertical zonation is observed. Both transect datasets can be divided into agglutinated-dominated assemblages (JD-A and BL-A), which are prominent at higher elevations of the salt-marsh environment, and a calcareous-dominated assemblage (JD-C and BL-C), which typically occupies lower elevations in the mid-low salt-marsh environment. A mixed foraminiferal assemblage zone (JD-B and BL-B) created overlap between the faunal zones at both sites, implying that sea-level inferences made from such assemblages are less precise from these sites.

Faunal zones dominated by agglutinated assemblages (JD-A and BL-A), with high relative abundances of *J. macrescens* and *T. inflata* and relatively few calcareous taxa, extended from above MHWST to near MTL. The vertical range of this assemblage zone was the same between sites (0.12 m), however, at Blace, it reached a higher elevation by comparison to Jadrtovac, extending to 0.40 m HVRs71. A second mixed faunal zone (JD-B and BL-B), again with relatively high abundances of *J. macrescens* and *T. inflata* coupled with an increased calcareous input (e.g., *Quinqueloculina* spp), spanned a greater vertical range also from around MHWST to below MTL. At Jadrtovac, this extended to 0.04 m HVRs71. A third faunal zone (JD-C and BL-C), characterized by an increased abundance of calcareous taxa (notably *Ammonia* spp. and *Quinqueloculina* spp.), was also observed and was vertically constrained below MTL. These distributions resemble typically observed intertidal zonation patterns whereby agglutinated species, *J. macrescens* and *T. inflata*, consistently dominate around MHWST in salt-marsh and mangrove environments (de Rijk & Troelstra, 1997; Horton et al., 1999b; Horton et al., 2003; Edwards et al., 2004). Calcareous foraminifera, including *Ammonia* spp., *Elphidium* spp and *Quinqueloculina* spp., however are more indicative of lower vegetated salt-marsh and mudflat environments (de Rijk & Troelstra, 1997; Horton et al., 1999b; Woodroffe et al., 2005).

The lack of comparative studies concerning the vertical zonation of intertidal foraminiferal assemblages for the purpose of sea-level studies on the Croatian coast hinders direct assessment of our findings at a local level. However, similarities with studies from salt-marshes in the northern Adriatic are possible; these display similar characteristics to the assemblage zones observed in this study. Using foraminiferal distributions to identify biotopes that characterize different environments in the Venice Lagoon, similarly high abundances of *T. inflata* have been reported (e.g., Serandrei-Barbero et al., 1999, 2011; Albani et al., 2007). In these studies, the genus *Trochammina* characterizes two altimetric zones between MSL and mean high water level (MHWL) (Petrucci et al., 1983; Serandrei-Barbero et al., 1997, 1999) and also the zone above MHWL (Albani et al., 1984). Indeed Petrucci et al. (1983) showed a *T. inflata*-dominated assemblage to indicate a ground height of about 15 cm above the local MSL in the Venice Lagoon area. Utilizing foraminiferal distributions as ecological indicators, Albani et al. (2007) also observed foraminiferal assemblages dominated by *T. inflata* (>60%) to be indicative of an environment above MSL. The authors also demonstrate that high abundances of calcareous species, *Ammonia* spp. and *Haynesina germanica*, characterize inner areas of the lagoon environment, which are influenced by more marine waters. The foraminiferal distributions from Jadrtovac and Blace parallel these observations, supporting their potential as proxies for tidal level in paleo-RSL reconstructions.

The quantitative analyses focused solely on dead foraminiferal assemblages. The selection of the most appropriate foraminiferal assemblage can have important effects on transfer-function performance. The choice of which assemblage should be used (e.g., Jorissen & Wittling, 1999) remains a discussion topic in salt-marsh-based foraminiferal RSL reconstructions. Several authors have argued that total (i.e., living and dead) assemblages are an

accurate representation of the modern environment and so offer a more reliable model in palaeoenvironmental reconstructions (e.g., Scott & Medioli, 1980b; Gehrels, 1994; Hayward et al., 1999a; Tobin et al., 2005). However, incorporating living assemblages into a training set includes foraminifera which are suited to the environmental conditions at the time of sampling (Callard et al., 2011). As this will fluctuate in line with seasonal changes, species diversity and abundance can change over time (Murray, 1991; 2000; Horton et al., 1999a). In a comprehensive study of foraminiferal assemblages from Cowpen Marsh, Great Britain, Horton (1999) concluded, dead foraminiferal populations are a better analogue for sub-surface samples in sea-level reconstructions. Using dead foraminiferal assemblages takes into account both live and dead populations over a greater time-average and so species diversity is generally greater (Murray, 1982, 2003).

The analyzed environments in this study contained very few living specimens by comparison to dead tests. Indeed many of the samples were void of living foraminiferal tests altogether. The contrast between concentrations of living and dead foraminifera is a common feature characterizing low sedimentation environments (Murray, 1976). Our observations from Jadrtovac and Blace conform to previous analyses of foraminiferal assemblages along the coast of Croatia. Cosovic et al. (2006) collected sediments from sample stations along transects extending from the coast out towards the open sea, up to depths of 55 m, and revealed dead foraminiferal tests to be much more abundant regardless of sampling season. Other studies near the Gulf of Venice have also shown greater concentration and increased species diversity in dead foraminiferal assemblages (Serandrei-Barbero et al., 2003).

Anomalously high abundances of *Quinqueloculina* spp. were observed at upper elevations at Blace (Fig. 4) and may be explained by strong, regional winds enabling miliolid

shells into areas where agglutinated taxa (e.g. *J. macrescens* and *T. inflata*) typically dominate. The influence of winds can significantly affect tidal regimes in intertidal environments (Allen, 2000; Kim et al., 2011; Bartholdy, 2012). In the Adriatic region, meteorological forcing associated with low atmospheric pressure coupled with persistent north-easterly Bora and south-easterly Sirocco winds can considerably alter tidal amplitude (Orlić et al., 1994; Raicich, 2003; Ferla et al., 2007). The influx of an allochthonous component into surface samples from higher elevations may have important consequences for the predictive ability of foraminiferal-based transfer functions, essentially broadening the vertical range of calcareous taxa. Inevitably, their inclusion will have an adverse effect on the strength of relationship with tidal level and so may warrant their removal from the training set if it can be justified in the context of a clearly identifiable allochthonous contribution. Such assessment of modern training sets prior to fossil calibration is regarded a useful procedure (Birks, 1995; Horton and Edwards, 2006).

#### POTENTIAL OF MEDITERRANEAN SALT-MARSH FORAMINIFERA TO RECONSTRUCT RSL TRENDS.

Using a training set derived from Jadrtovac and Blace, we developed a PLS transfer function for tidal level. Linear regression and calibration methods are typically less common in quantitative RSL reconstructions due to the often observed unimodal distribution of foraminiferal species in response to elevation in the tidal frame. However, the results from this study are comparable to other studies where PLS transfer functions have been employed. For example, in a study of foraminiferal distributions from Brittany, France, Rossi et al. (2011) also observed short environmental gradients (0.67 SD units), based on a modern training set comprising 36 surface samples. The authors demonstrated robust transfer-function performance

( $r^2_{\text{jack}} = 0.70$  ;  $\text{RMSEP}_{\text{jack}} = 0.07 \text{ m}$ ) and applied their PLS model to reconstruct RSL changes dating to AD 1850, showing comparable rates of change to direct observations from the nearby Brest tide-gauge. Using 43 samples from Tasmania, Callard et al. (2011) also used linear regression methods, although advocate caution in this approach. They showed that while PLS produced good statistical parameters and was comparable to unimodal, weighted-averaging, partial least-squares (WA-PLS) regression, unreliable predictions were produced in which the proxy reconstruction estimates were greater than both the sampled environment and tidal range.

Developing transfer-function models from within microtidal environments helps minimize vertical uncertainties, enabling more precise RSL reconstructions by comparison to those conducted under macrotidal settings (Southall et al., 2006; Callard et al., 2011; Barlow et al., 2013). The sampled vertical range of the contemporary training set has a strong impact on a model's predictive ability (Mills et al., 2013). The driver for foraminiferal vertical zonation in extreme microtidal environments, however, can be weaker by comparison to macrotidal settings and directly related to the small vertical range (Horton & Edwards, 2006) where other environmental parameters, such as salinity, can become important (Barlow et al., 2013). Prediction errors should typically be proportional to the tidal range at the sample site, hence the benefit of studies under microtidal regimes. A tidal range of ~20 cm should provide prediction errors of approximately 10% of the tidal range (i.e., ~2 cm) (Barlow et al., 2013). Where the strength of relationship observed is weaker, prediction errors ( $\text{RMSEP}_{\text{jack}}$ ) may offer a more realistic assessment of the model performance (Gehrels et al., 2001; Leorri et al., 2010). Based on the contemporary training set presented in this study, our prediction errors ( $\pm 0.08 \text{ m}$ ) equates to approximately 30% of the tidal range. While this is larger by comparison to other studies (Table 3; Barlow et al., 2013, Table 10; Mills et al., 2013), nonetheless the data can still be used

to examine paleo-RSL trends providing that the record is independently assessed by other means such as tide-gauge records (Donnelly et al., 2004; Gehrels et al., 2005; Kemp et al., 2009b).

While the application of subtidal foraminiferal-based transfer functions have been developed and applied in the Mediterranean, for example, reconstructing paleobathymetry (e.g., Rossi & Horton, 2009; Milker et al., 2011), we have documented the first quantitative use of foraminifera from intertidal environments and highlight their potential as proxy sea-level indicators for this region. Previous studies of sea-level change in the Mediterranean have primarily utilized geomorphological (e.g., tidal notches) and archeological (e.g., fish tanks) evidence (Flemming, 1969; Lambeck et al., 2004; Evelpidou et al., 2012; Antonioli et al., 2015). However, the nature and timing of their formation means their indicative meaning and range can often be hard to quantify with the necessary precision needed to delimit changes in late Holocene sea-level to the present. The use of salt-marsh foraminifera therefore significantly improves on the vertical accuracy if applied to fossil counterparts from sufficiently well-dated sediment cores (Shaw, 2013). Indeed, Marriner et al. (2014) recently highlighted high resolution records from salt-marsh environments and their underutilized potential in bridging the gap between geological and instrumental records of sea-level change for the Croatian coast, and more widely in the Mediterranean region.

## SUMMARY AND CONCLUSIONS

Foraminiferal assemblages from two microtidal sites along the coast of Croatia were documented to assess their utility as a proxy for tidal level in transfer-function reconstructions of RSL. Three faunal zones were identified and showed a relationship with tidal level in the modern

environment, similar to previous studies in the Adriatic region and elsewhere. Faunal zones dominated by agglutinated species *J. macrescens* and *T. inflata* were vertically constrained from MTL to above MHWST. A second, more diverse faunal zone comprising *J. macrescens* and *T. inflata*, and calcareous *Quinqueloculina* spp., occupied a similar, albeit greater vertical range. Assemblages dominated by higher relative abundances of calcareous taxa (*Ammonia* spp. and *Quinqueloculina* spp.) were indicative of lower intertidal environments below MTL.

The small environmental gradients observed suggested the use of linear regression modelling for establishing a sea-level transfer function, which indicated the training sets potential to relocate former RSL to within  $\pm 0.08$  m. This precision is comparable to previous studies utilizing salt-marsh foraminifera and highlights their potential for reconstructing RSL trends in the Mediterranean, and reducing the vertical uncertainties associated with sea-level indicators previously employed there. Future studies aimed at increasing the number of samples making up the modern training set for this region would ultimately improve the reconstructive potential of the transfer-function approach and simultaneously improve the modern analogues for application in paleo-RSL research.

## ACKNOWLEDGMENTS

This research was conducted as part of Shaw's Ph. D thesis at the Geography Department, University of Liverpool in collaboration with the National Oceanography Centre, Liverpool, Liverpool John Moores University and funded by a NERC studentship award. Technical staff at the University of Liverpool are thanked for their assistance in the laboratory, notably, Irene Cooper, Alan Henderson and Mike O'Connor. We also thank Hayley Mills for her



help with the statistical analyses. The authors are grateful to the Institute of Oceanography and Fisheries, Split, for their assistance in the field and with logistics. We are also grateful to Srdjan Cupic, Hydrographic Institute of the Republic of Croatia, for supplying tidal levels. Robin Edwards and Fabienne Marret-Davis are thanked for their useful input during discussions. The authors thank Stephen Culver for his taxonomic expertise and gratefully acknowledge Benjamin Horton for his support. Two anonymous reviewers are also thanked for their useful input in improving the manuscript. We also thank Pamela Hallock Muller for overseeing the editorial process.

## REFERENCES

- Albani, A., Barbero, R. S., and Donnici, S., 2007, Foraminifera as ecological indicators in the Lagoon of Venice, Italy: *Ecological Indicators*, v. 7, p. 239–253.
- Albani, A. D., Favero, V., and Serandrei-Barbero, R., 1984, Benthonic foraminifera as indicators of intertidal environments: *Geo-Marine Letters*, v. 4, p. 43–47.
- Allen, J. R. L., 2000, Morphodynamics of Holocene salt marshes: A review sketch from the Atlantic and Southern North Sea coasts of Europe: *Quaternary Science Reviews*, v. 19, p. 1155–1231.
- Alve, E., and Murray, J. W., 2001, Temporal variability in vertical distributions of live (stained) intertidal foraminifera, southern England: *Journal of Foraminiferal Research*, v. 31, p. 12–24.
- Andersen, H. V., 1953, Two new species of *Haplophragmoides* from the Louisiana coast: *Contributions from the Cushman Foundation for Foraminiferal Research*, v. 4, p. 21–22.

- Antonioli, F., Lo Presti, V., Rovere, A., Ferranti, L., Anzidei, M., Furlani, S., Mastronuzzi, G., Orru, P. E., Scicchitano, G., Sannino, G., Spampinato, C. R., Pagliarulo, R., Deiana, G., de Sabata, E., Sansò, P., Vacchi, M., and Vecchio, A., 2015, Tidal notches in Mediterranean Sea: A comprehensive analysis: *Quaternary Science Reviews*, v. 119, p. 66–84.
- Bačani, A., Koch, G., Bergant, S., Šparica, M., Viličić, D., Dolenc, T., Vreča, P., and Ibrahimpašić, H., 2004, Origin of recent organic-rich sediments from Morinje Bay (Northern Dalmatia, Croatia): aspects of hydrological and hydrogeological impact: conference presentation at; 32nd International Geological Congress, August 20–28, 2004, Florence, Italy.
- Baric, A., Grbec, B., and Bogner, D., 2008, Potential implications of sea-level rise for Croatia: *Journal of Coastal Research*, v. 24, p. 299–305.
- Barlow, N. L. M., Shennan, I., Long, A. J., Gehrels, W. R., Saher, M. H., Woodroffe, S. A., and Hillier, C., 2013, Salt marshes as late Holocene tide gauges: *Global and Planetary Change*, v. 106, p. 90–110.
- Barlow, N. L. M., Long, A. J., Saher, M. H., Gehrels, W. R., Garnett, M. H., and Scaife, R.G., 2014, Salt-marsh reconstructions of relative sea-level change in the North Atlantic during the last 2000 years: *Quaternary Science Reviews*, v. 99, p. 1–16.
- Bartholdy, J., 2012, Salt marsh sedimentation, *in* Davis Jr, R. A., and Dalrymple, R. W., (eds.), *Principles of tidal sedimentology*, Springer, Netherlands, p. 151–185.
- Berkeley, A., Perry, C. T., Smithers, S. G., Horton, B. P., and Taylor, K. G., 2007, A review of the ecological and taphonomic controls on foraminiferal assemblage development in intertidal environments: *Earth-Science Reviews*, v. 83, p. 205–230.

- Bernhard, J. M., 2000, Distinguishing live from dead foraminifera: Methods review and proper applications: *Micropaleontology*, v. 46, p. 38–46.
- Bernhard, J. M., Ostermann, D. R., Williams, D. S., and Blanks, J. K., 2006, Comparison of two methods to identify live benthic foraminifera: A test between Rose Bengal and CellTracker Green with implications for stable isotope paleoreconstructions: *Paleoceanography*, v. 21, p. 1–8.
- Birks, H. J. B., 1995, Quantitative palaeoenvironmental reconstructions, *in* Maddy, D., and Brew, J. S. (eds.), *Statistical Modelling of Quaternary Science Data: Quaternary Research Association*, Cambridge, p. 161–254.
- Brady, H. B., 1870, Foraminifera, *in* Bady, G. S., Robertson, D., and Brady, H. B., (eds.), *The ostracodes and foraminifera of tidal rivers: Annals and Magazine of Natural History*, London, England, Series 4, v. 6, p. 273–306.
- Brönnimann, P., Lutze, G. F., and Whittaker, J. E., 1989, *Balticammina pseudomacrescens*, a new brackish water trochamminid from the western Baltic Sea, with remarks on the wall structure; *Meyniana*, v. 41, p. 167–177.
- Callard, S. L., Gehrels, W. R., Morrison, B. V., and Grenfell, H. R., 2011, Suitability of salt-marsh foraminifera as proxy indicators of sea level in Tasmania: *Marine Micropaleontology*, v. 79, p. 121–131.
- Coccioni, R., 2000, Benthic foraminifera as bioindicators of heavy metal pollution - a case study from the Goro Lagoon (Italy), *in* Martin, R. E. (Ed.), *Environmental Micropaleontology: The Application of Microfossils to Environmental Geology*, Kluwer Academic/Plenum Publishers, New York, p. 71–103.

- Cosovic, V., Juracic, M., Moro, A., Kucenjak, M. H., Rukavina, S., Pugliese, N., Stuper, N., and Vlahov, I., 2006, Recent foraminifera from the Croatian Adriatic seacoast: *Anuário do Instituto de Geociências*, v. 29, p. 532–532.
- Culver, S. J., and Horton, B. P., 2005, Infaunal marsh foraminifera from the Outer Banks, North Carolina, USA: *Journal of Foraminiferal Research*, v. 35, p. 148–170.
- de Rijk, S., 1995, Salinity control on the distribution of salt marsh foraminifera (Great Marshes, Massachusetts): *Journal of Foraminiferal Research*, v. 25, p. 156–166.
- de Rijk, S., and Troelstra, S. R., 1997, Salt marsh foraminifera from the Great Marshes, Massachusetts: environmental control: *Palaeogeography, Palaeoclimatology, Palaeoecology* v. 130, p. 81–112.
- Donnelly, J. P., Cleary, P., Newby, P., and Ettinger, R., 2004, Coupling instrumental and geological records of sea-level change: Evidence from southern New England of an increase in the rate of sea-level rise in the late 19th century: *Geophysical Research Letters* v. 31, L05203.
- Duchemin, G., Jorissen, F. J., Redois, F., and Debenay, J. P., 2005, Foraminiferal microhabitats in a high marsh: Consequences for reconstructing past sea levels: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 226, p. 167–185.
- Edwards, R. J., Wright, A. J., and van de Plassche, O., 2004, Surface distribution of salt-marsh foraminifera from Connecticut, USA: Modern analogues for high-resolution sea level studies: *Marine Micropaleontology*, v. 51, p. 1–21.
- Edwards, R., and Wright, A., 2015, Foraminifera, *in* Shennan, I., Long, A. J., Horton, B. P. (eds.), *Handbook of Sea-Level Research*: John Wiley & Sons, Ltd, Chichester, UK, p. 191–217.

- Ehrenberg, C. G., 1840a, Eine weitere Erläuterung des Organismus mehrerer in Berlin lebend beobachteter Polythalamien der Nordsee: Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preussischen Akademie der Wissenschaften zu Berlin, 1840, p. 18–23.
- Ehrenberg, C. G., 1840b, Über noch jetzt zahlreich lebende Thierarten der Kreidebildung und den Organismus der Polythalamien: Physikalische Mathematische Abhandlungen der Königlich Akademie der Wissenschaften zu Berlin, 1839, p. 81–174.
- Ehrenberg, C. G., 1843, Verbreitung und einfluss des Mikroskopsichen Lebens in Süd- und Nord Amerika: physikalische Abhandlungen der Königl. Akademie der Wissenschaften zu Berlin, v. 1, p. 219–446.
- Evelpidou, N., Pirazzoli, P., Vassilopoulos, A., Spada, G., Ruggieri, G., and Tomasin, A., 2012, Late Holocene sea Level reconstructions based on observations of Roman fish tanks, Tyrrhenian Coast of Italy: *Geoarchaeology*, v. 27, p. 259–277.
- Fatela, F., and Taborda, R., 2002, Confidence limits of species proportions in microfossil assemblages: *Marine Micropaleontology*, v. 45, p. 169–174.
- Ferla, M., Cordella, M., Michielli, L., Rusconi, A., 2007, Long-term variations on sea level and tidal regime in the lagoon of Venice: *Estuarine, Coastal and Shelf Science*, v. 75, p. 214–222.
- Figueira, B. O., Grenfell, H. R., Hayward, B. W., and Alfaro, A. C., 2012, Comparison of rose bengal and celltracker green staining for identification of live salt-marsh foraminifera: *Journal of Foraminiferal Research*, v. 42, p. 206–215.
- Flemming, N. C., 1969, Archaeological evidence for eustatic change of sea level and Earth movements in the Western Mediterranean during the Last 2,000 Years: *Geological Society of America Special Papers*, v. 109, p. 1–98.

- Frontalini, F., and Coccioni, R., 2008, Benthic foraminifera for heavy metal pollution monitoring: A case study from the central Adriatic Sea coast of Italy: *Estuarine, Coastal and Shelf Science*, v. 76, p. 404–417.
- Frontalini, F., and Coccioni, R., 2011, Benthic foraminifera as bioindicators of pollution: A review of Italian research over the last three decades: *Revue de Micropaléontologie*, v 54, p. 115–127.
- Frontalini, F., Coccioni, R., and Bucci, C., 2010, Benthic foraminiferal assemblages and trace element contents from the lagoons of Orbetello and Lesina: *Environmental Monitoring and Assessment*, v. 170, p. 245–260.
- Gehrels, R. W., 1994, Determining relative sea-level change from salt-marsh foraminifera and plant zones on the Coast of Maine, USA: *Journal of Coastal Research*, v. 10, p. 990–1009.
- Gehrels, W. R., 2000, Using foraminiferal transfer functions to produce high-resolution sea-level records from salt-marsh deposits, Maine, USA: *The Holocene*, v. 10, p. 367–376.
- Gehrels, W. R., and van de Plassche, O., 1999, The use of *Jadammina macrescens* (Brady) and *Balticammina pseudomacrescens* Brönnimann, Lutze and Whittaker (Protozoa: Foraminiferida) as sea-level indicators: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 149, p. 89–101.
- Gehrels, W. R., and Woodworth, P. L., 2013, When did modern rates of sea-level rise start?: *Global and Planetary Change*, v. 100, p. 263–277.
- Gehrels, W. R., Roe, H. M., and Charman, D. J., 2001, Foraminifera, testate amoebae and diatoms as sea-level indicators in UK saltmarshes: A quantitative multiproxy approach: *Journal of Quaternary Science*, v. 16, p. 201–220.

- Gehrels, W. R., Kirby, J. R., Prokoph, A., Newnham, R. M., Achterberg, E. P., Evans, H., Black, S., and Scott, D. B., 2005, Onset of recent rapid sea-level rise in the western Atlantic Ocean: *Quaternary Science Reviews*, v. 24, p. 2083–2100.
- Grimm, E. C., 2004, Tilia View: Version 2.0.2. Research and Collections Center, Illinois State Museum, Research and Collections Center, Springfield, IL.
- Hawkes, A. D., Horton, B. P., Nelson, A. R., and Hill, D. F., 2010, The application of intertidal foraminifera to reconstruct coastal subsidence during the giant Cascadia earthquake of AD 1700 in Oregon, USA: *Quaternary International*, v. 221, p. 116–140.
- Hayward, B. W., Grenfell, H. R., and Scott, D. B., 1999a, Tidal range of marsh foraminifera for determining former sea-level heights in New Zealand: *New Zealand Journal of Geology and Geophysics*, v. 42, p. 395–413.
- Hayward, B. W., Grenfell, H. R., Reid, C. M., and Hayward, K. A., 1999b, Recent New Zealand shallow-water benthic foraminifera: Taxonomy, ecologic distribution, biogeography, and use in paleoenvironmental assessments, *Institute of Geological and Nuclear Sciences Monograph* 21, Lower Hutt, New Zealand, 264 p.
- Hippensteel, S. P., Martin, R. E., Nikitina, D., and Pizzuto, J. E., 2002, Interannual variation of marsh foraminiferal assemblages (Bombay Hook National Wildlife Refuge, Smyrna, DE): do foraminiferal assemblages have a memory?: *Journal of Foraminiferal Research*, v. 32, p. 97–109.
- Horton, B. P., 1997, Quantification of the indicative meaning of a range of Holocene sea-level index points from the western North Sea. Ph. D. Thesis, University of Durham.

- Horton, B. P., 1999, The distribution of contemporary intertidal foraminifera at Cowpen Marsh, Tees Estuary, UK: Implications for studies of Holocene sea-level changes: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 149, p. 127–149.
- Horton, B. P., and Culver, S. J., 2008, Modern intertidal foraminifera of the Outer Banks, North Carolina, U.S.A., and their applicability for sea-level studies: *Journal of Coastal Research*, v. 24, p. 1110–1125.
- Horton, B. P., and Edwards, R. J., 2003, Seasonal distributions of foraminifera and their implications for sea-level studies: *SEPM Special Publication*, v. 75, p. 21–30.
- Horton, B. P., and Edwards, R. J., 2005, The application of local and regional transfer functions to the reconstruction of Holocene sea levels, north Norfolk, England: *The Holocene*, v. 15, p. 216–228.
- Horton, B. P., and Edwards, R. J., 2006, Quantifying Holocene sea level change using intertidal foraminifera: Lessons from the British Isles: *Cushman Foundation for Foraminiferal Research, Special Publication*, v. 40, p.1–97.
- Horton, B. P., Edwards, R. J., and Lloyd, J. M., 1999a, Reconstruction of former sea levels using a foraminiferal-based transfer function: *Journal of Foraminiferal Research*, v. 29, p. 117–129.
- Horton, B. P., Edwards, R. J., and Lloyd, J. M., 1999b, UK intertidal foraminiferal distributions: implications for sea-level studies: *Marine Micropaleontology*, v. 36, p. 205–223.
- Horton, B. P., Larcombe, P., Woodroffe, S. A., Whittaker, J. E., Wright, M. R., and Wynn, C., 2003, Contemporary foraminiferal distributions of a mangrove environment, Great Barrier Reef coastline, Australia: Implications for sea-level reconstructions: *Marine Geology*, v. 198, p. 225–243.



Hydrographic Institute, 1956-2000, Report on sea level measurement along the eastern Adriatic coast. Split., Croatia.

Imbrie, J., and Kipp, N. G., 1971, A new micropaleontological method for quantitative paleoclimatology. Application to a late Pleistocene Caribbean core, *in* Turekian, K. K. (Ed.), *The Late Cenozoic Glacial Ages*: Yale University Press, New Haven, p. 71–131.

Jorissen, F. J., 1987, The distribution of benthic foraminifera in the Adriatic Sea: *Marine Micropaleontology*, v. 12, p. 21–48.

Jorissen, F. J., 1988, Benthic foraminifera from the Adriatic Sea : principles of phenotypic variation: *Utrecht micropaleontological bulletins*, v. 37, p. 1–174.

Jorissen, F. J., and Wittling, I., 1999, Ecological evidence from live–dead comparisons of benthic foraminiferal faunas off Cape Blanc (Northwest Africa): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 149, p. 151–170.

Juggins, S., 2003, C2: A Microsoft Windows program for developing and applying palaeoecological transfer functions and for visualising multi-proxy stratigraphic datasets. University of Newcastle, Newcastle Upon Tyne. 69 p.

Kemp, A. C., and Telford, R. J., 2015, Transfer functions, *in* Shennan, I., Long, A. J., Horton, B. P. (eds.), *Handbook of Sea-Level Research*: John Wiley & Sons, Ltd, Chichester, UK, p. 470–499.

Kemp, A. C., Horton, B. P., Corbett, D. R., Culver, S. J., Edwards, R. J., and van de Plassche, O., 2009a, The relative utility of foraminifera and diatoms for reconstructing late Holocene sea-level change in North Carolina, USA: *Quaternary Research*, v. 71, p. 9–21.

- Kemp, A. C., Horton, B. P., Culver, S. J., Corbett, D. R., van de Plassche, O., Gehrels, W. R., Douglas, B. C., and Parnell, A. C., 2009b, Timing and magnitude of recent accelerated sea-level rise (North Carolina, United States): *Geology*, v. 37, p. 1035–1038.
- Kemp, A. C., Horton, B. P., Donnelly, J. P., Mann, M. E., Vermeer, M., and Rahmstorf, S., 2011, Climate related sea-level variations over the past two millennia: *Proceedings of the National Academy of Sciences*, v. 108, p. 11017–11022.
- Kemp, A. C., Horton, B. P., Vann, D. R., Engelhart, S. E., Grand Pre, C. A., Vane, C. H., Nikitina, D., and Anisfeld, S. C., 2012, Quantitative vertical zonation of salt-marsh foraminifera for reconstructing former sea level; an example from New Jersey, USA: *Quaternary Science Reviews*, v. 54, p. 26–39.
- Kemp, A. C., Horton, B. P., Vane, C. H., Bernhardt, C. E., Corbett, D. R., Engelhart, S. E., Anisfeld, S. C., Parnell, A. C., and Cahill, N., 2013, Sea-level change during the last 2500 years in New Jersey, USA: *Quaternary Science Reviews*, v. 81, p. 90–104.
- Kim, D., Cairns, D. M., Bartholdy, J., 2011, Wind-driven sea-level variation influences dynamics of salt marsh vegetation: *Annals of the Association of American Geographers*, v. 101, p. 231–248.
- Lambeck, K., Anzidei, M., Antonioli, F., Benini, A., and Esposito, A., 2004, Sea level in Roman time in the Central Mediterranean and implications for recent change: *Earth and Planetary Science Letters*, v. 224, p. 563–575.
- Leorri, E., Gehrels, W. R., Horton, B. P., Fatela, F., and Cearreta, A., 2010, Distribution of foraminifera in salt marshes along the Atlantic coast of SW Europe: Tools to reconstruct past sea-level variations: *Quaternary International*, v. 221, p. 104–115.

- Leps, J., and Smilauer, P., 2005, Multivariate analysis of ecological data using CANOCO, Cambridge University Press, Cambridge, 284 p.
- Long, A. J., Barlow, N. L. M., Gehrels, W. R., Saher, M. H., Woodworth, P. L., Scaife, R. G., Brain, M. J., and Cahill, N., 2014, Contrasting records of sea-level change in the eastern and western North Atlantic during the last 300 years: *Earth and Planetary Science Letters*, v. 388, p. 110–122.
- Marriner, N., Morhange, C., Faivre, S., Flaux, C., Vacchi, M., Miko, S., Dumas, V., Boetto, G., and Radic Rossi, I., 2014, Post-Roman sea-level changes on Pag Island (Adriatic Sea): Dating Croatia's "enigmatic" coastal notch?: *Geomorphology*, v. 221, p. 83–94.
- Mihelčić, G., Lojen, S., Dolenec, T., and Kniewald, G., 2006, Trace metals conservation in Morinje Bay sediment: Historical record of anthropogenic imissions into a shallow Adriatic Bay: *Croatica Chemica Acta*, v. 79, p. 161–167.
- Milker, Y., Schmiedl, G., and Betzler, C., 2011, Paleobathymetric history of the Western Mediterranean Sea shelf during the latest glacial period and the Holocene: Quantitative reconstructions based on foraminiferal transfer functions: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 307, p. 324–338.
- Mills, H., Kirby, J. R., Holgate, S., and Plater, A. J., 2013, The distribution of contemporary saltmarsh foraminifera in a macrotidal estuary: An assessment of their viability for sea-level studies: *Journal of Ecosystem and Ecography*, v. 3, p. 1–16.
- Montagu, G., 1808, Supplement to Testacea Britannica: S. Woolmer, Exeter, 183 p.
- Murray, J. W., 1976, Comparative studies of living and dead benthic foraminiferal distribution, in Hedley, R. H. A., C. (Ed.), *Foraminifera*, v.2, Academic Press, London, p. 45–109.

- Murray, J. W., 1979, British nearshore foraminiferids, *in* Kermack, D. M., and Barners, R. S. K., (eds), Synopsis of the British Fauna (New Series) No 16: Academic Press, London, 62 p.
- Murray, J. W., 1982, Benthic foraminifera: the validity of living, dead or total assemblages for the interpretation of palaeoecology: *Journal of Micropalaeontology*, v. 1, p. 137–140.
- Murray, J. W., 1989, Syndepositional dissolution of calcareous foraminifera in modern shallow-water sediments: *Marine Micropaleontology*, v. 15, p. 117–121.
- Murray, J. W., 1991, Ecology and Palaeoecology of Benthic Foraminifera: Longman Scientific and Technical, Harlow, England, 397 p.
- Murray, J. W., 2000, The enigma of the continued use of total assemblages in ecological studies of benthic foraminifera: *Journal of Foraminiferal Research*, v. 30, p. 244–245.
- Murray, J. W., 2003, Patterns in the cumulative increase in species from foraminiferal time-series: *Marine Micropaleontology*, v. 48, p. 1–21.
- Murray, J. W., 2006, Ecology and Applications of Benthic Foraminifera, New York, Cambridge University Press. 426 p.
- Murray, J. W., and Bowser, S. S., 2000, Mortality, protoplasm decay rate, and reliability of staining techniques to recognize “living” foraminifera: A review: *Journal of Foraminiferal Research*, v. 30, p. 66–70.
- Orlić, M., Kuzmić, M., Pasarić, Z., 1994, Response of the Adriatic Sea to the bora and sirocco forcing: *Continental Shelf Research*, v. 14, p. 91–116.
- Ozarko, D. L., Patterson, R. T., and Williams, H. F. L., 1997, Marsh Foraminifera from Nanaimo, British Columbia (Canada); implications of infaunal habitat and taphonomic biasing: *Journal of Foraminiferal Research*, v. 27, p. 51–68.

- Pandža, M., Franjić, J., and Škvorc, Ž., 2007, The salt marsh vegetation on the East Adriatic coast: *Biologia*, v. 62, p. 24–31.
- Parker, F. L., 1952, Foraminiferal distribution in the Long Island Sound–Buzzards Bay area: *Harvard College, Museum of Comparative Zoology Bulletin*, v. 106, p. 428–473.
- Patterson, R. T., and Fishbein, E., 1989, Re-examination of the statistical methods used to determine the number of point counts needed for micropaleontological quantitative research: *Journal of Paleontology*, v. 63, p. 245–248.
- Petrucci, F., Medioli, F. S., Scott, D. B., Pianetti, F. A., and Cavazzini, R., 1983, Evaluation of the usefulness of foraminifera as sea level indicators in the Venetian Lagoon (N. Italy): *Acta Naturalia de l' Ateneo Parmense*, v. 19, p. 63–77.
- Raichich, F., 2003, Recent evolution of sea-level extremes at Trieste (Northern Adriatic): *Continental Shelf Research*, v. 23, p. 225–235.
- Romić, D., Zovko, M., Romić, M., Ondrašek, G., and Salopek, Z., 2008, Quality aspects of the surface water used for irrigation in the Neretva Delta (Croatia): *Journal of Water and Land Development*, v. 12, p. 59–70.
- Rossi, V., and Horton, B. P., 2009, The application of a subtidal foraminifera-based transfer function to reconstruct Holocene paleobathymetry of the Po delta, northern Adriatic Sea: *Journal of Foraminiferal Research*, v. 39, p. 180–190.
- Rossi, V., Horton, B. P., Corbett, D. R., Leorri, E., Perez-Belmonte, L., and Douglas, B. C., 2011, The application of foraminifera to reconstruct the rate of 20th century sea level rise, Morbihan Golfe, Brittany, France: *Quaternary Research*, v. 75, p. 24–35.

- Saunders, J. B., 1957, Trochamminidae and certain Lituolidae (Foraminifera) from the recent brackish-water sediments of Trinidad, British West Indies: Smithsonian Miscellaneous Collection, v. 134, p. 1–16.
- Scott, D. B., and Hermelin, J. O. R., 1993, A device for precision splitting of micropaleontological samples in liquid suspension: *Journal of Paleontology*, v. 67, p. 151–154.
- Scott, D. B., and Medioli, F. S., 1978, Vertical zonations of marsh foraminifera as accurate indicators of former sea-levels: *Nature*, v. 272, p. 528–531.
- Scott, D. B., and Medioli, F. S., 1980a, Quantitative studies of marsh foraminiferal distributions in Nova-Scotia Canada: Implications for sea level studies: Cushman Foundation for Foraminiferal Research Special Publication: v. 17, p. 1–58.
- Scott, D. B., and Medioli, F. S., 1980b, Living vs. total foraminiferal populations: Their relative usefulness in paleoecology: *Journal of Paleontology*, v. 54, p. 814–831.
- Scott, D. B., and Medioli, F. S., 1986, Foraminifera as sea-level indicators, *in* van de Plassche, O (ed.) *Sea-Level Research: A Manual for the Collection and Evaluation of Data*: GEO Books, Norwich, England, p. 435–456.
- Serandrei-Barbero, R., Albani, A. D., and Zecchetto, S., 1997, Palaeoenvironmental significance of a benthic foraminiferal fauna from an archaeological excavation in the Lagoon of Venice, Italy: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 136, p. 41–52.
- Serandrei-Barbero, R., Carbognin, L., Taroni, G., and Cova, E., 1999, Distribution of recent benthic foraminifera in the southern basin of the Venice Lagoon (Italy): Statistical evaluation of taxa significance: *Micropaleontology*, v. 45, p. 99–111.

- Serandrei-Barbero, R., Donnici, S., and Madricardo, F., 2011, Supratidal foraminifera as ecological indicators in anthropically modified wetlands (Lagoon of Venice, Italy): *Ecological Engineering*, v. 37, p. 1140–1148.
- Serandrei-Barbero, R., Morisieri, M., Carbognin, L., and Donnici, S., 2003, An inner shelf foraminiferal fauna and its response to environmental processes (Adriatic Sea Italy): *Revista Española de Micropaleontología*, v. 35, p. 1–24.
- Shaw, T., 2013, Reconstructing historical sea-level trends for the Croatian coast of the Adriatic Sea using salt-marsh foraminifera, Ph. D. Thesis, University of Liverpool, 234 p.
- Shennan, I., 1982, Interpretation of the Flandrian sea-level data from the Fenland, England: *Proceedings of the Geologists' Association*, v. 93, p. 53–63.
- Shennan, I., 1986, Flandrian sea-level changes in the Fenland. II: Tendencies of sea-level movement, altitudinal changes, and local and regional factors: *Journal of Quaternary Science*, v. 1, p. 155–179.
- Siddall, J. D., 1886, Report on the foraminifera of the Liverpool Bay District, in Herdman, W. A., *Fauna of Liverpool Bay: Proceedings of the Literary and Philosophical Society of Liverpool*, v. 40, p. 42–71.
- Southall, K. E., Gehrels, W. R., and Hayward, B. W., 2006, Foraminifera in a New Zealand salt marsh and their suitability as sea-level indicators: *Marine Micropaleontology*, v. 60, p. 167–179.
- Šparica, M., Bačani, A., Koch, G., Anda, A., Slobodan, M., Viličić, D., Galovć, I., Šparica, M. M., Ibrahimpšarić, H., Bargant, S., and Dolenec, T., 2005, Ecosystem of Morinje Bay (Adriatic Sea, Croatia): Aspects of the sediment/water interface: *RMZ - Materials and Geoenvironment*, v. 52, p. 115–118.

- Strachan, K. L., Hill, T. R., Finch, J. M., and Barnett, R. L., 2015, Vertical zonation of foraminifera assemblages in Galpins salt marsh, South Africa: *Journal of Foraminiferal Research*, v. 45, p. 29–41.
- Telford, R. J., and Birks, H. J. B., 2005, The secret assumption of transfer functions: problems with spatial autocorrelation in evaluating model performance: *Quaternary Science Reviews*, v. 24, p. 2173–2179.
- ter Braak, C. J. F., and Juggins, S., 1993, Weighted averaging partial least squares regression (WA-PLS): An improved method for reconstructing environmental variables from species assemblages: *Hydrobiologia*, v. 269-270, p. 485–502.
- ter Braak, C. J. F., and Šmilauer, P., 2002, CANOCO reference Manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5) USA: Microcomputer Power, Ithaca, New York. 500 p.
- Tobin, R., Scott, D. B., Collins, E. S., and Medioli, F. S., 2005, Infaunal benthic foraminifera in some north American marshes and their influence on fossil assemblages: *Journal of Foraminiferal Research*, v. 35, p. 130–147.
- van de Plassche, O., 1986, *Sea-Level Research: A manual for the collection and evaluation of data*. Geobooks, Norwich, England, 617 p.
- Walton, W. R., 1952, Techniques for recognition of living foraminifera: *Cushman Foundation Foraminiferal Research*, v. 3, v. 56–60.
- Watcham, E. P., Shennan, I., and Barlow, N. L. M., 2013, Scale considerations in using diatoms as indicators of sea-level change: Lessons from Alaska: *Journal of Quaternary Science*, v. 28, p. 165–179.



- Woodroffe, S. A., Horton, B. P., Larcombe, P., and Whittaker, J. E., 2005, Intertidal mangrove foraminifera from the central Great Barrier Reef shelf, Australia: Implications for sea-level reconstruction: *Journal of Foraminiferal Research*, v. 35, p. 259–270.
- Woodworth, P. L., 1999, High waters at Liverpool since 1768: The UK's longest sea level record: *Geophysical Research Letters*, v. 26, p. 1589–1592.
- Wright, A. J., Edwards, R. J., and van de Plassche, O., 2011, Reassessing transfer-function performance in sea-level reconstruction based on benthic salt-marsh foraminifera from the Atlantic coast of NE North America: *Marine Micropaleontology*, v. 81, p. 43–62.

*Received 14 September 2015*

*Accepted 9 November 2015*

## APPENDICIES

APPENDIX A. Taxonomic reference list of species presented in text and Appendix B.

APPENDIX B. Contemporary foraminiferal counts of dead and live assemblages including sample station numbers and elevation (m HVRS71).

## TABLE CAPTIONS

TABLE 1. Tide levels (m HVR571) derived from the Split tide-gauge (Hydrographic Institute, 1956-2000). MLWST = Mean low water spring tide. MLWN = Mean low water neap. MTL = Mean tidal level. MHWN = Mean high water neap. MHWST = Mean high water spring tide.

TABLE 2. Summary of DCCA results.

TABLE 3. Statistical summary of the PLS transfer function performance. C = component.

## FIGURE CAPTIONS

FIGURE 1. Location of study area along the coast of Croatia (A) and samples sites Jadrtovac (B) and Blace (C) showing location of modern surface transects presented in Figures 3 and 4.

FIGURE 2. Scanning electron microscope (SEM) images of foraminiferal species observed from salt-marshes at Jadrtovac and Blace, Croatia. **1, 2** *Jadammina macrescens*; **3, 4, 5** *Trochammina inflata*; **6** *Miliammina fusca*; **7, 8** *Siphotrochammina lobata*; **9** *Haplophragmoides wilberti*; **10** *Scherochorella moniliformis*; **11** *Textularia earlandi*; **12** *Spirillina vivipara*; **13** *Elphidium* sp.; **14** *Ammonia* sp.; **15** *Quinqueloculina* sp.; **16** *Haynesina germanica*. White scale bars = 100  $\mu\text{m}$ .

FIGURE 3. Modern distribution of the relative abundances (%) of dead foraminifera plotted by distance for transect J-J1 at Jadrtovac. Foraminiferal abundance (per 5  $\text{cm}^3$ ), elevation (m HVR571) and salt-marsh zones are also shown. Transect location is shown in Fig. 1B.

FIGURE 4. Modern distribution of the relative abundance (%) of dead foraminifera plotted by distance for transect B-B1 at Blace. Foraminiferal abundance (per 5  $\text{cm}^3$ ), elevation (m HVR571) and salt-marsh zones are also shown. Transect location is shown in Fig. 1C.

FIGURE 5. Unconstrained cluster analysis identifying faunal assemblage zones from transect J-J1 at Jadrtovac (A) and transect B-B1 from Blace (C) and boxplots of faunal zones plotted by elevation m HVR571 (B, D) with tidal levels superimposed. JD = Jadrtovac; BL = Blace;

MHWST = Mean high water spring tide; MTL = mean tidal level. Samples 16, 17 and 18 (C) are from similar locations and altitudes to sample stations 1 to 4 from transect B-B<sub>1</sub>.

FIGURE 6. Scatter plot from a screened PLS transfer function (component 2) showing observed versus predicted elevation (A) and residual values versus observed elevation (B).

2359 Shaw, Table 1

MLWST	MLWN	MTL	MHWN	MHWST
-0.036	+0.034	+ 0.128	+0.233	+0.256

2359 Shaw, Table 2

<b>Axes</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>Total inertia</b>
Eigenvalues:	0.264	0.315	0.107	0.045	1.280
Lengths of gradient:	1.594	2.220	1.635	1.790	
Sum of all Eigenvalues:					1.280
Sum of all Canonical Eigenvalues:					0.264

Statistical Parameters	C1	C2	C3	C4	C5
Unscreened training set					
$r^2$	0.37	0.44	0.44	0.45	0.45
RMSE (m)	0.11	0.10	0.10	0.10	0.10
Max_bias	0.16	0.14	0.14	0.14	0.14
$r^2_{\text{jack}}$	0.27	0.32	0.32	0.28	0.25
RMSEP <sub>jack</sub> (m)	0.12	0.11	0.11	0.12	0.12
Max_bias <sub>jack</sub>	0.17	0.16	0.16	0.16	0.16
Screened training set					
$r^2$	0.56	0.62	0.63	0.63	0.63
RMSE (m)	0.08	0.07	0.07	0.07	0.07
Max_bias	0.10	0.09	0.09	0.10	0.09
$r^2_{\text{jack}}$	0.47	0.55	0.56	0.55	0.54
RMSEP <sub>jack</sub> (m)	0.08	0.08	0.07	0.08	0.08
Max_bias <sub>jack</sub>	0.11	0.10	0.10	0.10	0.12



*Ammonia* spp. Murray, 1979, p. 57, fig. 18a-l; Horton and Edwards, 2006; p. 73, P3, fig. 10a-c, fig. 11a-c, fig. 12a-c.

*Balticammina pseudomacrescens* Brönnimann, Lutze and Whittaker, 1989. Gehrels and van de Plassche, 1999, p.98, P1, fig. 6-10; Horton and Edwards, 2006, p. 63, P1, fig. 1a-d; Wright et al., 2011, p. 58, fig. A1/1.

*Elphidium* spp. Murray, 1979, p. 53, fig. 16a-d; Hayward et al., 1999b, p. 219, P17, fig. 1-28; Murray, 2006, p. 65, fig. 4.2, 11; Horton and Edwards, 2006; p. 75, P4, fig. 15-20.

*Haplophragmoides wilberti* (Andersen, 1953). Hayward et al., 1999b, p. 217, P1, fig. 25, 26; Horton and Edwards, 2006, p. 63, P1, fig. 3a-d; Hawkes et al., 2010, p. 133, P1, fig. 2a, b; Wright et al., 2011, p. 58, fig. A1/7.

*Haynesina germanica* (Ehrenberg, 1840a, b). Murray, 1979, p. 55, fig. 17a, b; Horton and Edwards, 2006; p. 75, P4, fig. 21a, b.

*Jadammina macrescens* (Brady, 1870). Murray, 1979, p. 27, fig. 6k-m; Gehrels and van de Plassche, 1999, p.98, P1, fig. 1-5; Hayward et al., 1999b, p. 217, P1, fig. 27-29; Horton and Edwards, 2006; p. 67, P1, fig. 4a-d; Hawkes et al., 2010, p. 133, P1, fig. 7a-d; Wright et al., 2011, p. 58, fig. A1/5.

*Miliammina fusca* (Brady, 1870). Murray, 1979, p. 24, fig. 5d-f; Hayward et al., 1999b, p. 217, P1, fig. 25, 6; Edwards et al., 2004; p. 16, P1, fig. 7; Horton and Edwards, 2006; p. 67, P1, fig. 5a, b. Wright et al., 2011, p. 59, fig. A2/2.

*Quinqueloculina* spp. Murray, 1979, p. 35, fig. 9a-i; Hayward et al., 1999b, p. 223; P4, fig. 26-28; p. 225, P5, fig. 9, 10; Horton and Edwards, 2006; p. 71, P2, fig. 9a, b.

*Scherchorella moniliformis* Siddall, 1886. Murray, 1979, p. 24, fig. 5b; Horton and Edwards, 2006; p. 67, P1, fig. 6a-c; Wright et al., 2011, p. 58, fig. A1/6.

*Siphotrochammina lobata* (Saunders, 1957). Edwards et al., 2004; p. 16, P1, fig. 9, 10; Wright et al., 2011, p. 58, fig. A1/10; Kemp et al., 2012; p. 29, P1, fig. 13, 14.

*Spirillina vivipara* Ehrenberg, 1843. Ehrenberg, 1843, p. 422, P3, fig. 41, sec. 7; Murray, 1979, p. 39, fig. 11a; Hayward et al., 1999b, p. 221, P3, fig. 7.

*Textularia earlandi* Parker, 1952. Hayward et al., 1999b, p. 219, P2, fig. 22, 23; Edwards et al., 2004; p. 16, P1, fig. 11; Wright et al., 2011, p. 58, fig. A1/3.

*Trochammina inflata* (Montagu, 1808). Hayward et al., 1999b, p. 219, P2, fig. 6-8; Edwards et al., 2004; p. 16, P1, fig. 14, 15; Horton and Edwards, 2006; p. 71, P2, fig. 8a-d; Wright et al., 2011, p. 58, fig. A1/9; Kemp et al., 2012; p. 29, P1, fig. 7, 8.

Transect J-J1 (Jadrto vac)		Sample Station Number																					
Species Name	Assemblage	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Ammonia spp.	Dead	0	0	0	4	0	0	0	0	0	231	0	0	0	2	1	67	59	3	1	58	15	23
	Live	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	11	6	0	3	3	1	0
Balticammina pseudomacrescens	Dead	0	0	3	0	2	9	1	5	1	0	1	4	0	8	0	3	8	16	0	0	1	8
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elphidium spp.	Dead	0	0	90	312	0	0	0	0	0	5	0	0	0	0	0	12	17	0	3	19	7	14
	Live	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	5	3	0	3	6	0	1
Haplophragmoides wilberti	Dead	0	0	5	0	0	1	1	2	2	2	7	1	0	0	7	3	31	6	1	4	12	13
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Haynesina germanica	Dead	0	0	0	0	0	0	0	0	0	35	0	0	0	0	0	11	21	0	0	10	3	4
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jadammina macrescens	Dead	0	7	83	90	91	108	113	323	184	240	214	143	95	277	265	90	59	162	160	144	199	243
	Live	0	0	0	0	0	4	0	13	11	16	4	4	0	53	4	2	5	1	8	8	19	8
Miliammina fusca	Dead	0	0	34	0	10	69	34	16	13	12	8	5	1	0	0	0	0	1	1	4	0	8
	Live	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0
Quinqueloculina spp.	Dead	0	0	14	8	0	0	0	0	0	193	10	0	0	0	3	334	314	1	19	598	63	384
	Live	0	0	0	0	0	0	0	0	0	50	0	0	0	0	1	87	47	2	26	74	10	137
Scherochorella moniliformis	Dead	0	0	0	0	0	0	0	0	0	0	12	30	0	0	0	0	0	0	0	2	0	0
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphotrochammina lobata	Dead	0	0	0	2	0	0	13	7	2	0	0	5	0	0	2	0	2	1	0	0	3	0
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spirillina vivipara	Dead	0	0	0	0	0	0	0	0	0	4	0	1	0	0	1	19	3	0	0	6	1	7
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	3	0	0	2	2	0
Textularia earlandi	Dead	0	0	0	0	0	0	0	0	0	3	2	0	0	2	2	0	0	8	2	0	7	10
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trochammina inflata	Dead	0	2	519	515	63	312	232	316	548	60	58	16	28	69	105	235	250	319	570	431	335	1050
	Live	0	0	9	28	0	1	6	36	67	11	7	1	1	15	10	34	37	10	52	64	35	121
Total	Dead	0	9	748	931	166	499	394	669	750	785	312	205	124	358	386	774	765	517	757	1280	646	1764
Total	Live	0	0	9	28	0	5	6	50	80	104	11	5	1	68	15	146	101	13	94	157	67	265
Elevation (m HVRST1)		0.48	0.44	0.27	0.22	0.20	0.18	0.19	0.15	0.14	0.09	0.06	0.08	0.05	0.08	0.08	0.11	0.10	0.06	0.05	0.06	0.10	0.04

Transect B-B1 (Blace)		Sample Station Number																	
Species Name	Assemblage	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Ammonia</i> spp.	Dead	1	0	0	0	0	0	0	0	0	87	103	58	35	98	78	0	25	74
	Live	0	0	0	0	0	0	0	0	0	0	1	0	15	13	13	0	1	4
<i>Balticammina pseudomacrescens</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Elphidium</i> spp.	Dead	1	0	1	0	0	0	0	0	0	5	16	30	6	7	29	0	0	0
	Live	0	1	2	0	0	0	0	0	2	2	15	0	0	0	0	0	0	0
<i>Haplophragmoides wilberti</i>	Dead	5	17	17	4	22	7	0	5	9	3	0	0	1	0	0	0	1	1
	Live	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Haynesina germanica</i>	Dead	0	0	0	0	0	0	0	0	0	33	42	12	16	17	8	0	4	13
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Jadammina macrescens</i>	Dead	78	295	200	90	488	289	507	240	280	140	79	25	23	5	4	101	170	240
	Live	1	3	2	1	12	19	18	11	10	21	16	13	22	0	0	4	10	12
<i>Miliammina fusca</i>	Dead	45	10	5	3	38	70	34	7	42	0	17	0	0	2	1	30	0	1
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Quinqueloculina</i> spp.	Dead	643	178	50	0	0	0	0	0	0	240	1117	95	68	21	39	1	197	510
	Live	0	19	4	0	0	0	0	0	0	34	14	36	45	19	25	0	9	30
<i>Scherochorella moniliformis</i>	Dead	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Siphotrochammina lobata</i>	Dead	0	0	0	1	0	0	2	0	0	0	0	0	1	0	0	0	1	0
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spirillina vivipara</i>	Dead	10	3	1	0	0	0	0	0	0	31	170	8	4	3	5	0	13	5
	Live	0	2	1	0	0	0	0	0	0	7	0	0	0	0	1	0	7	0
<i>Textularia earlandi</i>	Dead	0	0	0	0	1	0	1	0	2	0	3	5	3	4	4	0	0	0
	Live	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0
<i>Trochammina inflata</i>	Dead	695	450	400	139	200	145	303	285	638	245	95	41	24	17	7	343	650	720
	Live	30	9	35	3	10	9	9	12	10	20	13	15	13	1	0	15	16	33
<b>Total</b>	<b>Dead</b>	<b>1478</b>	<b>953</b>	<b>674</b>	<b>237</b>	<b>749</b>	<b>511</b>	<b>847</b>	<b>537</b>	<b>971</b>	<b>784</b>	<b>1642</b>	<b>274</b>	<b>181</b>	<b>174</b>	<b>175</b>	<b>475</b>	<b>1061</b>	<b>1564</b>
<b>Total</b>	<b>Live</b>	<b>31</b>	<b>34</b>	<b>45</b>	<b>6</b>	<b>22</b>	<b>28</b>	<b>27</b>	<b>23</b>	<b>20</b>	<b>84</b>	<b>46</b>	<b>79</b>	<b>95</b>	<b>34</b>	<b>41</b>	<b>19</b>	<b>43</b>	<b>83</b>
<b>Elevation (m HVR571)</b>		<b>0.37</b>	<b>0.37</b>	<b>0.36</b>	<b>0.34</b>	<b>0.32</b>	<b>0.29</b>	<b>0.28</b>	<b>0.29</b>	<b>0.3</b>	<b>0.26</b>	<b>0.2</b>	<b>0.17</b>	<b>0.18</b>	<b>0.05</b>	<b>0.01</b>	<b>0.4</b>	<b>0.34</b>	<b>0.29</b>













