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Distributions of salt-marsh foraminifera along the coast of SW California, USA: implications for sea-level reconstructions

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Abstract

Salt-marsh foraminifera are frequently used around the world as proxies in paleoenvironmental studies of sea-level change. Quantitative reconstructions of sea-level change use transfer functions which are based on the vertical zonation of salt-marsh foraminifera with respect to the tidal frame. This paper explores for the first time the environmental factors that control the foraminiferal assemblages in Southern California marshes using modern surface samples (1 cm thick) from two marshes Seal Beach and Tijuana Estuary. The dead foraminiferal assemblages demonstrate distinct zonation across the salt-marsh surfaces which is primarily related to elevation. Other variables less important than elevation such as O_2, temperature, salinity and pH additionally control the distribution pattern of these assemblages.

The tidal flat and low marshes are characterized by high abundances of *Miliammina fusca* and calcareous species. The middle marsh is dominated by *Jadammina macrescens* and *Trochammina inflata*, while the high marsh zone is dominated by *Trochamminita irregularis*, *Miliammina petila*, *J. macrescens* and *T. inflata*. Regression modelling was used for the development of a sea-level transfer function based on a combined training set of surface samples from the two study sites. The performance of the Weighted Average – Partial Least Squares (WA-PLS) transfer function suggests a robust relationship between the observed and estimated elevations ($r^2_{\mathrm{Jack}} = 0.72$), and is capable of predicting former sea levels to a precision of ±0.09 m. Our results can be used for future paleoenvironmental reconstructions along the Southern California coast, an area that has experienced changes in sea level in the past and will be affected by future sea-level rise coupled with climate and anthropogenic changes, resulting in wide impacts on the natural coastal habitats in this region.

Keywords: foraminiferal assemblages; California; salt marshes; environmental relations; redundancy analysis; transfer function; relative sea level;

1 Introduction

Salt-marsh sediment records are used to quantitatively reconstruct late Holocene relative sea-level changes (e.g., Kemp et al., 2011), with fairly high precision (up to ±0.05 m, cf. Gehrels and Woodworth, 2013). In combination with long-term tide gauge records they have provided sea-level reconstructions of the transition from relatively low rates of change during the late Holocene in the order of tenths of mm yr^{-1} to accelerated modern rates (early 20th century) in the order of mm yr^{-1}, both in the Northern and Southern Hemispheres (Gehrels and Woodworth, 2013). Quantifying regional patterns of sea-level change using proxies from salt-marsh sediments provides information on drivers of local to regional sea-level change and ultimately on global climate change (e.g., mass–balance changes of ice sheets and glaciers) (e.g., Milne et al., 2002; Milne et al., 2009; Kopp et al., 2016). Benthic foraminifera preserved in salt-marsh sediments are frequently used for reconstructing past sea-level changes due to their vertical zonation in the modern intertidal zone (e.g., Scott and Medioli, 1980; Scott et al., 1984; Gehrels, 1994; Horton et al., 1999a; Kemp et al., 2009a; Horton and Edwards, 2005), especially in micro- to mesotidal settings (e.g., Scott et al., 2001; Barlow et al., 2013 and references therein; Kemp and Telford, 2015 and references therein). Elevation relative to the tidal frame (or frequency of tidal submergence) is the controlling environmental parameter that is of interest to sea-level studies (Gehrels, 2000). Studies exploring the ecology of modern salt-marsh foraminifera show that their spatial distribution can also be controlled by other environmental factors, such as salinity (e.g., Murray, 1971; Patterson, 1990; de Rijk and Troelstra, 1997), pH (e.g., Woodroffe et al., 2005; Barnett et al., 2016), grain-size (e.g., Matera and Lee, 1972; de Rijk and Troelstra, 1997; Scott et al., 1998; Barnett et al., 2016) and organic carbon concentration (e.g., de Rijk and Troelstra, 1997; Milker et al., 2015a). However, these environmental parameters and others (e.g., vegetation cover, geochemical properties) are significantly correlated with tidal elevation in many salt marshes (e.g., de Rijk and Troelstra, 1997; Horton, 1999a; Horton et al., 2003; Horton and Edwards, 2005; Milker et al., 2015a).

Many quantitative sea-level studies use regression methods to develop predictive transfer functions, capable of inferring past relative sea levels from fossil foraminifera in subsurface salt-marsh deposits (e.g., Gehrels, 1999; Horton et al.,1999b; Edwards and Horton, 2000; Gehrels, 2000; Edwards et al., 2004b; Gehrels et al., 2006; Horton and Edwards, 2006; Kemp et al., 2009b; Gehrels et al., 2012). In marshes where salt-marsh foraminifera are unimodally distributed along the environmental gradient, Weighted Averaging (WA), Locally Weighted Weighted-Averaging (LW-WA) and even to a higher degree, Weighted Averaging Partial Least-Squares (WA-PLS), are considered as the most robust models for reconstructing sea level (ter Braak and Juggins, 1993; ter Braak et al., 1993; Birks, 1995, 2010; Juggins and Birks, 2012; Kemp and Telford, 2015). Where linear species–environment responses are demonstrated, Partial Least Squares (PLS) is the most widely used technique (e.g., Stone and Brooks, 1990; Rossi et al., 2011). These methods are reviewed in detail by Birks (1995, 2003, 2010), Barlow et al. (2013) and Kemp and Telford (2015), and have been applied to reconstruct past sea-level changes in a wide range of geographical areas, including the Atlantic coast of the USA (e.g., Gehrels, 2000; Edwards et al., 2004a,b; Gehrels et al., 2002, 2004, 2005; Horton et al., 2006; Kemp et al., 2009a, 2009b, 2011, 2013, 2015; Wright et al., 2011), the Atlantic coast of Europe (e.g., Gehrels et al., 2001; Horton and Edwards, 2005, 2006; Leorri et al., 2010; Long et al. 2014; Barlow et al., 2014; Barnett et al., 2015), eastern Canada (e.g., Patterson et al., 2004; Gehrels et al., 2005; Barnett et al., 2016), west coast of Canada (Guilbault et al., 1996), South Africa (Franceschini et al., 2005; Strachan et al., 2014), Iceland (Gehrels et al., 2006; Saher et al., 2015), Australia (Woodroffe, 2009; Gehrels et al., 2012), New Zealand (Gehrels et al., 2008; Grenfell et al., 2012) and Malaysia (Culver et al., 2015). Despite this vast literature, few studies have been conducted along the Pacific coast of the USA. Exceptions are the studies of intertidal foraminifera from Oregon, USA, to reconstruct relative sea-level changes caused by co-seismic subsidence (e.g., Hawkes et al., 2010, 2011; Engelhart et al., 2013) and to investigate the influence of taphonomic processes, small-scale variability and infaunal distribution on the accuracy of sea-level reconstructions (Milker et al., 2015a). However, neither a comprehensive modern training set, nor transfer function based on recent developments and methodological recommendations (Barlow et al., 2013; Kemp and Telford, 2015) have been developed for salt marshes in California. With that being said, previous studies, during the mid-late 1970's, from Tijuana salt-marsh, Southern California, qualitatively divided the marsh into foraminiferal zones (Scott, 1976; Scott and Medioli, 1978) which were applied in Holocene paleoenvironmental reconstructions (Scott et al., 2011).

Salt-marsh ecosystems are of high economic value and societal and ecological significance. They provide ecosystem services for tourism and commercial fisheries, as nurseries and refuge areas for a variety of organisms, for carbon sequestration, and for protecting water quality by filtering runoff and reducing the pollutant load entering estuaries. Moreover, salt marshes are a natural protection against coastal flooding, erosion and sea-level rise (e.g., Gedan et al., 2010). For the Southern California coast, with its dense population and ongoing disappearance of natural coastal habitats due to anthropogenic modification, variable tectonic regimes and climate change, the need to investigate the coastal marshes is pressing. In order to create a reference baseline for future regional paleogeographic, paleoecological and paleo sea-level study this study aims to: (1) identify and describe the distribution patterns of the living and dead foraminiferal assemblages in two coastal salt marshes: Tijuana and Seal Beach; (2) constrain by quantitative ordination methods the relationships between foraminiferal assemblages and the most important environmental drivers influencing their distribution; (3) examine whether the recent foraminiferal assemblages in these salt marshes show a distinct zonation relative to the tidal frame; (4) develop an ecological response function using the modern training set (i.e., a foraminifera based transfer function) suitable for precise relative sea-level reconstructions in an area that is susceptible to both sea-level change and tectonic land movements.

2 Study area

The salt marsh at Tijuana is part of the Tijuana River Estuary located north of the US-Mexico border (32° 33’ N, 117° 07’ W; Fig. 1). The salt marsh is part of the National Estuarine Research Reserve which has over 1000 ha of coastal marsh environments (Zedler et al., 1986). Just over 150 km to the northwest of Tijuana, Sea Beach consists of approximately 390 ha of salt marshes incorporated in a National Wildlife Refuge that lies within the US Naval Weapons Station at Seal Beach (33° 44’ N, 118° 05’ W). The Seal Beach and Tijuana sites represent salt marshes with generally similar tidal characteristics and overall climatic and oceanographic settings representative of Southern California. Tides are semidiurnal and have an observed mean range close to the upper micro-tidal range, <2 m (Table 1), as measured from 1983 to 2001 at the National Oceanic and Atmospheric Administration (NOAA) tide-gauge stations in Los Angeles, ~16 km north of Seal Beach, and Imperial Beach, ~2 km north of Tijuana.

Historically, salt marshes on the Southern California coast have developed in response to the drowning of river valleys when sea levels reached their approximate current position about 5000 years before present (Zedler, 1982). Although salt marshes in California have seen a great reduction in area due to human influence, Tijuana salt marsh is considered a pristine ecosystem that preserves many of its natural qualities. Moreover the northern arm of the marsh, which was chosen for this study, is known for its simple elevation gradient and its relative physical stability (Zedler, 1977). The marsh at Seal Beach is a similar habitat that has been least affected by human disturbance thanks to its designation as a wildlife reserve. Moreover, this marsh is the only remaining undeveloped part of the Anaheim Bay estuary. Prior to development, this estuary had large fringing freshwater wetlands, salt flats, and alkali meadows, and freshwater creeks may have flowed perennially into it (Grossinger et al., 2011). Reclaimed areas of the estuary adjacent to the Seal Beach salt marsh include military, municipal and industrial infrastructure.

Natural hydrologic disturbances at Tijuana include extreme flood events which can deposit up to 8 or 9 cm of sediment in low marsh areas near channels (Cahoon et al., 1996; Wallace et al., 2005). In the past century, some reduction in streamflow has been observed due to damming upstream in the watershed. Even so, hydrologic extremes of flood and drought at Tijuana have been known to cause periods of tidal closure and hypersalinity leading to vegetation die-off (Zedler, 2010).

The most significant natural hydrologic change at the salt marsh at Seal Beach occurred about 300 years before present with the isolation of the marsh due to changes in the flow of the Santa Ana River (Leeper III, 2015). Historically sedimentation at Seal Beach appears to have kept pace with sea-level rise in the recent past, but the lack of terrestrial sediment input makes the marsh at Seal Beach all the more vulnerable to accelerated sea-level rise (Kirwan and Megonigal, 2013). This danger is compounded by the fact that Seal Beach lies directly along the San Andreas Fault and is suspected to have suffered elevation loss due to tectonic subsidence (Leeper III, 2015). Additionally, the region surrounding Seal Beach has observed a 4.13 mm/yr average lowering in surface elevation from 1994 to 2012 (Takekawa et al., 2013) due to oil extraction.

Marsh vegetation in Southern California is often classified into zones based on elevation (Peinado et al., 1994; Zedler et al., 1986; Zedler, 1977). Zonation is due to a complex combination of biotic tolerances and interspecific competition (Engels et al., 2011). The low elevations, high salinity habitats of Southern California salt marshes are dominated by *Spartina alterniflora*. Mid-marsh regions are frequently co-dominated by a number of species including *Sarcocornia pacifica*, *Batis maritima*, and *Jaumea carnosa*. Species such as *Distichlis spicata*, *Frankenia grandifolia* and *Limonium californicum* are found in the mid-to-high marsh areas. However, the boundary between mid and high marsh vegetation is less definite, and plants from these zones also colonize the marsh-upland transition area. *Arthrocnemum subterminale* and *Monanthochloe littoralis* are species which show a preference for the highest elevations in the marsh. Marsh-upland transition can most clearly be seen by the appearance of shrub-type plants, often those of the native chaparral vegetation such as *Artemisia californica*, *Rhus lauriana*, and *Baccharis pilularis*.

The climate of Southern California is Mediterranean and experiences hot, dry summers and warm, wet winters. At Tijuana Estuary, the average annual high temperature is 21°C with an average low of 12.9°C and an average annual precipitation of 26.6 cm. At Seal Beach, average annual high temperatures are 23.4°C and lows are 13°C with an annual average of 31.1 cm of precipitation (usclimatedata.com). Drought and extreme flooding, as previously mentioned, are not uncommon and pose the most significant climatic impacts on marsh vegetation (Zedler et al., 1986; Zedler, 2010).

3 Materials and methods

3.1. Field sampling

We established twenty stations in Seal Beach salt marsh and seventeen stations in Tijuana salt marsh (Fig. 1, Table 2) along transects perpendicular to the primary direction of tidal inundation. Stations covered the sub-environments within the intertidal zone from high marsh to the tidal flat, where possible. Sampling coincided with approximately spring tide in the fall in order to standardize the timing of collection and to maintain perennial persistency in foraminiferal distribution (i.e., we avoided sampling during bloom periods) (e.g., Buzas, 1965; Jones and Ross, 1979; Horton and Edwards, 2003; Horton and Murray, 2006, 2007; Schönfeld et al., 2012). The stations at Seal Beach were sampled in mid-October 2015 and resampled (only for faunal analysis) three days after storm activity generated by Hurricane Patricia on 23 October, 2016 (www.nhc.noaa.gov). However, our results showed that the study area was not impacted by the storm and we used the replicate dead foraminiferal data at Seal Beach to enhance our interpretations. The stations at Tijuana were sampled in early December, 2015.

Station locations were determined with Differential Global Positioning System (DGPS) and post processed with the Online Positioning User Service (OPUS) generated by NOAA in order to provide simplified access to high-accuracy National Spatial Reference System (NSRS) coordinates i.e., to standardize and correct for spatial changes in MSL. The elevations, with a precision of ≤4cm (3cm in average), were referenced to the North American vertical datum (NAVD88) computed using GEOID12B.

At each station vegetation cover was described and pore-water salinity, temperature, O_2 concentration and pH were measured using hand-held EXTECH DO700 meter following de Rijk (1995).

Fifty seven surface marsh sediment samples with a standardized volume of 10 cm^3 from the uppermost centimeter (10 cm^2 by 1 cm thick) were sampled for foraminiferal analysis. This sampling strategy follows the assumption that the intertidal foraminifera are primarily shallow infaunal (classification follows Buzas et al. (1993)), thus our surface samples sufficiently represent the modern intertidal environment. This hypothesis is supported by research in other salt marshes, for example in Oregon (Hawkes et al., 2010; Milker et al., 2015a), Nova Scotia (Scott and Medioli, 1980), Maine (Gehrels, 1994), Massachusetts (de Rijk, 1995), North Carolina (Culver and Horton, 2005), New Brunswick, Canada (Patterson et al., 2004) and the UK (Horton, 1997; Horton and Edwards, 2006). Nevertheless, there are a considerable number of studies that reported living infaunal salt-marsh foraminifera which might alter the composition of fossil assemblages (e.g., Hippensteel et al., 2002; Culver and Horton, 2005 and references therein) due to seasonal and local environmental conditions and bioturbation (Buzas et al., 1993; de Stigter et al., 1998; Culver and Horton, 2005; Tobin et al., 2005; Horton and Edwards, 2006). We tested the influence of infaunal foraminifera in the marshes of Southern California by analyzing foraminifera at 1 cm resolution down 10cm long mini cores from the mid-marsh (one core along each transect).

All foraminifera surface and core samples were preserved on the day of sampling in rose Bengal solution (2 g rose Bengal /l 95%- ethanol) for two weeks to distinguish living from dead specimens at the time of collection (Walton, 1952; Murray and Bowser, 2000; Schönfeld et al., 2012). Specimens were considered living at the time of collection when all chambers were stained completely bright red, except for the last chamber (e.g., Horton and Edwards, 2006; Milker et al., 2015a). Additionally the solution was buffered by calcium carbonate powder to prevent dissolution of calcareous tests. At each sampling station a second set of sediment samples (one per station) was taken and stored in sealed plastic bags for grain-size distribution and loss on ignition (LOI) analyses. All samples were stored in the refrigerator at 4°C prior to further laboratory analyses.

3.2. Laboratory techniques

Quantitative Sedimentological Analyses

Grain-size distributions of the surface samples were determined using a Malvern Mastersizer 2000 Laser Diffraction Particle Size Analyzer coupled to a Hydro 2000G large-volume sample dispersion unit at the Paleoclimatology and Paleotsunami Laboratory, California State University, Fullerton. Prior to analysis, samples were treated with 25-50 ml of 30% hydrogen peroxide (H_2O_2) to remove organic matter. Standard laboratory procedures for grain-size distributions are detailed in Kirby et al. (2015).
Loss-on-Ignition (LOI; a proxy for percent organic matter- %TOM) at 550 °C and 950 °C (% total carbonate - %TC) were measured according to the method of Heiri et al. (2001). For LOI measurements, samples were wet sieved to remove the material larger than 2 mm, dehydrated at 105°C for 24 hours, and burned in a muffle furnace at

550°C for 4 hours. LOI was calculated by the difference in sample dry weight at 105°C and 550°C. Samples were then burned in a furnace at 950°C for 1 hour to calculate carbonate content.

Foraminiferal analysis

A total of fifty seven surface samples and 20 core samples were analyzed for foraminifera from the two marshes. These samples were wet-sieved through 500 μm and 63 μm sieves. The >500 μm fraction was examined for larger foraminifera before being discarded. The fraction between 63 and 500 μm was subdivided into eight equal aliquots following the most reliable method for splitting a foraminiferal sample described in Horton and Edwards (2006) using a wet splitter (Scott and Hermelin, 1993). Where possible, at least 300 tests (dead and live) were counted in water which enabled easy detection of rose Bengal stained foraminifera and prevented drying of the organic residue (e.g., de Rijk, 1995; Horton and Edwards, 2006). In the short core samples, living specimens from below the surface (1-10 cm) sediment layer were considered as infaunal.

Taxonomic identifications follow Gehrels and van de Plassche (1999), Horton and Edwards (2006), Hawkes et al. (2010), Wright et al. (2011), and Milker at al. (2015a, b). The genus *Jadammina* is now considered a junior synonym of *Entzia* (Kaminski and Filipescu, 2011). However, we still employ the genus *Jadammina* in this study in order to avoid confusion since the majority of salt-marsh foraminiferal researchers use it. Juvenile specimens of *Trochammina inflata* and *Jadammina macrescens* that were difficult to distinguish from each other because of their small sizes were lumped into a single group and assigned as juvenile Trochamminids. Specimens of the genus *Ammobaculites* were combined into a single group, because these species were often broken making it difficult to identify them to the species level (Kemp et al., 2009a; Milker et al., 2015a). All counts were expressed as numerical abundance of living and dead foraminifera numbers per 10 cm^3 bulk sediment and as a relative abundance (%) of species out of the total group. All foraminiferal data can be found in the supplementary material (Supplementary data 1, 2 and 3). Scanning electron microscope photographs of key species were taken at the Department of Earth, Planetary and Space Sciences, UCLA.

3.3. Statistical analysis

Dead surface foraminiferal assemblages were statistically analyzed to minimize the seasonal fluctuations commonly recorded in live populations and because they most accurately reflect the subsurface assemblages indicating that taphonomic processes are minimal (e.g., Culver and Horton, 2005, Milker et al., 2015a and references therein). Two samples with low counts (<4 specimens) were removed from the statistical analyses while the remaining 55 surface samples (average of 417 individuals per sample) with 84 as the lowest specimens number were included.

Multivariate statistical methods (unconstrained Cluster Analysis, CA, and detrended correspondence analysis, DCA) are used to identify and classify the distribution of groups and subgroups in the foraminiferal community into homogeneous faunal zones (clusters) along each transect (e.g., Frezza and Carboni, 2009; Phipps et al., 2010).

A Q-mode CA was processed by PRIMER version 6 software (Plymouth Routines In Multivariate Ecological Research, UK). The data of the common benthic species (>1% relative abundance) were double-root transformed in order to down-weight the relative contribution of highly abundant species. These transformed abundances were used to build a similarity matrix calculated between every pair of samples comprising a Bray–Curtis similarity (Bray and Curtis, 1957) as the distance metric, and used to reconstruct a dendrogram for hierarchical clustering (group average linkage). 'Similarity profile' (SIMPROF) permutation tests were used to identify significant groupings, such that the group being subdivided had a significant ($p < 0.05$) internal structure. A 'similarity percentages' (SIMPER) routine was used in order to identify species that contributed most to the similarity within each sample cluster, as well as to dissimilarities with other clusters.

A DCA was carried out in order to provide further information about the patterns of variation in the faunal data and to determine the type of response displayed by the species distribution to one or more environmental gradients, a unimodal or linear response (e.g., Leps and Smilauer, 2003). Choosing an appropriate ordination technique to quantify the direct species–environment relationships relies on determining the extent of species turnover (the beta diversity in community composition) measured in standard deviation (SD) units along an environmental gradient, as calculated by DCA (e.g., Leps and Smilauer, 2003; Barlow et al., 2013). Gradient lengths of SD <3 point toward linear faunal response along the environmental gradient, whereas those of SD >4 indicate unimodal species–environment relationships. DCA showed a linear species response and therefore RDA was used. RDA was applied to quantify the direct relationship between the distribution of benthic foraminifera to the elevation and abiotic ecological variables including pore-water and sediment properties (Table 2). This ordination technique is based on a linear species–environment relationship, where the axes are linear combinations of the environmental variables. It integrates variance as well as correlation in its search for relationships between the two sets of biotic and abiotic variables (Leyer and Wesche, 2007). In order to further test the correlation between the species distribution and elevation we used the parametric correlation coefficient Pearson's r.

Both DCA and RDA were applied using Canoco, version 4.55 software (Leps and Smilauer, 2003; Ter Braak and Smilauer, 2002). For DCA, detrending by segments was selected and for RDA environmental parameters were standardized and Monte Carlo permutation tests (2000 permutations) were performed. In both statistical methods species data were log transformed because they don't show normal distribution based on the Shapiro-Wilk test calculated using the PAST software package vs. 3.11 (Hammer et al., 2001) and also due to the rather uneven vertical distribution of the samples (Gehrels, 2000; Telford and Birks, 2011). We calculated inter-correlations between environmental parameters and statistical significance as well as the Pearson's correlation coefficient (r value) with the PAST software package vs. 2.15 (Hammer et al., 2001).

DCA results were also used as an initial step for choosing an appropriate unimodal or linear-based transfer function. In order to develop transfer functions ('ecological response functions') for predicting marsh surface elevations, the relationship between water depth and the relative abundances of foraminiferal taxa within the combined training data set was empirically modeled in the C2 program (version 1.7.4; Juggins, 2011). Although the difference in tidal range between the two sites is small, sample elevations were normalized using the Standardised Water Level Index (SWLI), commonly applied in salt-marsh sea-level studies (Gehrels, 1999; Horton et al., 1999; Wright et al., 2011; Barlow et al., 2013; Kemp and Telford, 2015). The SWLI value is calculated as: (100 × (sample elevation − local mean tidal level) / (high water reference level − local mean tidal level)) + 100. We used the mean higher high water as the high water reference level (Kemp and Telford, 2015). Although Wright et al. (2011) recommend to use the highest occurrence of foraminifera as the high water reference level in SWLI calculations, we could not establish this datum because our highest samples still contained foraminifera. All elevations are expressed relative to the same datum and a SWLI of 100 is MTL and 200 is MHHW.

Model performance was evaluated based on the cross-validated (leave-one-out/ jack-knifed) correlation between model prediction elevation and measured elevation (r^2_{jack}), the root mean squared error of prediction (RMSEP) and the tendency of the model to overestimate (underestimate) parts of the training set gradient, as mean and maximum bias (Birks, 1998; Juggins and Birks, 2012; Kemp and Telford, 2015). The observed residual scatter and observed and predicted values after model prediction in the produced scatterplots were also taken in consideration as complementing the evaluated model performance (Telford et al., 2004).
Sampling of the modern analogue along transects (e.g., evenly stratified by elevation and or within one site/marsh) may lead to spatial autocorrelation (increased resemblance of samples) and thus might negatively impact the transfer function model performance (Legendre and Fortin, 1989; Telford and Birks, 2009). The issue of spatial autocorrelation is reduced by sampling two different salt marshes and combining the results into one modern training set. Consequently, we present a robust foraminifera-based transfer function from a modern analogue potentially suitable for RSL reconstructions in Southern California.

4 Results

4.1. The environmental properties of surface sediment

Water temperature (WT) varies between 24 °C and 32 °C and between 15 °C and 20 °C in Seal Beach and Tijuana salt marshes, respectively (Fig. 2; Table 2). Differences in WT between the two marshes are related to differences in sampling months (October vs. December) and differences within each marsh are related to sampling hours during the day, in each transect. The pH values of the pore-water show no observable spatial trend and range commonly from 6.1 to 7.8 in Seal Beach excluding one sample with the lowest pH (4.3) and from 6.4 to 7.3 in Tijuana. Low O_2 concentration is measured in the most elevated stations of Seal Beach and thereafter a decreasing trend is observed ranging from 8 to 0.3 mg/l. O_2 concentration were rather low, <1.6 3 mg/l, at all stations in Tijuana excluding two stations with values of 6.6 and 3.3 mg/l. Salinity values in Seal Beach show a decreasing trend from the high marsh samples (~40 ‰) to the low marsh samples (~34 ‰) whereas in Tijuana the values varies between 27 ‰ and 38 ‰ in all stations apart of one high marsh sample with 20 ‰. The organic matter content is fluctuating in both transects and ranges from 67 to 1% and from 12 to 75% in Seal Beach and Tijuana salt marshes, respectively. The organic matter content in both transects was the highest in the mid marsh sediments (apart from two samples in Seal Beach in which sparse vegetation occurs) and it decreases somewhat towards the low marsh edge due to the decrease in vegetation cover. The carbonate content varied between 1% and 22% and between 1% and 11% in Seal Beach and Tijuana salt marshes, respectively, with the higher values occurring in the mid marsh samples in both transects (apart from two samples in Seal Beach which had also low organic matter content). There was no clear trend in the grain-size distribution along the intertidal zone of both transects. Tijuana salt marsh is dominated generally by silty sediment (62-77%), except in two sandy high marsh stations (TJE1, TJE2; Fig. 2; Table 2). Seal Beach stations are characterized by silty to sandy sediments with low concentrations of clay (<14%). Increasing sand concentrations in the lower salt-marsh stations of Seal Beach (SB8-SB17) are probably related to a tidal velocity gradient.

4.2. Distribution of live (rose Bengal stained) foraminifera in the surface samples

The distribution of the live dominant taxa identified along transects from Seal Beach and Tijuana salt marshes are summarized in Figs. 3 and 4, respectively.
Nine different agglutinated taxa were found in the live (rose Bengal stained) populations from both sites which were dominated by *Jadammina macrescens*, *Trochammina inflata, Miliammina fusca,* and *Ammobaculites* spp. Other species such as *Trochamminita irregularis, Miliammina petila* and *Scherochorella moniliformis* were observed in rather low numbers (Plate 1). Calcareous species were found mainly in the tidal flat and low marsh sediments. High abundances of juvenile calcareous miliolids were encountered in several high marsh samples. These were probably transported by tides via nearby tidal creeks (Plate 2) as suggested by the high sand content in the same samples.

The live species exhibit observable zonation relative to elevation. At both sites, the relative abundance of *M. fusca* is larger at lowest elevations. The tidal flat sediments at Seal Beach (St. 16) are dominated by this species with general abundances between 92 and 496 specimens/10 cm^3 sediment volume and *S. moniliformis* with 108 and 216/10 cm^3 (Fig. 3). In the low marsh sediments at Seal Beach (St. SB8-SB17) and at Tijuana (St. TJE10-TJE 15) these two species occur in decreasing numbers (Figs. 3 and 4). In the middle marsh these species are replaced by high concentrations of *J. macrescens* and *T. inflata* (St. TJE7-TJE 9 and TJE 16), while at Seal Beach (St. SB3-SB7) *Ammobaculites* spp. also occur. The highest stations (St. SB1 and SB18-SB20 and St. TJE1-TJE 3 and TJE17) are characterized by higher numbers of *J. macrescens* and *T. inflata* and occurrence of *T. irregularis* and *M. petila* (Figs. 3 and 4, Supplementary data 1 and 2).

4.3. Distribution patterns of dead foraminiferal assemblages in the surface samples

The dead foraminiferal assemblages are dominated by the same taxa as the live (rose Bengal stained) populations at the same stations with occasional higher concentrations in both marshes (Figs. 3 and 4).
The dead foraminiferal zonation defined by the Q mode cluster analyses mimics the vascular plant zonation in Seal Beach saltmarsh whereas in Tijuana it differs slightly from the zonation of vascular plants. Three main sample groups (clusters 1, 2 and 3) were distinguished in each salt marsh (Figs. 5 and 6).

At Seal Beach, cluster 1 contains samples from the low marsh (St. SB17 and SB8-SB15 and their replicates) with elevations between 1.37-1.67 m NAVD88 designated as cluster 1b and samples from tidal flat (St. SB16, 2SB16) with only one elevation of 0.98 m NAVD88 labeled as cluster 1a. Both sub-clusters are characterized by *J. macrescens* (7-68%), *T. inflata* (18-57%), calcareous species (1-25%) and *M. fusca* (1-29%). The latter species is more abundant in cluster 3a where it is also accompanied by *S. moniliformis* (5-11%). Cluster 2 consists entirely of mid marsh stations (St. SB2-SB7 and their replicates) with elevations between 1.48 and 1.58 m NAVD88 (Fig. 5, Table 2, Supplementary data 1). This cluster is divided into two sub-clusters 2a and 2b. Sub cluster 2a is characterized by *J. macrescens* (21-75%), *Ammobaculites* spp. (12-62%) and *T. inflata* (<20%). Sub cluster 2b is dominated by *J. macrescens* (57-89%) and accompanied by *T. inflata* (<29%) and calcareous species (<5%). Cluster 3 includes stations from the high marsh (St. SB1, SB18-SB20 and their replicates) with elevations between 1.56 and 1.79 m NAVD88. The most significant species contributing to this cluster are *J. macrescens* (>46%), *T. inflata* (<38%) and *T. irregularis* (<7%).

At Tijuana, cluster 1 consists in part of the low marsh stations (St. TJE12-TJE15) with the lowest elevations between 1.39 and 1.48 m NAVD88 (Fig. 6, Table 2, Supplementary data 2). This cluster is dominated by *J. macrescens* (21-52%), *Trochammina inflata* (18-48%), calcareous species (11-38%), *M. fusca* (4-9%) and by *S. moniliformis* (1-3%). Cluster 2 contains samples from the mid to low marsh (St. TJE4 – TJE11and TJE16) with elevations between 1.42-1.59 m NAVD88. Samples in this cluster are dominated by *J. macrescens* (35-72%), *T. inflata* (20-51%) and calcareous species (1-13%). Cluster 3 encompasses the high marsh samples (St. TJE1-3 and TJE17) with elevations between 1.57- 1.93 m NAVD88. The dominant species in this cluster are similar to those occurring in cluster 3 at Seal Beach including *J. macrescens* (>40%), *T. inflata* (12-44%), *T. irregularis* (4-12%) and *M. petila* (<7%) (Fig. 6).

4.4. Surface and infaunal foraminiferal distribution in the short cores

The infaunal foraminiferal distributions in the short cores are shown in Fig. 7. The down core distribution of dead foraminifera is given in Supplementary data 1 and 2. Similar foraminiferal species are currently living (rose Bengal stained) at the surface (0-1 cm depth) of the transition from mid to low marsh (St. SB5) of Seal Beach and of the mid marsh (St. TJE8) of Tijuana with general abundances of 872/10 cm^3 and 340/10 cm^3, respectively. The living assemblage at the surface of Seal Beach is dominated by *J. macrescens* (624/10 cm^3), calcareous species (192/10 cm^3) and *T. inflata* (56/10 cm^3). The living assemblage at the surface of Tijuana is dominated by *T. inflata* (188/10 cm^3), *J. macrescens* (108/10 cm^3), and calcareous species (24/10 cm^3). Living infaunal specimens of the same surface living species are observed between 1 cm and maximum down to 6 cm, showing general decreasing numbers with core depth. In the shallowest depths (1-2 cm), the total highest numbers of infaunal specimens representing 16% and 10% out of the total assemblages, in Seal Beach and Tijuana, respectively, are observed. The most abundant infaunal species is *T. inflata* (672/10 cm^3 or 80/10 cm^3 at 1-2 cm in Seal Beach and Tijuana, respectively) which also found deeper (down to 6 cm) compared to other infaunal species.

4.5. The relationship between foraminiferal composition and environmental variables

The short lengths of the first DCA axis in turnover (less than 2 SD) units for each transect and for the combined surface assemblage of both marshes (Table 3a-c) indicate that the foraminifera demonstrate a linear response to one or more environmental gradients and thus a linear ordination method (i.e., RDA) is expected to perform well. The applied Monte Carlo tests suggest a significant influence ($p < 0.05$; Table 4a) of several environmental parameters on the species distribution in the modern data set of Seal Beach. O_2 explains 24.1% of the variance in the data set, elevation, salinity, carbonate content and temperature, each justifying values between 16.3% and 19.9% of the variance in the data set. These significant environmental variables in Seal Beach are correlated to the first two axes, calculated with the RDA, which explain 51% of the cumulative variance of the species data and 94% of the species-environment relationship (Table 4a, Fig. 8A). However, in Tijuana, elevation and TOM were found to be the significant environmental parameters, explaining 43.2 % and 8.3% of the variance in the data set, respectively (Table 4b, Fig. 8B). Axes one and two explain 56% of the total variance in the foraminiferal data (Table 4b).

The combined RDA results for both salt marshes show that elevation is the most significant environmental parameter explaining 17.1% of the variance in the data set. Other parameters explaining the variance in the data set include O_2 (12.2%), temperature (7.6%), salinity (10.9%), pH (2.1%) with the remainder (50%) consisting of inter-correlations between variables (Table 4c). The first two axes calculated with the RDA explain 38% of the cumulative variance of the species data and 93% of the species-environment relationship (Table 4c, Fig. 9).

In general, the results of the RDA (Figs. 8 and 9) support the Q-mode CA for both sites (Figs. 5 and 6). The distance between the samples with relatively good separation of the three assemblages within each transect is distinguished in the three dendrograms (1, 2, 3; Figs. 8 and 9) and shows the dissimilarities between the sample clusters and the similarities within each sample cluster. In the RDA ordination diagrams, cluster 3 samples representing high marsh sediments in both salt marshes are plotting around the elevation arrow while cluster 1 samples, representing mid to low marsh and low to tidal flat sediments, with lower elevations plotting mostly in the opposite direction.

Several samples of cluster 2 plot close to the carbonate content, temperature and O_2 arrows, all pointing in the same direction (Figs. 8A and 9). The arrow of salinity is in the same direction as the arrow of elevation in Seal Beach indicating an inter-correlation between the two and reflecting a similar general trend from higher values in the high marsh to lower values towards the low marsh (Figs. 8 and 2).

The relationships between elevation, the most significant environmental parameter (Table 4c) and abundance of the six strongly correlative foraminiferal species are shown in Fig. 9. *Jadammina macrescens* and *T. irregularis* are positively correlated with elevation, although rather weakly ($r = 0.2$). *Miliammina petila* occurs in low relative abundances at high marsh sites (i.e., in Tijuana) does not seem to have any correlation with elevation ($r = -0.03$). Conversely, *M. fusca*, calcareous spp. and *S.*

moniliformis occurring in the low marsh to tidal flat stations, are negatively correlated with elevation (Figs. 5, 6, 8 and 9) (*r* values range from -0.3 to -0.5). *Trochammina inflata* occurs in high relative abundances at low marsh as well as at high marsh sites, notably in Seal Beach, and does not seem to have any correlation with elevation ($r = -0.1$) (Fig. 8A). *Ammobaculites* spp. that have higher abundances in the mid marsh sediments, cluster 2 of Seal Beach, are positively correlated with O_2 (Figs. 8A and 9).

4.6. Development of a foraminifera-based transfer function

DCA of the Southern California training set, combining Seal Beach and Tijuana salt marshes with the SWLI as the environmental variable, produced a gradient length of 1.98 (Table 3c), allowing us to apply linear regression models, i.e., PLS (Birks, 1995). Nonetheless, WA-PLS also performs well for a linear species distribution along such an environmental gradient and while providing 'the minimal adequate model' (Birks, 1998 and reference therein), occasionally it outperforms PLS (Ter Braak et al., 1993). For this reason we tested also the WA-PLS model predictions.

Prior to the development of the foraminifera-based transfer function we performed a screening exercise. Three samples that contain high abundances of *Ammobaculites* species (>26%) and belonging to cluster 2a (Fig. 5) were excluded from the original 55 salt-marsh samples. The reasoning behind this decision is that these species are usually found broken in surface marsh sediments (Kemp et al., 2009a; Milker et al., 2015a) and to a greater extent they are hardly preserved within the subsurface fossilized record and thus, are not considered as useful proxy species for sea-level studies.

In order to improve the predictive ability of the transfer function we removed samples that have a difference between the predicted and observed values larger than 25% of the total observed elevation range, between 120.7 and 222.8 m NAVD88 (following Edwards et al., 2004). Consequently, PLS was developed from a screened training set of 43 samples and 8 species whereas a WAPLS was developed from 44 samples and 8 species. The final component in each transfer function was chosen according to the highest r^2 and the lowest RMSEP and maximum bias values if the reduction in prediction error exceeds 5% for this component compared to the next lowest component (Ter Braak and Juggins, 1993). This decision path was merely applied to the first three components in order not to add statistical complexity (Wright et al., 2011; Barlow et al., 2013).

The performance of both regression methods is presented in Table 5. The statistical output of the PLS foraminiferal transfer function shows that the second component of our model performed better than the first component providing the highest correlation between the observed and predicted values with $r^2_{\text{Jack}} = 0.49$, and the lowest root-mean squared-error of prediction ($\text{RMSEP}_{\text{Jack}}$) of 14.7 SWLI. Whereas the WAPLS-based- transfer-function shows that the third component performed significantly better than the other components and also compared to the PLS model, with the lowest $\text{RMSEP}_{\text{Jack}}$ of 11.9 SWLI, higher $r^2_{\text{Jack}} = 0.72$ and lower maximum bias values (22.7). The transfer function shows a stronger performance between observed and predicted SWLIs as also reflected in the scatter plots for the WAPLS (Fig. 10). A trend was found in the residuals of the WAPLS component 2, but this trend was weaker with the use of component 3. Nevertheless the residual scatter is suggesting that some elevation predictions are underestimated especially from the landward upper edge of the gradient (high marsh).

5 Discussion

5.1. Environmental controls on modern foraminiferal distribution

Among the environmental variables controlling the spatial foraminiferal distribution across salt marshes (e.g., salinity, organic carbon concentration, grain-size, pH) (e.g., Patterson, 1990; de Rijk and Troelstra, 1997; Scott et al., 1998; Woodroffe et al., 2005; Milker et al., 2015a; Barnett et al., 2016), elevation which is associated with tidal inundation (or subaerial exposure) is frequently identified as the primary control, at least indirectly, responsible for their zonation (Gehrels, 2000; Horton et al., 2003; Edwards et al., 2004; Horton and Edwards, 2005; Barlow et al., 2013; Milker et al., 2015a). Consequently, these organisms have been extensively used as proxies for sea-level reconstruction (e.g., Scott and Medioli,1980; Patterson et al., 2004; Barlow et al., 2013).

The results of the Q-mode CA and the RDA from Southern California further support the hypothesis that foraminiferal assemblages are strongly related to elevation and hence tidal submergence. At Tijuana elevation explains 43% of the total variance in the foraminiferal assemblages whereas at Seal Beach, 16% of the variance of the species data is explained by elevation (Fig. 8, Table 4a-b). Despite the difference in the elevational control between marshes, the combined RDA results of both data sets still show that elevation is the primary factor influencing the foraminiferal zonation, explaining 17.1% of the variance in the data set (Fig. 9, Table 4c) similar to studies in the Magdalen Islands in the Gulf of St. Lawrence, Canada (Barnett et al., 2016), Oregon, USA (Hawkes et al., 2010) and the UK (Horton and Edwards, 2006). Elevation is followed by four additional environmental variables explaining lower variance in the data set including O_2 (12.2%), temperature (7.6), salinity (10.9), pH (2.1) and with the remainder (50%) consisting of inter-correlations between variables (Table 4c). Inter-correlations between environmental variables and foraminifera are known from other intertidal studies since varied factors also may be governed by the frequency and duration of tidal exposure as controlled by elevation (Horton et al., 2003; Horton and Edwards, 2005). For example in Seal Beach a significant ($p < 0.05$, $r = 0.36$) correlation between elevation and salinity was observed (Fig. 8b). Pore-water salinity is an additional key factor (after elevation) known to control marsh foraminiferal distributions (Murray, 2006), for example in tidal marshes with extremely low gradients having complex topography such as of the Great Marshes of eastern Massachusetts (e.g., de Rijk and Troelstra, 1997). Salinity of the sediment pore-water generally varies considerably due to the combined influence of the tidal cycle and infiltration of seawater, desiccation, precipitation and seepage of fresh ground water. The Southern California marshes experience frequent droughts under dry climate conditions. Pore-water salinity decreases from the high marsh (~40 ‰) to the low marsh (~34 ‰) at Seal Beach marsh (Fig. 2). This trend is also measured by the RDA results where salinity explains 16.8% of the variance in the species data and it has a positive correlation with elevation (Fig. 8b, Table 4b). On the other hand, salinity values at Tijuana were more variable and thus had no significant influence on the distribution pattern of the foraminifera. It seems that this difference between both marshes is associated with their topographic characteristics with Tijuana transect having a simple gradient with no topographic complications whereas Seal Beach has more complex and irregular topography. Other studies also imply that when the topography is irregular, there is no very clear vertical foraminiferal zonation with respect to the tidal frame (de Rijk, 1995; de Rijk and Troelstra, 1997; Müller-Navarra et al., 2016). Nonetheless, since salinity varies considerably through the tidal cycle and our measurements were done only at the time of the sample collection during summer when evaporation is playing an important role, not much significance is attached to our measurements of this environmental parameter.

At Tijuana marsh, elevation is followed by TOM explaining 8.3% of the variance in the data set (Fig. 8b, Table 4b). Mainly mid to low samples dominated by *J. macrescens* and *T. inflata* were positively related to the TOM (Figs. 6, 8b). These species are known to prefer higher amounts of organic matter (Armynot du Châtelet et al., 2009). When the data are combined, the clear control of TOM on the distribution of foraminifers in Tijuana becomes masked.

Further environmental parameters probably affect the distributions patterns of foraminifera in Seal Beach, for example O_2 and temperature (Fig. 8). Substrate oxygenation is an important factor determining the degree of infaunal foraminiferal dispersion into the substrate (Walker and Goldstein, 1999). O_2 and temperature also influence organic matter degradation and thus the preservation of agglutinant species organic cement (Berkeley et al., 2007 and references therein). However, the potential of preservation of agglutinant species is also inherent selectively by different species (Berkeley et al., 2007 and references therein). At Seal Beach, O_2 and temperature are positively related to mid marsh sediment that are the only samples characterized by higher abundances of *Ammobaculites* spp. (Fig. 8A). It may be that their preservation specifically at the mid marsh is associated with more stable environmental conditions compared to the salt marsh edges. Similar fragility was related to the coarseness of the grains making up the tests of *M. fusca* explained their poor preservation (de Rijk and Troelstra, 1999) compared to other more packed grains of relatively robust species such as *T. inflata* (Berkeley et al., 2007 and references therein). It is worth mentioning that this study was not designed to determine the temporal variability of intertidal foraminifera in the surface sediments from a time series survey (e.g., by monthly sampling). Consequently, we cannot attribute more significance to these factors which fluctuate daily, through the tidal cycle and seasonally.

5.1.1. Vertical zonation of dead foraminifera

The comparison between the dead foraminiferal assemblages across the salt-marsh surfaces of Seal Beach and Tijuana show that their distributions are very similar to each other and are also comparable to foraminiferal distributions in other parts of the world. This indicates that despite the recent hydrological changes, the foraminiferal distributions are robust to these changes and their prominent elevational zonation (with site-specific differences) is not affected.

The dead foraminiferal assemblages of the tidal flat and low marsh of the studied sites are characterized by the occurrence of *M. fusca* and calcareous species. The agglutinant *M. fusca* is known as an indicative species of lower elevations, for example along the North America's Pacific coast (e.g., Nelson et al., 2008; Hawkes et al., 2010; Engelhart et al., 2013, Milker et al., 2015a) and the North America's Atlantic coast (e.g., Edwards et al., 2004). In the middle marsh the dominant dead species include *J. macrescens*, *T. inflata* and *Ammobaculites* spp. *Trochammina inflata* and more prominently *J. macrescens* are also dominating higher elevations of the high marshes at both sites where they are accompanied by *T. irregularis* and *M. petila. Jadammina macrescens* and *T. inflata* have frequently been reported from middle marsh (Guilbault et al., 1996; Jennings and Nelson, 1992; Nelson et al., 2008; Hawkes et al., 2010; Engelhart et al., 2013, Milker et al., 2015a ,b) and the highest marsh environments (e.g., Patterson, 1990; de Rijk and Troelstra, 1997; Horton et al., 1999; Wang and Chappell, 2001; Hippensteel et al., 2002; Horton et al., 2003; Edwards et al., 2004a; Franceschini et al., 2005; Woodroffe et al., 2005). *Trochamminita irregularis* (often grouped with *T. salsa*) has commonly been detected as a dominant species in the high and highest marsh in North American Pacific marshes (Hawkes et al., 2010; Engelhart et al., 2013; Milker et al., 2015a, b) and in New Zealand (e.g., Hayward et al., 2004; Southall et al., 2006) and Tasmania (Callard et al., 2011). Similarly *M. petila* has been also observed in the middle and high marshes from Oregon (Engelhart et al., 2013). The agglutinant *Balticammina pseudomacrescens* is an important sea-level indicator (Gehrels and van de Plassche, 1999) dominating higher elevation of mid to highest marsh zones in North American Pacific marshes, for example in Oregon salt marshes (Hawkes et al., 2010, 2011; Engelhart et al., 2013; Milker et al., 2015a, b) but is absent in the studied salt marshes in California.

5.2. The influence of taphonomic processes

Processes as sub-surface foraminiferal production (infauna) and taphonomic changes vary temporally and spatially, from one intertidal system to another, and may influence the fossil assemblages (e.g., Martin, 1999; Berkeley et al., 2007). Accordingly there is a clear need to explore these processes in each depositional environment, as a base for employing an adequate surface sampling strategy aiming at accurate paleoenvironmental interpretations based on the microfossil record. At Seal Beach and Tijuana, test production mirrors rather proportionally the standing crop numbers, a principle discussed in Berkeley et al. (2007) (Figs. 3 and 4). Samples with high numbers of standing crops yielded high total numbers (per 10 cm^3 sediment volume) of dead foraminifera though exceeding the living ones, often by over an order of magnitude. This observation applies to most species excluding *S. moniliformis* and calcareous species in both marshes which showed opposite trends with higher numbers of live specimens compare to the dead numbers. This is probably due to taphonomic processes and low preservation potential (Figs. 3 and 4). Dead agglutinant specimens of *S. moniliformis* were found only in lower elevations. These are very fragile and tend to break easily due to the loss of organic cement by oxidation (Berkeley et al., 2007). On the low marsh and tidal flat lower numbers of dead calcareous species were observed compared to the live foraminifera (Figs. 3 and 4, Supplementary data 1 and 2). This difference along with apparent dissolution (Plate 2, Fig. 6b) is probably associated with reduced mean pH values of 6.5 and 6.9 in Seal Beach and in Tijuana, respectively, causing carbonate dissolution and lower preservation of the calcareous tests. Early diagenetic dissolution and loss of calcareous tests related to a pH <~7, which results in a carbonate undersaturation is a known process from intertidal environments along the North-West American coastal marshes (e.g., Hawkes et al., 2010; Milker et al., 2015a), salt marshes in the Mediterranean region (Cundy et al., 2000; Shaw et al 2016) as well as from other temperate and tropical coasts (Wang and Chappell, 2001; Edwards and Horton, 2000; Horton and Murray, 2006; Berkeley et al., 2009). Moreover, a general spatial trend of better preservation at higher elevations was observed at Tijuana (Fig. 4), possibly associated with diagenetic controls on the preservation potential of calcareous and agglutinated tests.

5.3. Surficial vs. subsurface foraminifera

Most paleoenvironmental studies of intertidal marshes use the foraminiferal assemblages in surface sediment (upper 1 to 2 cm) as a modern counterpart assuming that they are characterized primarily by epifaunal production (e.g., Scott and Medioli, 1980; Gehrels, 1994; de Rijk, 1995; Horton, 1999; Patterson et al., 2004; Woodroffe et al., 2005; Horton and Edwards 2006; Kemp et al., 2009a) or shallow infaunal (Buzas et al., 1993). However, several studies have shown that intertidal foraminifera can live infaunally as deep as several decimeters in some marsh settings (e.g., Goldstein et al., 1995; Ozarko et al., 1997; Goldstein and Watkins, 1998; Saffert and Thomas, 1998; Goldstein and Watkins, 1999; Patterson et al., 1999; Hippensteel et al., 2002; Culver and Horton, 2005; Duchemin et al., 2005; Tobin et al., 2005; Berkeley et al., 2007; Leorri and Martin, 2009; Milker et al., 2015a). In such cases sampling the uppermost surface sediment (0-1 cm) would produce poor modern analogues (Duchemin et al., 2005). For example Ozarko et al. (1997) and Patterson et al. (1999) relied on a deeper surface sampling (to 10 cm), covering the entire distribution of the living infauna. Relying on such thick intervals may be misleading as they might represent a longer time span, in some cases a decade or longer, in some salt marsh settings (Milker et al., 2015a).

At Seal Beach and Tijuana the highest numbers of living specimens at the transition to middle marsh (St. SB5) and middle marsh (St. TJE8) are found in the surface samples (Fig. 7). The numbers of infaunal specimens, restricted to the first six cm of the cores, are low compared to the total foraminiferal assemblage and show a decreasing trend from 16% and 10% between 1 and 2 cm at Seal Beach and Tijuana, respectively, to nil (Fig. 7). These results are in accordance with other salt-marsh studies reporting living species predominantly in the top few centimeters of salt marsh in North Carolina (Culver and Horton, 2005), New Brunswick, Canada (Patterson et al., 2004) and the UK (Horton, 1997; Horton and Edwards, 2006).

Furthermore, the same infaunal species are presently living in the surface samples indicating that none of them are exclusively infaunal. Additionally the dominant infaunal species *T. inflata*, *J. macrescens* and calcareous miliolids are also dominating the dead surface and fossil assemblages in both marshes. Consequently, our results show that the influence of infaunal species on the dead assemblage is minor since most reproduction is concentrated near the sediment surface and that the same post-depositional processes influence fossil assemblages as the dead surface assemblages. These observations enable us to use the dead assemblages in the upper surface sediments as an adequate modern analogue for accurate quantitative paleoenvironmental interpretations.

The dead fossil assemblages in the mini cores analyzed also reveal interesting results. At Tijuana, similar species that dominate the surface dead assemblages occur along the entire 10 cm core with similar ratios and abundances. However at Seal Beach the down core shows a fossilized dead assemblage different from the surface dead assemblage. *Miliammina fusca* dominates the entire foraminiferal assemblage in the lower part of the core (Supplementary data 1 and 2) and numbers gradually decrease towards the top. This faunal change is indicating a change from a low marsh setting to a mid-marsh setting (Figs. 3-6).

5.4. Robustness of the transfer functions for relative sea-level estimates

This study demonstrates that elevation related to tidal inundation is a primary control on the foraminiferal distributions across the two salt marshes in Southern California and our data are thus suitable for developing a transfer function for reconstructing past sea-level changes (described in chapter 5.1). The WAPLS transfer function (component 3) is the favored model with the best statistical performance compared to the PLS model (described in chapter 4.6) (Table 5, Fig. 10, Supplementary data 4). The performance of the transfer function is also evaluated by the positive correlation between transfer function model prediction error ($\mathrm{RMSEP}_{\mathrm{Jack}}$) and tidal and elevation ranges at the studied sites (e.g., Callard et al., 2011; Barlow et al., 2013; Mills et al., 2013). Earlier studies show that salt-marsh foraminifera-based transfer function models produce RMSEPs values between ~3–23% of the tidal range in a micro-tidal setting characterized by a <2 m tidal range (summaries in Callard et al. (2011) and Barlow et al. (2013)). The elevation range of the modern analogue is additionally influencing the error terms of RSL reconstruction, with a common RMSEPs between 5 and 15% of the elevation range of samples produced in most studies. In the current study the RMSEP value (11.9 SWLI or 0.09 m NAVD88) is 5.7% of the tidal range (1.6 m; Table 1) and 10% of the elevation range of the samples (0.95 m; Table 2). These values are within the common ranges presented by Barlow et al. (2013).

6 Conclusions

This study, for the first time, quantifies the environmental drivers controlling the distribution of foraminiferal assemblages in two coastal salt marshes along the Southern California coast, Seal Beach and Tijuana. The Q-mode CA and the RDA results show that elevation is the primary factor influencing the foraminiferal zonation. Seal Beach has more topographical complexity than Tijuana salt marsh, and thus more environmental parameters (e.g., O_2, salinity), apart from elevation, affect the foraminiferal distribution. The dead assemblages in the upper surface sediments are an adequate modern analogue for quantitative paleoenvironmental interpretations due to i) concentrated presence in the upper cm of sediment enabling statistical analyses, ii) presence of the same dominant foraminifera in the live and dead assemblages in both marshes indicating similar influence of post-depositional processes, iii) exceedance of the abundances of the surface dead foraminifera compared to the live abundances, reflecting preservation of several generations of foraminifera.

The dead surface assemblages in both marshes show a distinct zonation with respect to elevation, similar to earlier studies, however with some notable site-specific variability. The tidal flat and low marsh are characterized by higher concentrations of *M. fusca* and calcareous species, the middle marsh is dominated by *J. macrescens*, *T. inflata* and *Ammobaculites* spp (primarily at Seal Beach) and the high marsh zone is dominated by *J.macrescens*, *T. inflata* accompanied by *T. irregularis* and *M. petila*.

The development of WA-PLS foraminiferal transfer functions based on the training set combining data from two salt marshes increases the likelihood that fossil assemblages are adequately represented in the modern training set. The regional training set also reduces problems of spatial autocorrelation. The performance of the transfer functions is supported statistically by a robust relationship between the observed and the predicted elevations ($r^2_{\mathrm{Jack}} = 0.72$), the lower maximum bias values in the training set and by a precision of the reconstructions of 0.09 m NAVD88 ($\mathrm{RMSEP}_{\mathrm{Jack}}$) which is 5.7% of the tidal range and 10% of the elevation range of the samples. Our results agree with other foraminiferal studies from micro-tidal saltmarsh environments and can be used for future paleoenvironmental reconstructions in the study area.

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Table captions

Table 1. The nearest tide gauge station for each site with observations of Mean Higher High Water (MHHW), Mean Tide Level (MTL) and Mean Sea-Level (MSL). Tidal water level heights (m), above North American vertical datum (NAVD88), are measured over the period from 1983 to 2001 at the National Oceanic and Atmospheric Administration (NOAA).

Table 2. Sample locations, elevation, pore-water and sediment properties of the surface marsh samples collected at Seal Beach (denoted with the initials SB) and Tijuana (denoted with the initials TJE) during spring tide on mid-October, and early December 2015, respectively. TOM (total organic matter) and carbonate content were determined by Loss-on-Ignition at 550 and 950 °C, respectively. Detailed granulometric data detailed in Supplementary data No. 1 and 2. (nd = no data; asterisk denote stations in which a mini core was collected in addition to the surface sample).

Table 3. Statistical results of Detrended Correspondence Analysis (DCA) for Seal Beach (a), Tijuana (b) and the combined surface assemblage of both marshes (c).

Table 4. Statistical results of Redundancy Analysis (RDA) for Seal Beach (a), Tijuana (b) and the combined surface assemblage of both marshes (c).

Table 5. Results of the transfer functions performance criteria for foraminifera training set using two regression models: Partial Least Squares and Weighted Averaging-Partial Least Squares (see text for details). Given are the cross-validated (jack-knifed) correlation (r^2) between observed and estimated elevation in the modern data, the mean and maximum bias, the Root Mean Squared Error of Prediction (RMSEP) and the change of the RMSEP (in %) from one component to the next.

Figure captions

Fig. 1. Location of the study area on the North American Pacific coast, southern California (A), and sites mentioned in the text including Seal Beach salt-marsh (B) and Tijuana salt-marsh (C) with transects highlighted showing the surface station

locations (asterisk denote stations in which a mini core was collected in addition to the surface sample). See also Tables 1 and 2.

Fig. 2. Environmental variables from sampled transects in Seal Beach and Tijuana salt marshes including: temperature, pH, O_2, salinity, organic matter, carbonate content, sand, silt and clay content and vertical profile relative to the North American vertical datum (NAVD88). Sample elevation profiles with the tidal datum for MHHW (mean highest high water). See also Tables 1 and 2.

Fig. 3. Absolute abundances of the most abundant live (rose Bengal stained) (A) and dead foraminifera B) and their counts in the Seal Beach salt-marsh surface samples collected during mid-and late October, 2015. Sample elevation profiles are shown.

Fig. 4. Absolute abundances of the most abundant live (rose Bengal stained) (A) and dead foraminifera (B) and their counts in the Tijuana salt- marsh surface samples collected during December, 2015. Sample elevation profiles are shown

Fig. 5. Dendrogram of Q-mode cluster analysis of the dead foraminifera from Seal Beach salt-marsh. The most significant species contributing to each cluster, based on the 'similarity percentages' (SIMPER) routine, are shown on top of each cluster (*J.m. – J. macrescens*; *A.*spp. *– Ammobaculites* spp.; *T.in. – T. inflata*; Cal. – Calcareous species; *T.ir. – T. irregularis*; *M.f. – M. fusca*; *S.m – S. moniliformis*. The percentages of the most common dead species are given below the dendrogram.

Fig. 6. Dendrogram of Q-mode cluster analysis of the dead foraminifera from Tijuana salt-marsh. Taxa that make significant contributions to the similarity within each cluster, based on SIMPER routine, are shown on top of each cluster (abbreviations are given in Fig. 5) and the percentages of the most common dead species are given below the dendrogram.

Fig. 7. Total and individual live (rose Bengal stained) foraminiferal numbers (per $10cm^3$ sediment volume), and total percentages of live (rose Bengal stained) specimens relative to the total populations in each mini core (10cm deep) taken from the middle marshes of Seal Beach and Tijuana, St. 5 and St. 8, respectively.

Fig. 8. Redundancy Analysis (RDA) ordination triplots with forward selected significant environmental variables (Table 4) showing retrospective projection of the surface samples—species—environmental variables for Seal Beach (A) and Tijuana (B). Clusters sample distinguished in the Q-mode CA (Figs. 5 and 6) were incorporated into the RDA results.

Fig. 9. Redundancy Analysis (RDA) ordination triplot with forward selected significant environmental variables (Table 4) showing retrospective projection of the surface samples—species—environmental variables for the combined data sets of Seal Beach and Tijuana. Clusters sample distinguished in the Q-mode CA (Figs. 5 and 6) were incorporated into the RDA results.

Fig. 10. Scatterplots showing the relationship between observed standardized water level index (SWLI) against model predicted SWLI and residuals versus observed

SWLI using WA-PLS (component 3) transfer function in the modern data set derived from the southern California salt marshes.

Plate captions

Plate 1. Agglutinant foraminifera from surface sediments collected in Seal Beach and Tijuana salt marches, along the coast of southern California.
The scale bars of Figs. 2c, 3b equal 20 µm, of Figs. 2a-b equal 50 µm, of Figs. 1a-c, 4a-b, 5b, 6a-c, 7c, 8, 9c, 10b-e equal 100 µm, of Figs. 3a, 5a, 7a-b, 9a-b, 10a equal 200 µm.

(1a-b) *Miliammina fusca* (Brady, 1870), side view. (1c) *M. fusca*, aperture view. (2a-b) *Miliammina petila* Saunders, 1958, side view. (2c) *M. petila*, aperture view. (3a) *Scherochorella moniliformis* (Siddall, 1886), side view. (3b) *S. moniliformis*, aperture view. (4a) *Trochamminita irregularis* Cushman & Brönnimann, 1948 , side view. (4b) *T. irregularis*, side and aperture view. (5a) *Ammobaculites dilatatus* Cushman & Brönnimann, 1948 , side view. (5b) *A.dilatatus*, aperture view. (6a-b) *Ammobaculites* sp., side view. (6c) *Ammobaculites* sp., aperture view. (7a-b) *Ammobaculites* spp., side view. (7c) *Ammobaculites* spp., aperture view. (8) *Ammobaculites* spp., side view. (9a) *Trochammina inflata* (Montagu, 1808), spiral view. (9b) *T. inflata,* umbilical view. (9c) *T. inflata*, aperture view. (10a-b) *Jadammina macrescens* (Brady, 1870), spiral view. (10c) *J. macrescens*, umbilical view. (10d) *J. macrescens*, umbilical view showing collapsed chambers occurred soon after the specimen was dried. (10e) *J .macrescens*, aperture view with secondary apertures.

Plate 2. Calcareous intertidal taxa from surface sediments collected in Seal Beach and Tijuana salt marches, along the coast of southern California.
The scale bars of Figs. 1, 3 and 5c equal 50 µm, of Figs. 2, 4a-b, 5a-b and 6a-b equal 100 µm.

(1) *Cornuspira* sp., side view. (2) *Quinqueloculina* sp. side view. (3) miliolid, side view. (4a) *Trichohyalus aguayoi* (Bermúdez), spiral view. (4b) *T. aguayoi,* umbilical view. (5a) *Ammonia* sp. spiral view. (5b) *Ammonia* sp. umbilical view. (5c) *Ammonia* sp. aperture view. (6a) *Elphidium* sp side view. (6b) *Elphidium* sp. aperture view.

Supplementary data captions

Supplementary data 1. Seal Beach salt-marsh: general data and census foraminiferal data.

Supplementary data 2. Tijuana salt-marsh: general data and census foraminiferal data.

Supplementary data 3. Taxonomic reference list of species presented in text and in Supplementary data 1 and 2.

Supplementary data 4. Scatterplots showing the relationship between observed standardized water level index (SWLI) against model predicted SWLI and residuals versus observed SWLI using PLS (component 2) transfer function in the modern data set derived from the southern California salt marshes.

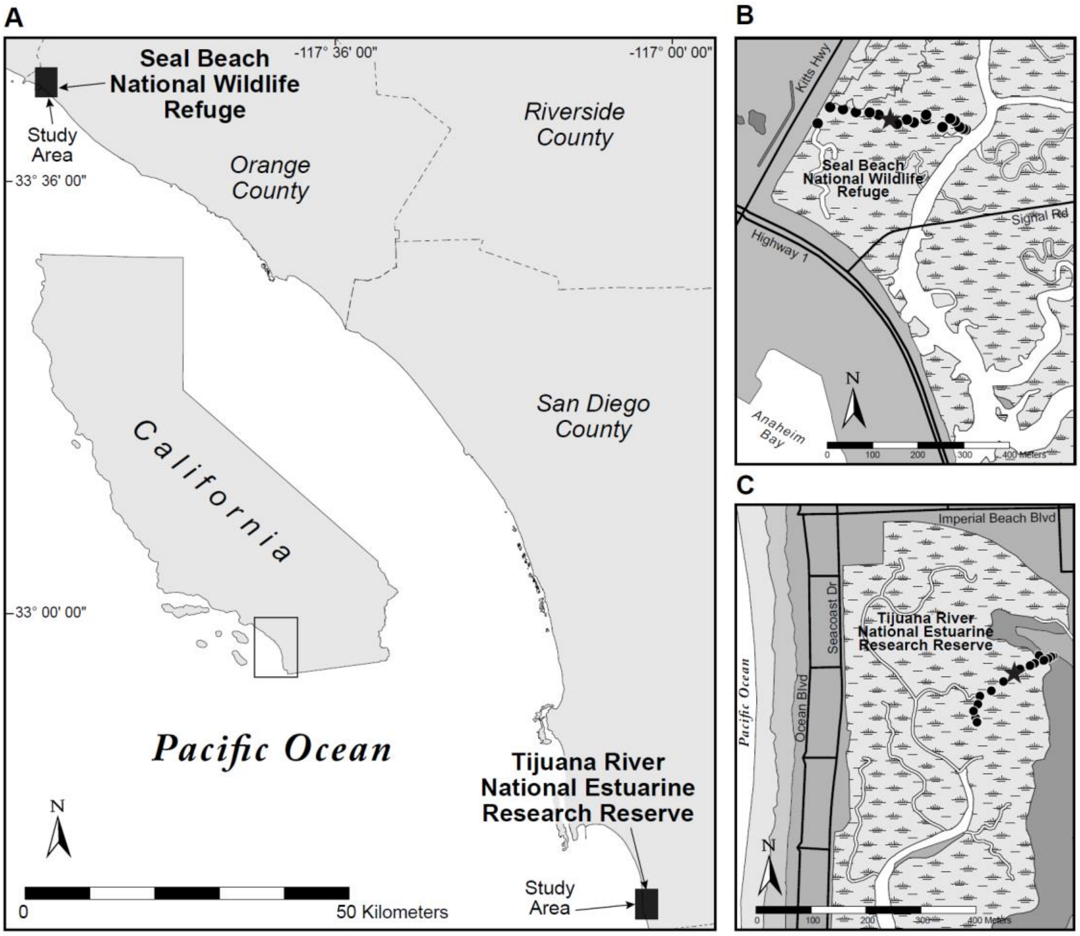

A
Seal Beach
National Wildlife
Refuge
Study
Area
-117° 36' 00"
-117° 00' 00"
Riverside
County
Orange
County
-33° 36' 00"
California
-33° 00' 00"
San Diego
County
Pacific Ocean
Tijuana River
National Estuarine
Research Reserve
N
Study
Area
0
50 Kilometers
B
Kitts Hwy
Seal Beach
National Wildlife
Refuge
Signal Rd
Highway 1
N
Anaheim
Bay
0
100
200
300
400 Meters
C
Imperial Beach Blvd
Seacoast Dr
Tijuana River
National Estuarine
Research Reserve
Pacific Ocean
Ocean Blvd
N
0
100
200
300
400 Meters

Figure 1

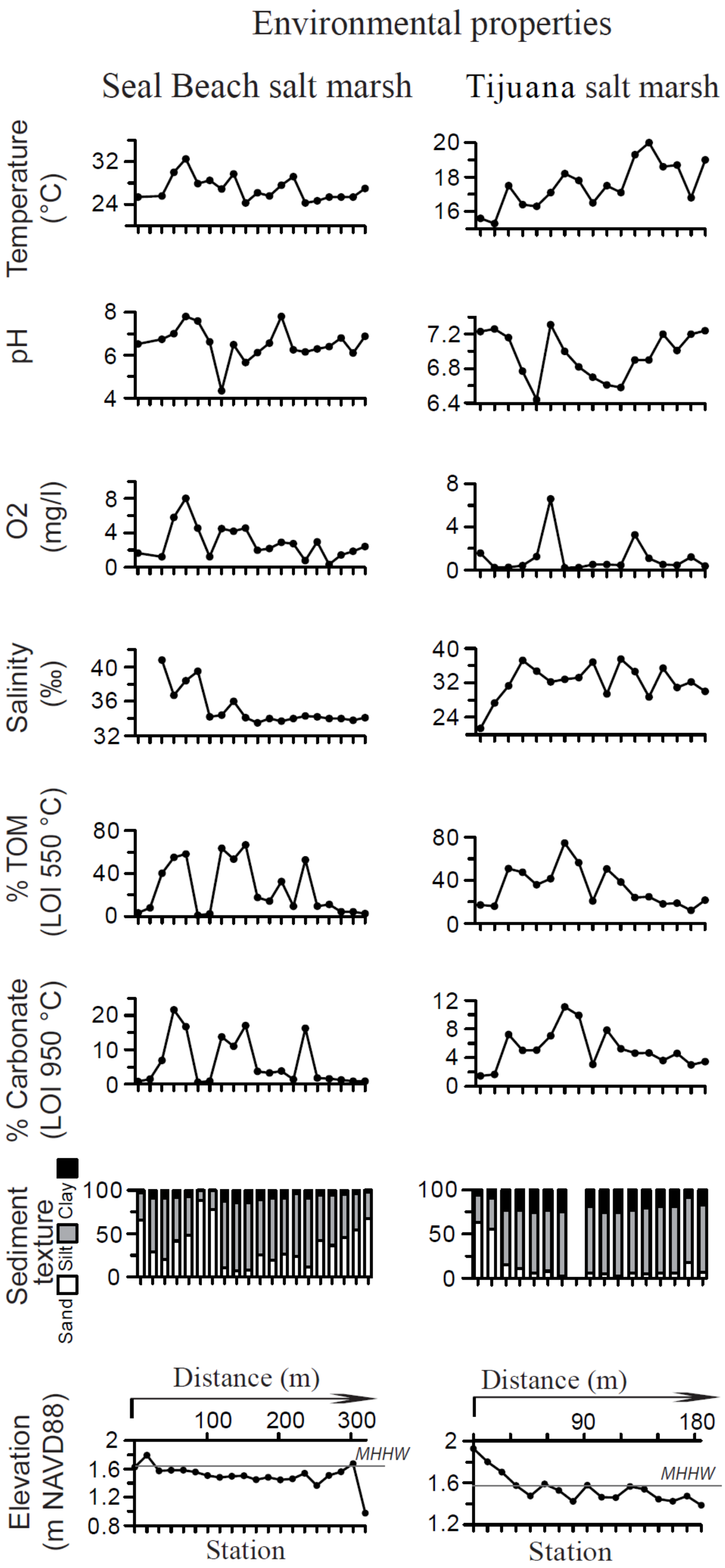

Environmental properties
Seal Beach salt marsh
Tijuana salt marsh
Temperature (°C)
32
24
20
18
16
pH
8
6
4
7.2
6.8
6.4
O2 (mg/l)
8
4
0
Salinity (‰)
40
36
32
24
% TOM (LOI 550 °C)
80
40
0
% Carbonate (LOI 950 °C)
20
10
12
8
4
Sediment texture
Sand
Silt
Clay
100
50
0
Distance (m)
100
200
300
90
180
Elevation (m NAVD88)
2
1.6
1.2
0.8
MHHW
Station

Figure 2

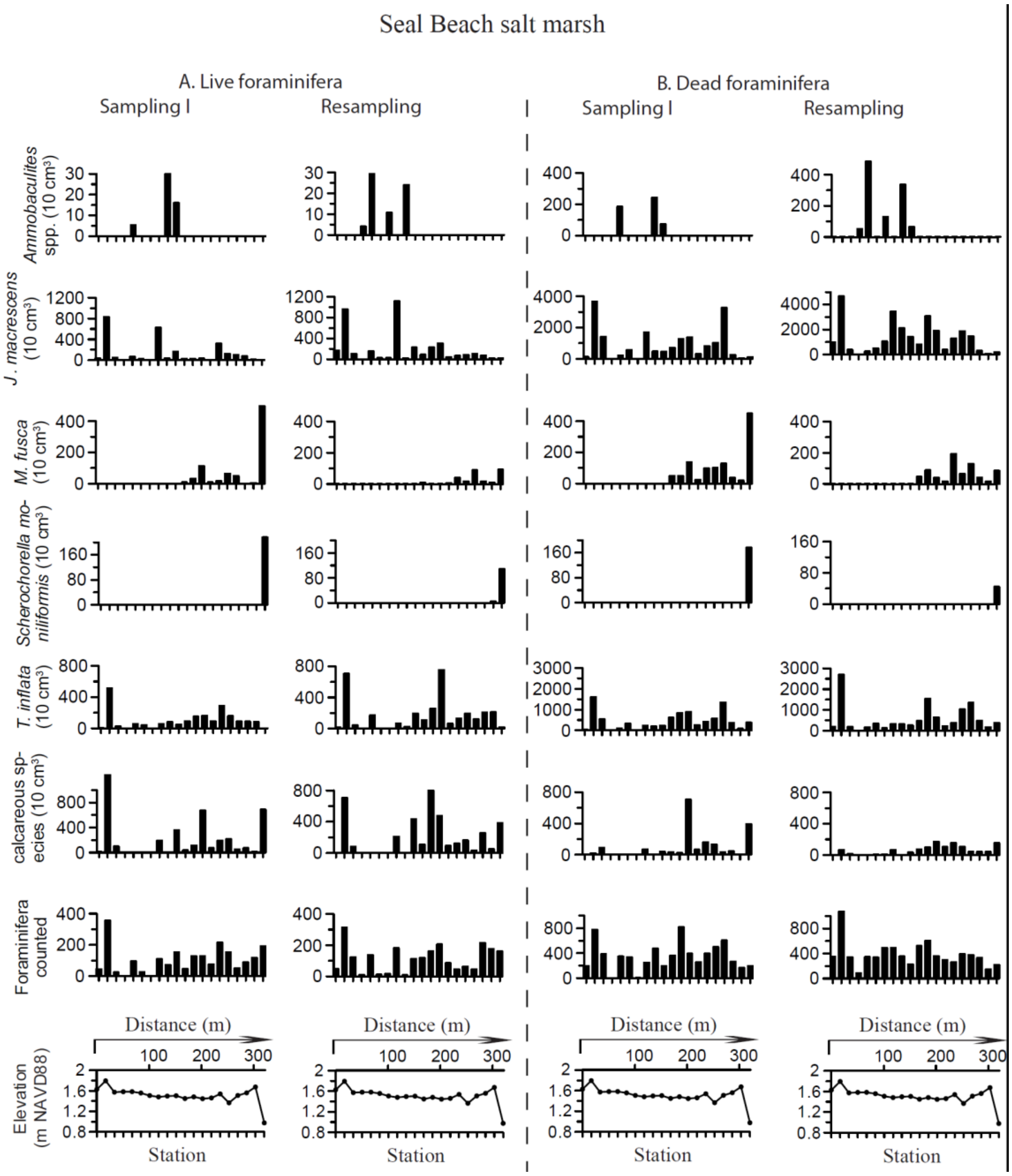

Seal Beach salt marsh
A. Live foraminifera
B. Dead foraminifera
Sampling I
Resampling
Sampling I
Resampling
Ammobaculites spp. (10 cm³)
J. macrescens (10 cm³)
M. fusca (10 cm³)
Scherochorella moniliformis (10 cm³)
T. inflata (10 cm³)
calcareous species (10 cm³)
Foraminifera counted
Elevation (m NAVD88)
0
10
20
30
0
200
400
0
400
800
1200
0
2000
4000
0
200
400
0
80
160
0
400
800
0
1000
2000
3000
0
400
800
0
200
400
0
400
800
Distance (m)
100
200
300
2
1.6
1.2
0.8
Station

Figure 3

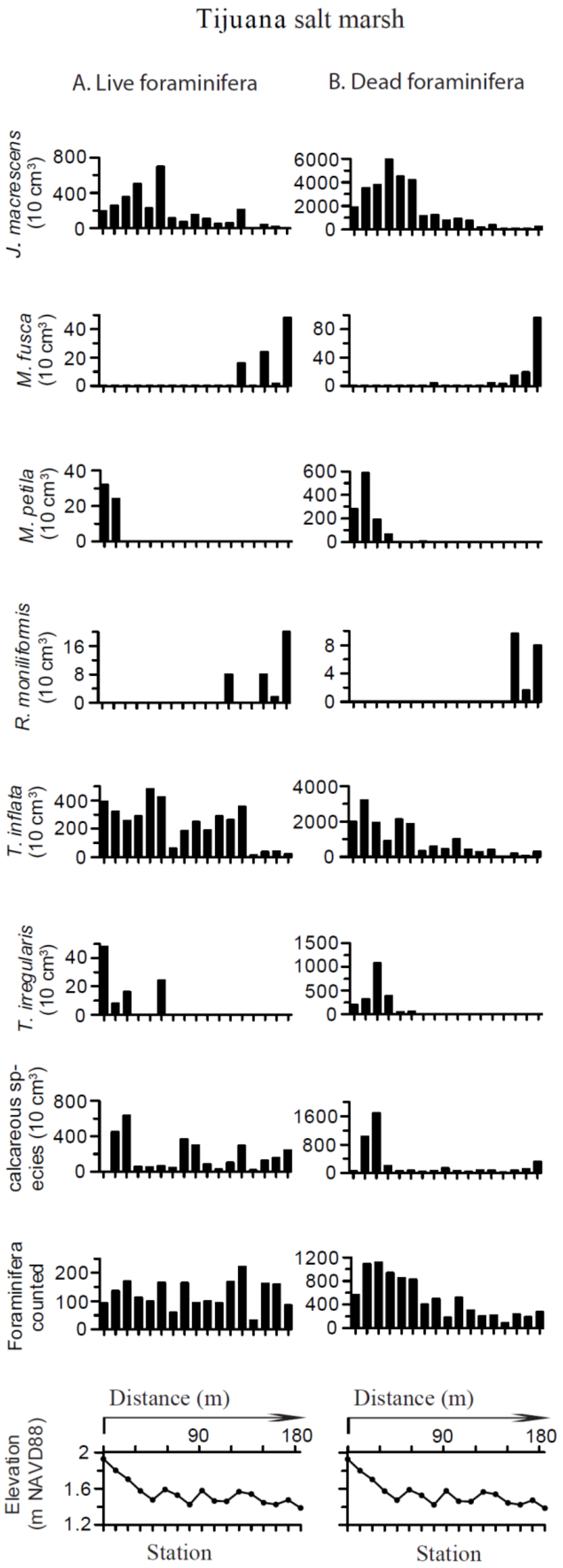

Tijuana salt marsh
A. Live foraminifera
B. Dead foraminifera
J. macrescens (10 cm³)
0
400
800
0
2000
4000
6000
M. fusca (10 cm³)
0
20
40
0
40
80
M. petila (10 cm³)
0
20
40
0
200
400
600
R. monilliformis (10 cm³)
0
8
16
0
4
8
T. inflata (10 cm³)
0
200
400
0
2000
4000
T. irregularis (10 cm³)
0
20
40
0
500
1000
1500
calcareous species (10 cm³)
0
400
800
0
800
1600
Foraminifera counted
0
100
200
0
400
800
1200
Distance (m)
90
180
Elevation (m NAVD88)
1.2
1.6
2
Station
Distance (m)
90
180
Station

Figure 4

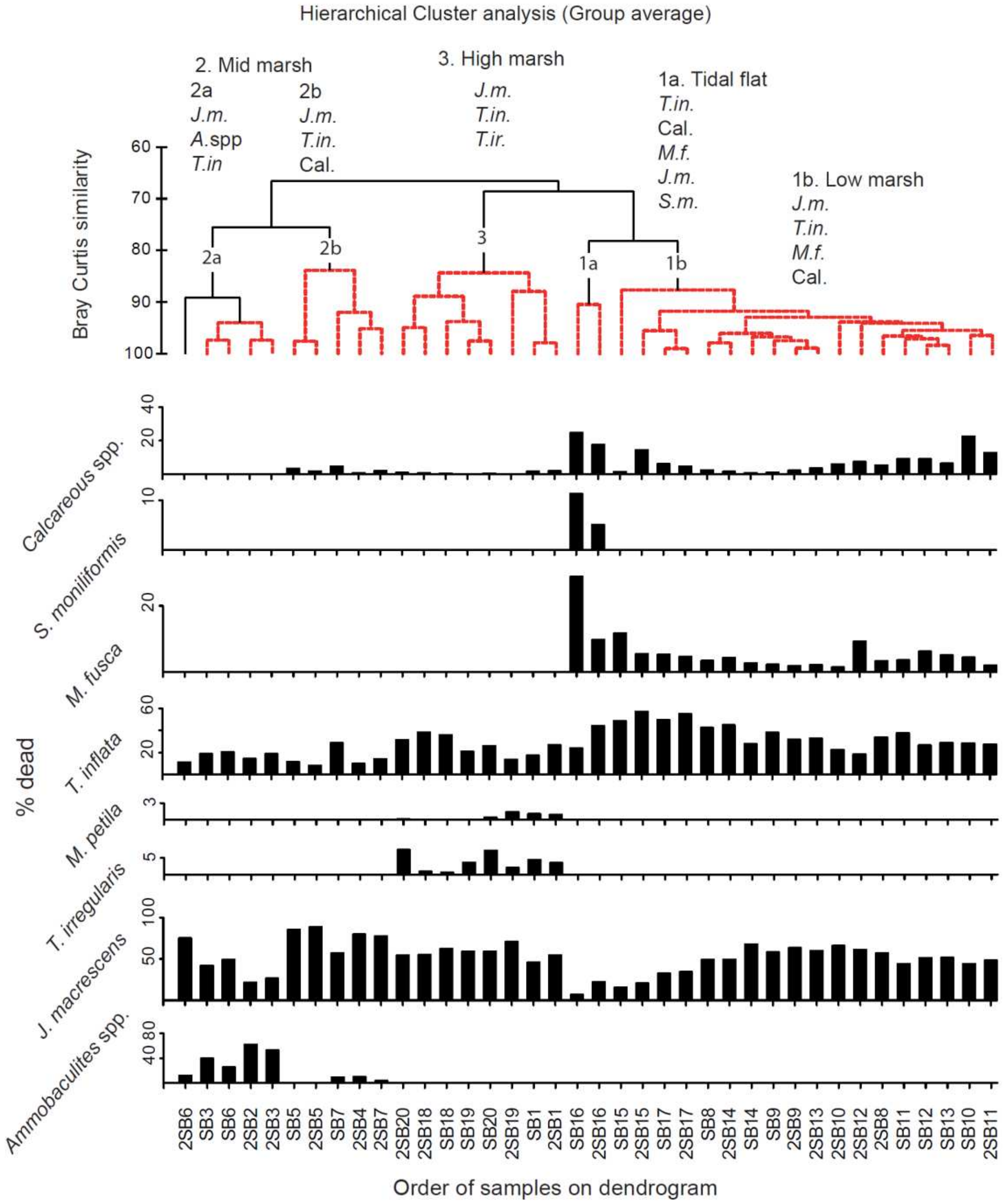

Hierarchical Cluster analysis (Group average)
2. Mid marsh
2a
J.m.
A.spp
T.in
2b
J.m.
T.in.
Cal.
3. High marsh
J.m.
T.in.
T.ir.
1a. Tidal flat
T.in.
Cal.
M.f.
J.m.
S.m.
1b. Low marsh
J.m.
T.in.
M.f.
Cal.
Bray Curtis similarity
60
70
80
90
100
2a
2b
3
1a
1b
Calcareous spp.
S. moniliformis
M. fusca
T. inflata
M. petila
T. irregularis
J. macrescens
Ammobaculites spp.
% dead
40
20
10
20
60
20
3
5
100
50
40 80
2SB6
SB3
SB6
2SB2
2SB3
SB5
2SB5
SB7
2SB4
2SB7
2SB20
2SB18
SB18
SB19
SB20
2SB19
SB1
2SB1
SB16
2SB16
SB15
2SB15
SB17
2SB17
SB8
2SB14
SB14
SB9
2SB9
2SB13
2SB10
2SB12
2SB8
SB11
SB12
SB13
SB10
2SB11
Order of samples on dendrogram

Figure 5

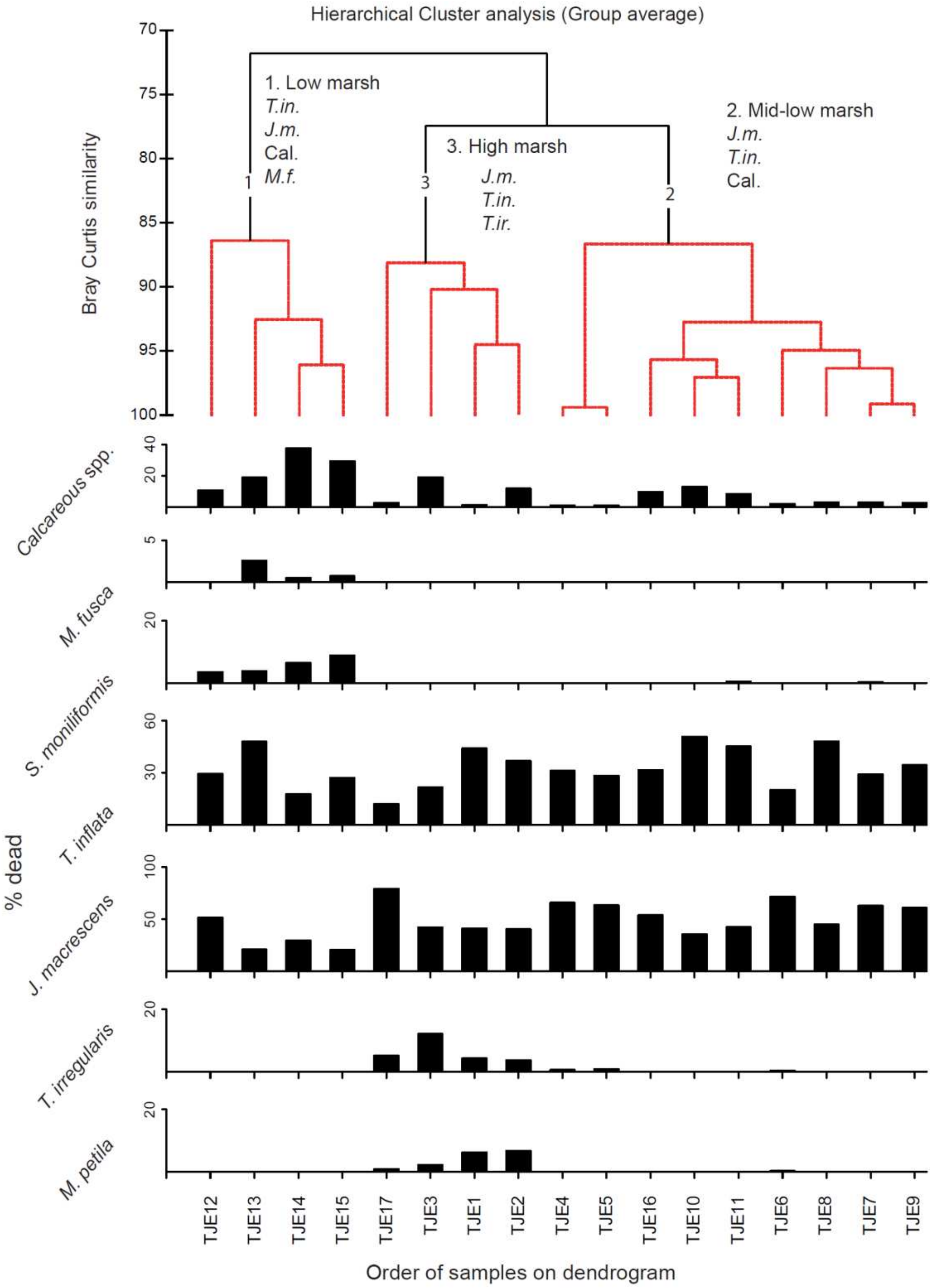
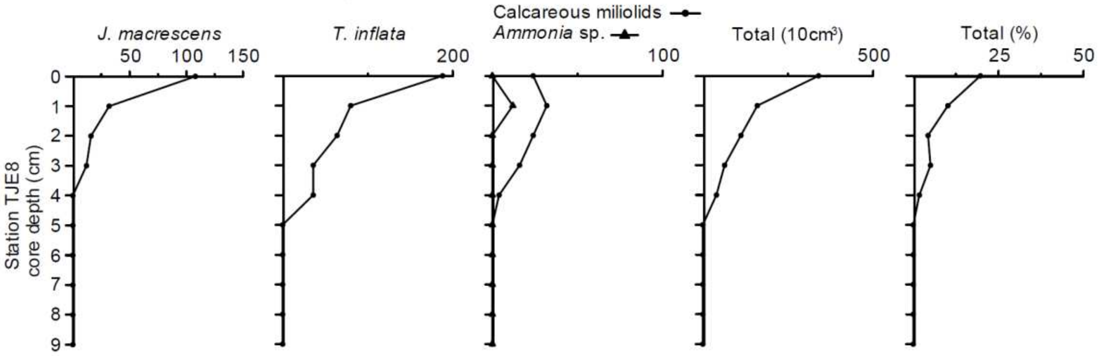

Hierarchical Cluster analysis (Group average)
Bray Curtis similarity
70
75
80
85
90
95
100
1. Low marsh
T.in.
J.m.
Cal.
M.f.
3. High marsh
J.m.
T.in.
T.ir.
2. Mid-low marsh
J.m.
T.in.
Cal.
1
3
2
% dead
Calcareous spp.
M. fusca
S. moniliformis
T. inflata
J. macrescens
T. irregularis
M. petila
20
40
5
20
30
60
50
100
20
20
TJE12
TJE13
TJE14
TJE15
TJE17
TJE3
TJE1
TJE2
TJE4
TJE5
TJE16
TJE10
TJE11
TJE6
TJE8
TJE7
TJE9
Order of samples on dendrogram

Figure 6


A. Live foraminifera in Tijuana salt marsh

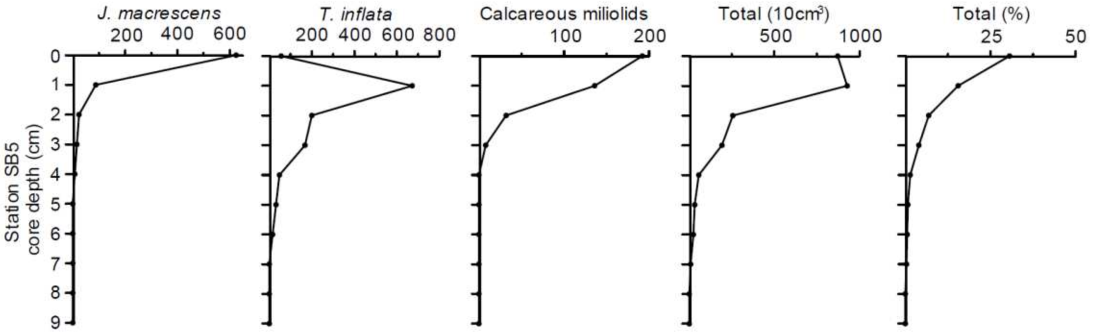

B. Live foraminifera in Seal Beach salt marsh

Figure 7

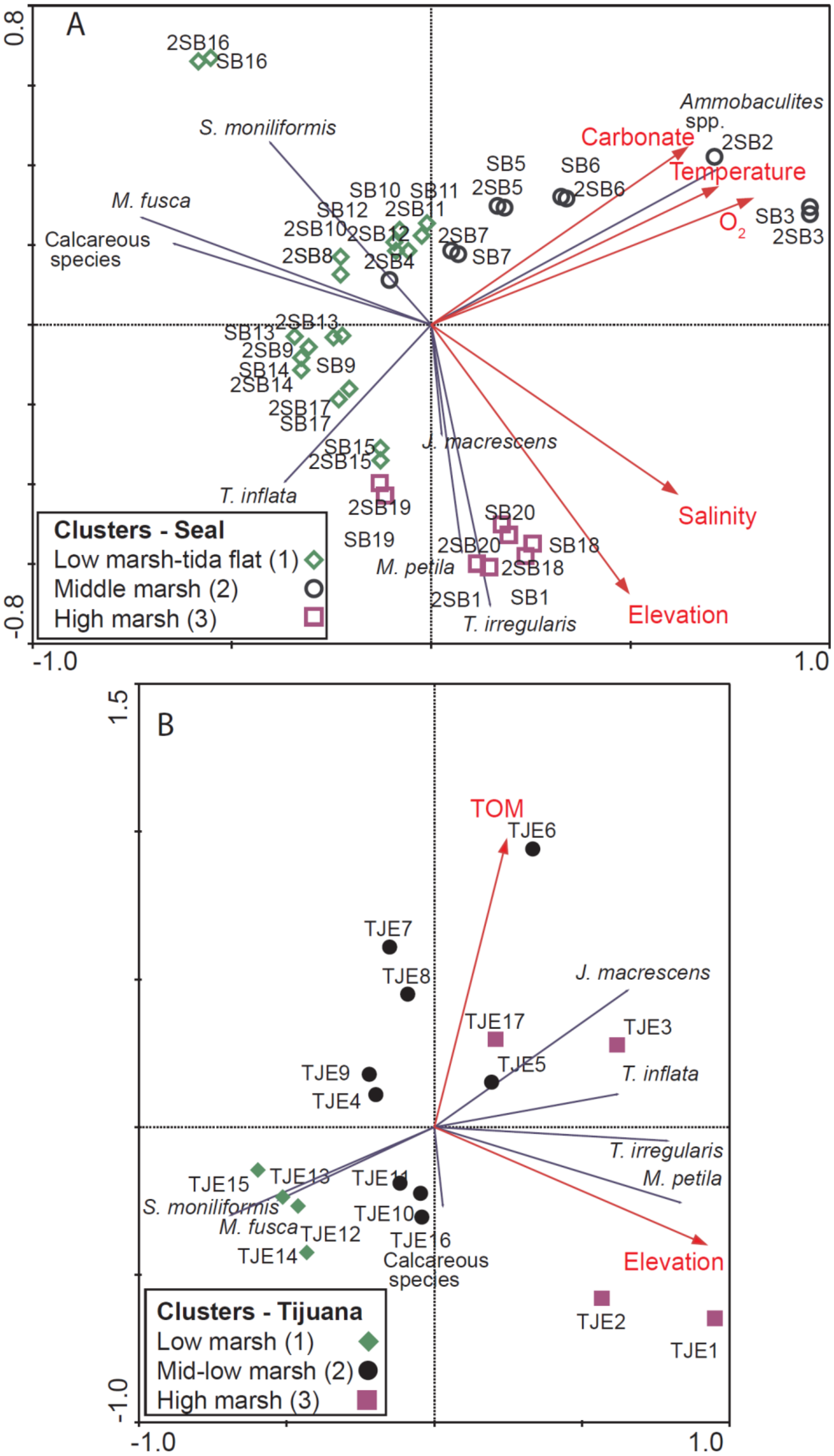

A
0.8
-0.8
-1.0
1.0
2SB16
SB16
S. moniliformis
M. fusca
Calcareous species
Ammobaculites spp.
Carbonate
Temperature
O_2
2SB2
SB3
2SB3
SB5
2SB5
SB6
2SB6
SB10
SB11
2SB11
SB12
2SB10
2SB12
2SB7
SB7
2SB8
2SB4
SB13
2SB13
2SB9
SB14
SB9
2SB14
2SB17
SB17
SB15
2SB15
J. macrescens
T. inflata
2SB19
SB19
SB20
2SB20
SB18
2SB18
M. petila
2SB1
SB1
T. irregularis
Salinity
Elevation
Clusters - Seal
Low marsh-tida flat (1) ◇
Middle marsh (2) ○
High marsh (3) □
B
1.5
-1.0
-1.0
1.0
TOM
TJE6
TJE7
TJE8
J. macrescens
TJE17
TJE3
TJE5
T. inflata
TJE9
TJE4
T. irregularis
M. petila
TJE15
TJE13
TJE11
S. moniliformis
TJE10
M. fusca
TJE12
TJE16
TJE14
Calcareous species
Elevation
TJE2
TJE1
Clusters - Tijuana
Low marsh (1) ◆
Mid-low marsh (2) ●
High marsh (3) ■

Figure 8

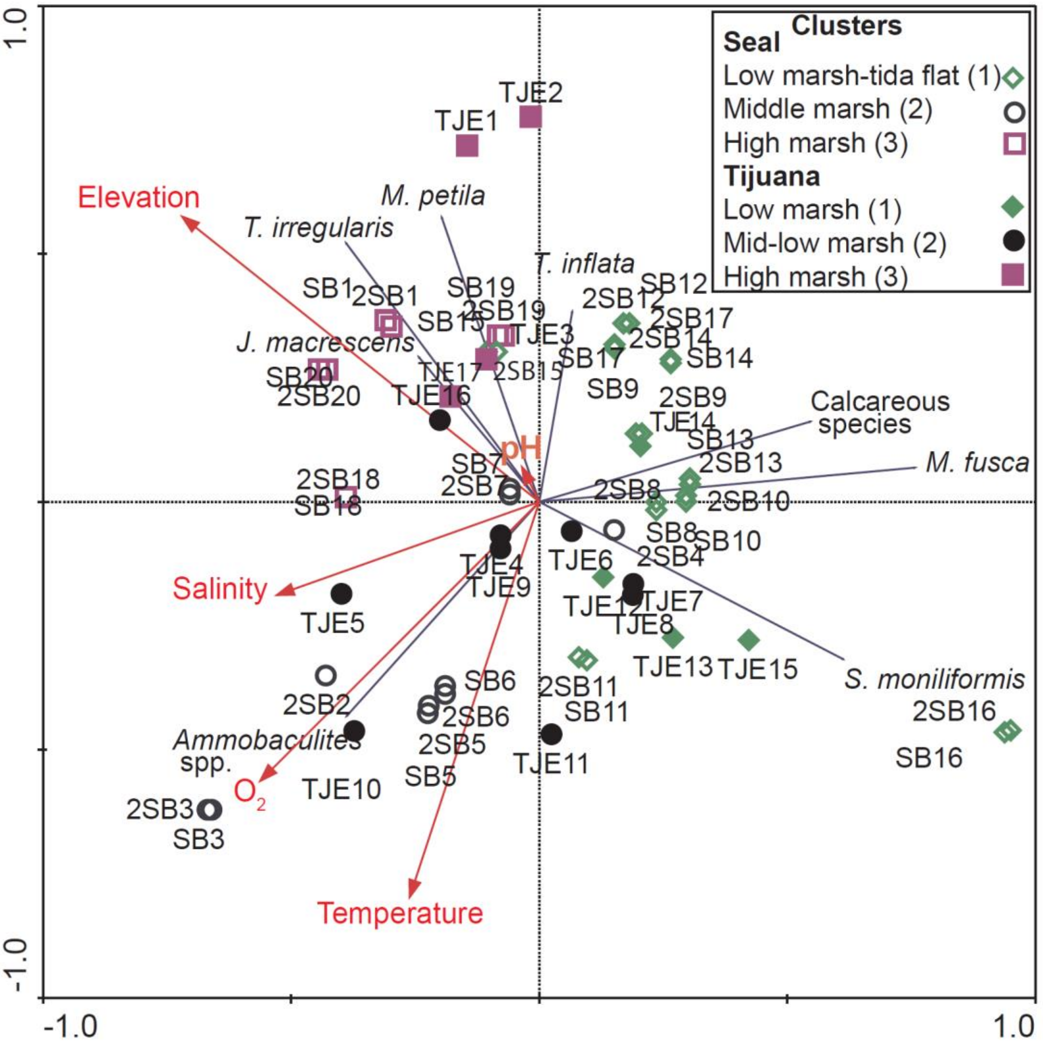


Figure 9

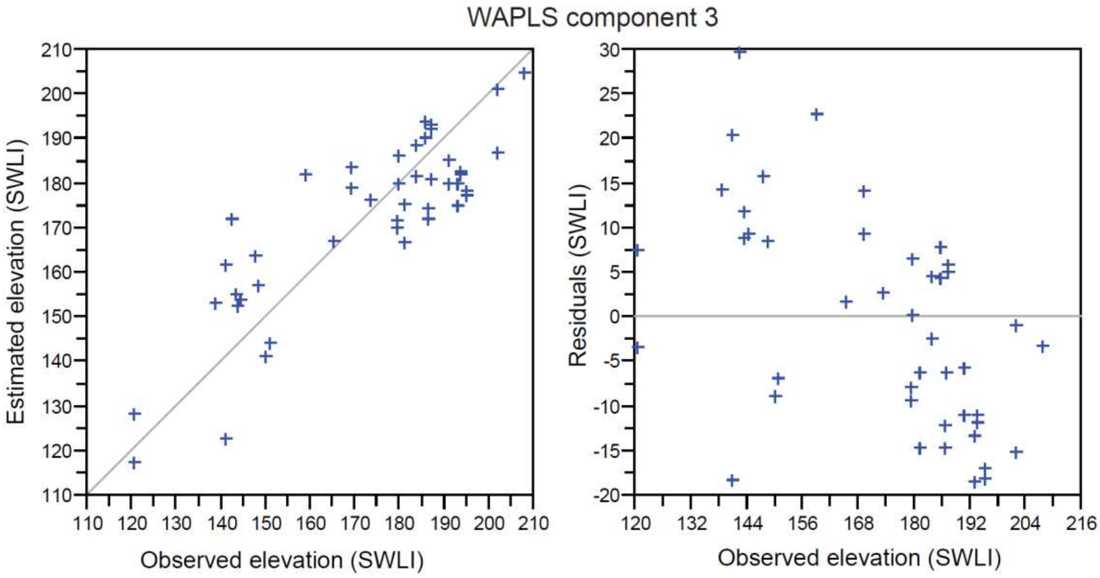


Figure 10

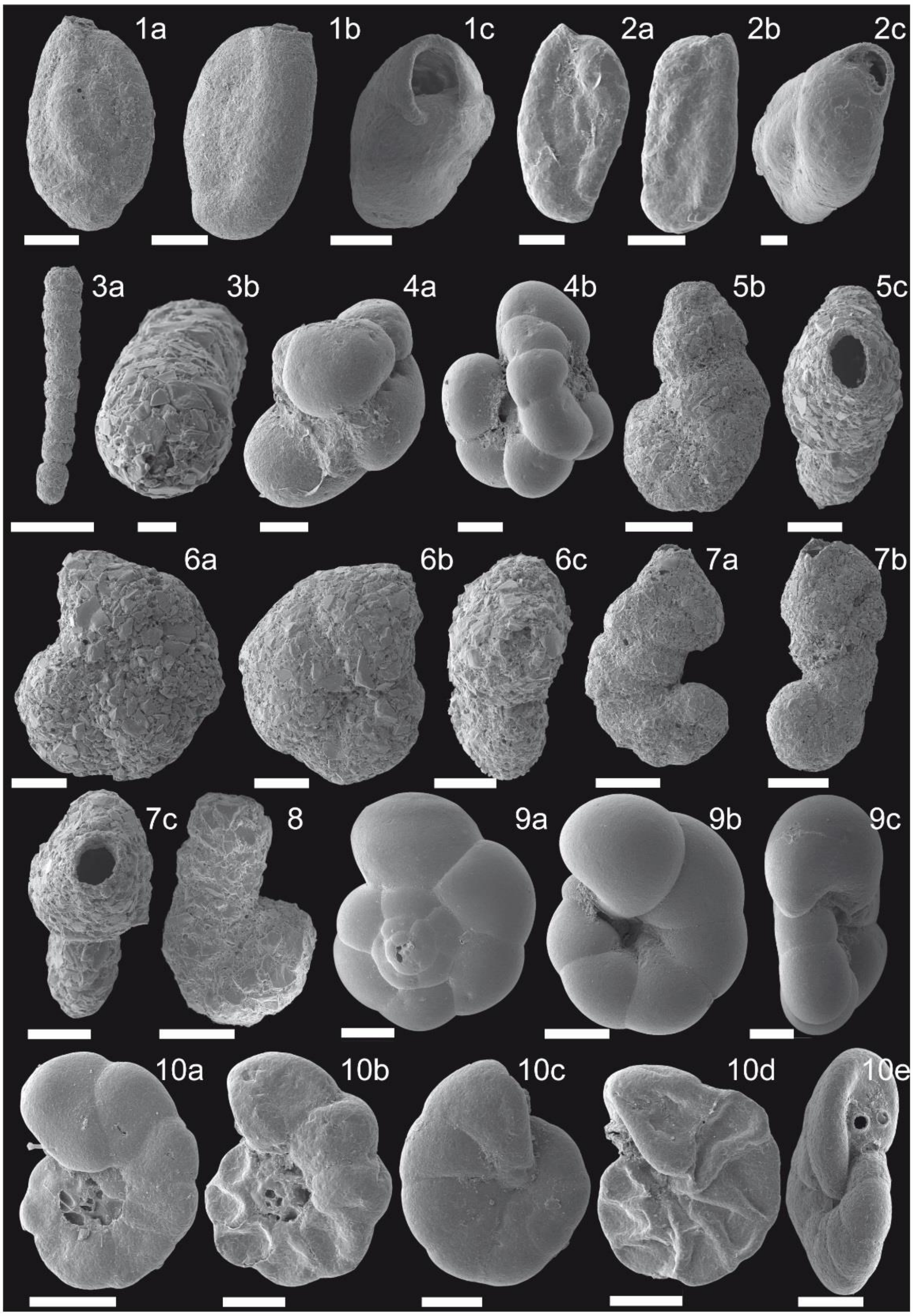

1a
1b
1c
2a
2b
2c
3a
3b
4a
4b
5b
5c
6a
6b
6c
7a
7b
7c
8
9a
9b
9c
10a
10b
10c
10d
10e

Plate 1

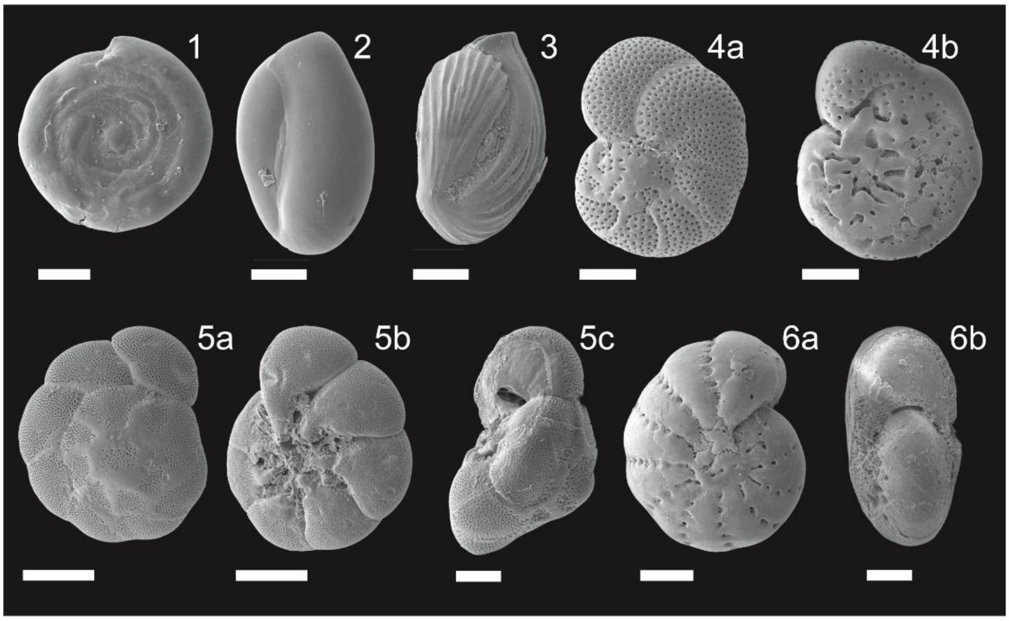


Plate 2

Site	Nearest tidal station (ID)	MHHW	MTL	MSL	MLLW	Mean diurnal range
Seal Beach	Los Angeles (9410660)	1.61	0.81	0.8	-0.06	1.67
Tijuana River Estuary	Imperial Beach (9410120)	1.56	0.77	0.77	-0.07	1.64

Table 1

Sample name	Coordinates		Elevation (m NAVD88)	Pore-water properties				Sediment properties (%)				
	Latitude (N)	Longitude (E)		pH	Temp. (˚C)	O_2 (mg/l)	Salinity (‰)	TOM	Carbonat	Sand	Silt	Clay
SB19	33 44 25.3116	-118 5 17.7163	1.63±0.03	6.5	25.4	1.7	nd	3.4	0.7	65.4	32.1	2.5
SB20	33 44 25.3334	-118 5 17.8292	1.79±0.04	nd	nd	nd	nd	8.1	1.5	29.1	62.0	8.8
SB1	33 44 26.4765	-118 5 16.7351	1.57±0.04	6.7	25.6	1.2	40.8	40.2	6.9	20.7	70.7	8.5
SB2	33 44 26.3093	-118 5 15.6391	1.58±0.04	7.0	30.0	5.8	36.7	55.1	21.6	41.7	50.1	8.1
SB3	33 44 26.0878	-118 5 14.5482	1.58±0.04	7.8	32.5	8.0	38.4	58.1	16.7	48.3	44.1	7.5
SB18	33 44 26.0348	-118 5 13.3831	1.56±0.03	7.6	27.9	4.6	39.5	1.2	0.6	88.0	12.0	0.0
SB4	33 44 25.8576	-118 5 12.6228	1.51±0.03	6.6	28.5	1.2	34.2	2.6	0.9	77.6	21.7	0.6
SB5*	33 44 25.5088	-118 5 11.7917	1.48±0.03	4.3	26.9	4.5	34.4	63.5	13.7	10.9	76.9	12.1
SB6	33 44 25.1860	-118 5 11.0653	1.50±0.03	6.5	29.7	4.2	36.0	53.4	11.0	7.5	78.6	13.8
SB7	33 44 25.4806	-118 5 10.2254	1.50±0.03	5.7	24.3	4.6	34.1	66.6	17.0	8.3	77.5	14.1
SB8	33 44 25.2602	-118 5 9.6482	1.45±0.03	6.1	26.2	2.0	33.5	17.7	3.7	25.2	64.3	10.4
SB9	33 44 25.4797	-118 5 8.6051	1.48±0.03	6.6	25.6	2.2	34.0	14.4	3.3	19.4	71.6	8.9
SB10	33 44 25.7897	-118 5 8.5703	1.45±0.03	7.8	27.6	2.9	33.7	32.6	3.8	26.4	65.0	8.5
SB11	33 44 24.8903	-118 5 7.2019	1.46±0.03	6.3	29.2	2.8	34.0	9.5	1.4	24.0	71.8	4.1
SB12	33 44 25.4888	-118 5 6.5347	1.54±0.04	6.2	24.3	0.8	34.3	52.7	16.2	11.4	79.7	8.8
SB13	33 44 25.3204	-118 5 6.1613	1.37±0.04	6.3	24.7	3.0	34.2	9.6	1.8	42.1	52.0	5.7
SB14	33 44 24.8828	-118 5 5.76425	1.51±0.03	6.4	25.4	0.3	34.0	11.3	1.6	36.4	58.0	5.5
SB17	33 44 24.8615	-118 5 5.6192	1.56±0.03	6.8	25.4	1.4	34.0	4.4	1.2	45.2	50.2	4.5
SB15	33 44 24.7418	-118 5 5.4418	1.67±0.03	6.1	25.4	1.9	33.8	4.4	0.8	54.0	42.2	3.8
SB16	33 44 24.6803	-118 5 5.2340	0.98±0.04	6.9	27.0	2.4	34.1	2.7	0.8	67.2	31.1	1.6
TJE1	32 34 27.0512	-117 7 39.3707	1.93±0.03	7.2	15.6	1.6	21.4	17.0	1.5	63.2	30.9	5.9
TJE2	32 34 27.0115	-117 7 39.5918	1.80±0.01	7.3	15.3	0.2	27.3	15.8	1.7	55.3	35.7	9.0
TJE3	32 34 26.9140	-117 7 39.8134	1.71±0.03	7.2	17.5	0.2	31.3	50.8	7.2	15.0	61.6	23.2
TJE17	32 34 27.1192	-117 7 40.4346	1.58±0.03	6.8	16.4	0.4	37.2	47.4	5.0	11.3	65.6	22.9
TJE4	32 34 26.8188	-117 7 40.1039	1.48±0.03	6.4	16.3	1.2	34.7	35.8	5.1	6.0	67.9	25.9
TJE5	32 34 26.7614	-117 7 40.4217	1.59±0.03	7.3	17.1	6.6	32.2	41.4	7.1	8.0	69.3	22.6
TJE6	32 34 26.6542	-117 7 40.7628	1.53±0.03	7.0	18.2	0.2	32.8	74.5	11.1	1.9	73.3	24.6
TJE7	32 34 26.5336	-117 7 41.0782	1.42±0.03	6.8	17.8	0.2	33.2	56.3	9.9	nd	nd	nd
TJE16	32 34 26.3524	-117 7 41.7866	1.58±0.03	6.7	16.5	0.5	36.8	20.7	3.1	5.7	75.6	18.6
TJE8*	32 34 26.1397	-117 7 42.1450	1.46±0.03	6.6	17.5	0.5	29.4	50.5	7.9	4.9	69.8	25.1
TJE9	32 34 25.6358	-117 7 42.9642	1.46±0.03	6.6	17.1	0.4	37.5	38.3	5.2	2.0	72.4	25.4
TJE10	32 34 25.1096	-117 7 43.8299	1.57±0.03	6.9	19.3	3.3	34.6	23.9	4.6	5.9	70.8	23.1
TJE11	32 34 24.8189	-117 7 44.6329	1.54±0.03	6.9	20.0	1.1	28.7	24.6	4.7	5.0	74.3	20.6
TJE12	32 34 24.3459	-117 7 44.7942	1.45±0.03	7.2	18.6	0.5	35.4	18.0	3.6	6.1	74.8	19.0
TJE13	32 34 23.9469	-117 7 45.1092	1.42±0.03	7.0	18.7	0.4	30.9	18.7	4.6	5.6	75.9	18.3
TJE14	32 34 23.5376	-117 7 44.9764	1.48±0.03	7.2	16.8	1.2	32.2	12.0	3.0	17.7	74.1	8.1
TJE15	32 34 23.2793	-117 7 44.8901	1.39±0.03	7.2	19.0	0.4	30.0	21.5	3.5	6.7	76.6	16.6

Table 2

a. Seal Beach	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.318	0.165	0.024	0.012
Lengths of gradient	2.017	1.519	1.19	1.214
Cumulative percentage variance of species data	40.6	61.7	64.7	66.3
b. Tijuana				
Eigenvalues	0.252	0.012	0.008	0.002
Lengths of gradient	1.468	0.447	0.407	0.438
Cumulative percentage variance of species data	62.1	65.1	67.2	67.7
c. Combined sites				
Eigenvalues	0.318	0.214	0.022	0.009
Lengths of gradient	1.981	1.847	0.907	1.004
Cumulative percentage variance of species data	40.9	68.3	71.1	72.3

Table 3

a. Seal Beach	Axis 1	Axis 2	Axis 3	Axis 4	F-value	*P* value	Captured variance
Eigenvalues	0.344	0.164	0.019	0.008			
Species-environment correlation	0.826	0.813	0.517	0.427			
Cumulative percentage variance							
Of species data	34.4	50.8	52.7	53.5			
Of species-environment relatio	63.8	94.2	97.7	99.1			
Correlations							
O_2 (mg/L)					11.41	0.0005	24.1
Elevation					8.92	0.0005	16.3
Salinity (‰)					3.66	0.0105	16.7
Carbonate (wt.%)					2.79	0.0255	17.7
Temperature (°C)					3.02	0.0215	19.9
b. Tijuana							
Eigenvalues	0.501	0.06	0.235	0.102			
Species-environment correlation	0.886	0.578	0	0			
Cumulative percentage variance							
Of species data	50.1	56.1	79.6	89.8			
Of species-environment relatio	89.4	100	0	0			
Correlations							
Elevation					11.39	0.0005	43.2
TOM (wt.%)					4.11	0.007	8.6
c. Combined sites							
Eigenvalues	0.238	0.141	0.023	0.006			
Species-environment correlation	0.805	0.66	0.535	0.319			
Cumulative percentage variance							
Of species data	23.8	37.9	40.2	40.7			
Of species-environment relatio	58.2	92.7	98.3	99.7			
Correlations							
Elevation					10.95	0.0005	17.1
O_2 (mg/L)					8.41	0.0005	12.2
Salinity (‰)					3.66	0.0075	7.6
Temperature (°C)					2.88	0.027	10.9
pH					3.15	0.0175	2.1

Table 4

PLS	R^2_{Jack}	Ave.Bias$_{Jack}$	Max.Bias$_{Jack}$	RMSEP$_{Jack}$	%Change
Component 1	0.242	-0.030	32.224	18.033	
Component 2	0.492	-0.696	21.553	14.737	18.281
Component 3	0.507	-0.628	20.451	14.527	1.420
Component 4	0.543	-0.481	26.127	14.218	2.132
Component 5	0.578	-0.253	28.639	13.557	4.643
WAPLS					
Component 1	0.338	0.148	27.778	18.576	
Component 2	0.511	-0.180	20.976	16.002	13.860
Component 3	0.724	0.621	22.757	11.964	25.232
Component 4	0.680	-0.016	26.186	12.995	-8.620
Component 5	0.683	-0.289	27.531	12.964	0.240

Table 5

Sample Name	SB5 0-1	SB5 1-2	SB5 2-3	SB5 3-4	SB5 4-5	SB5 5-6	SB5 6-7	SB5 7-8	SB5 8-9	SB5 9-10
	0	1	2	3	4	5	6	7	8	9
Aliquot/8	1	1	1	1	1	1	1	1	1	1
Aliquot sample size	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125
Census live										
Jadammina macrescens	78	11	3	2	1					
Calcareous miliolids	24	17	4	1						
Trochammina inflata	7	84	25	21	6	4	2			
juvenile Trochamminids		4					1	1		
Total live	109	116	32	24	7	4	3	1	0	0
Census dead										
Ammobaculites dilatatus										1
Ammobaculites sp.									4	9
Jadammina macrescens	211	386	207	320	254	373	346	168	232	184
Miliammina fusca		1	7	25	11	3	4	39	178	339
Calcareous miliolids	8	9	4	1	2	3	2	1	3	
Scherochorella moniliformis (forma R									1	1
Textulariid sp.				1	1	1				
Trochammina inflata	28	204	184	192	151	118	148	49	26	32
Trochammina sp.				2						
juvenile Trochamminids		31	31	38	57	27	41	15	9	4
Total dead	247	631	433	579	476	525	541	272	453	570
Total live+dead	356	747	465	603	483	529	544	273	453	570
Proccessed data										
Live BF/10 cm^3										
Jadammina macrescens	624	88	24	16	8	0	0	0	0	0
Calcareous miliolids	192	136	32	8	0	0	0	0	0	0
Trochammina inflata	56	672	200	168	48	32	16	0	0	0
total live populations 10cm 3	872	928	256	192	56	32	24	8	0	0
%live relative to the total populations	31	16	7	4	1	1	1	0	0	0
Dead BF/10 cm^3										
Jadammina macrescens	1688	3088	1656	2560	2032	2984	2768	1344	1856	1472
Miliammina fusca	0	8	56	200	88	24	32	312	1424	2712
Calcareous miliolids	64	72	32	8	16	24	16	8	24	0
Trochammina inflata	224	1632	1472	1536	1208	944	1184	392	208	256

Supplementary Data 1

Sample Name		Hour	HGPS Latitude	HGPS Longitude	Name	DGPS Latitude	DGPS Longitude	Elevation	Error	Distrance between srations 01 as ref.	pH	Temp. C	O_2 (mg/L)	Salinity ppt (‰)	% Organic Content	% Carbonate Content	% sand	% silt	% clay	Top cm	Sediment Bulk	Flora	Remarks during field		Remarks during analysis	Aliquot/8		*Ammobaculites* spp.	*Ammonia* sp.	*Bolivina* sp.	*Cornuspira involvens*	*Elphidium* spp.	*Jadammina macrescens*	*Miliammina fusca*	*Miliammina petila*	Calcareous miliolids	*Scherochorella moniliformis (forma R*	*Reophax* spp.	Textulariid sp.	*Trichohyalus aguayoi*	*Trochammina inflata*	*Trochamminita irregularis*	juvenile Trochamminids	Unidentified very coarse agglutinated
TJE1	1	10:31	32° 34.451	117° 07.656	TJE1	32 34 27.05128	-117 7 39.37079	1.93	0.026	0	7.2	16	1.6	21	17	1.46	63	31	6	x	x	*Frankenia salina* ; *Distichlis*	High Marsh			1	0.125						24		4						49	6	9	
TJE2	2	10:45	32° 34.452	117° 07.660	TJE2	32 34 27.01151	-117 7 39.59188	1.803	0.011	5.09902	7.3	15	0.2	27	16	1.67	55	36	9	x	x	*Frankenia salina* ; *Distichlis*	High Marsh			1	0.125						32		3	56					40	1	4	
TJE3	3	11:14	32° 34.450	117° 07.665	TJE3	32 34 26.91408	-117 7 39.81347	1.705	0.028	11.7047	7.2	18	0.2	31	51	7.23	15	62	23	x	x	*Frankenia salina* ; *Sarcocor*	High Marsh,			1	0.125						44			72				7	32	2	12	
TJE17	4	16:30	32° 34.451	117° 07.677	TJE17	32 34 27.11920	-117 7 40.43469	1.576	0.03		6.8	16	0.4	37	47	5.02	11	66	23	x	x	*Frankenia salina* ; Sarcocor	High Marsh			1	0.125						63			7					36		6	
TJE4	5	11:30	32° 34.448	117° 07.670	TJE4	32 34 26.81880	-117 7 40.10398	1.476	0.023	20.24846	6.4	16	1.2	35	36	5.06	6	68	26	x	x	*Sarcocornia californica* ; so	Mid marsh (			1	0.125						28			6					60		4	
TJE5	6	11:54	32° 34.446	117° 07.675	TJE5	32 34 26.76148	-117 7 40.42177	1.591	0.025	28.4605	7.3	17	6.6	32	41	7.05	8	69	23	x	x	*Sarcocornia californica* ; Ja	Mid marsh (			1	0.125		4				87			4					53	3	14	
TJE6	7	12:20	32° 34.445	117° 07.680	TJE6	32 34 26.65428	-117 7 40.76285	1.529	0.027	37.94733	7	18	0.2	33	75	11.1	2	73	25	x	x	*Transition from Sarcocorni*	High to mid			2	0.25		5			1	28			5					15		5	
TJE7	8	12:32	32° 34.442	117° 07.684	TJE7	32 34 26.53361	-117 7 41.07826	1.424	0.029	46.8188	6.8	18	0.2	33	56	9.91				x	x	*Frankenia salina* ; Spartina	Midmarsh			2	0.25		1			1	18			89					46		9	
TJE16	9	15:40			TJE16	32 34 26.35243	-117 7 41.78665	1.579	0.025	66.7308	6.7	17	0.5	37	21	3.07	6	76	19	x	x	Jaumea carnosa; Sarcocorn	Midmarsh			1	0.125				1		19			36					31		6	
TJE8	10	12:56	32° 34.436	117° 07.704	TJE8	32 34 26.13974	-117 7 42.14508	1.464	0.027	77.25283	6.6	18	0.5	29	51	7.85	5	70	25	x	x	*Jaumea carnosa* ; Sarcocor	Midmarsh; 1			2	0.25						27			21					47		5	
TJE9	11	13:12	32° 34.426	117° 07.716	TJE9	32 34 25.63580	-117 7 42.96428	1.46	0.025	102.8834	6.6	17	0.4	38	38	5.25	2	72	25	x	x	*Jaumea carnosa* ; Batis ma	Mid-to-low			2	0.25						12							6	72		2	
TJE10	12	13:25	32° 34.421	117° 07.732	TJE10	32 34 25.10969	-117 7 43.82999	1.567	0.027	130.5986	6.9	19	3.3	35	24	4.63	6	71	23	x	x	Sarcocornia californica; Sp	Low marsh			3	0.375		32				23			6	3				98		5	
TJE11	13	14:00	32° 34.414	117° 07.743	TJE11	32 34 24.81891	-117 7 44.63298	1.541	0.027	153.3949	6.9	20	1.1	29	25	4.66	5	74	21	x	x	Pure Spartina foliosa	Low marsh			2	0.25		41			2	52	4		28			1	2	89		2	
TJE12	14	14:27	32° 34.406	117° 07.747	TJE12	32 34 24.34597	-117 7 44.79428	1.445	0.033	163.6154	7.2	19	0.5	35	18	3.61	6	75	19	x	x	Spartina foliosa on mudfla	Low marsh			8	1		8			3	4			5					12			
TJE13	15	14:38	32° 34.400	117° 07.753	TJE13	32 34 23.94699	-117 7 45.10929	1.425	0.025	177.2484	7	19	0.4	31	19	4.61	6	76	18	x	x	Pure Spartina foliosa	Low marsh			5	0.625	1	52			2	25	15		21	5		2	2	23		12	1
TJE14	16	14:54	32° 34.392	117° 07.750	TJE14	32 34 23.53768	-117 7 44.97645	1.475	0.025	181.604	7.2	17	1.2	32	12	3	18	74	8	x	x	Pure Spartina foliosa	Low marsh			5	0.625		59	1		7	12	1		30	1	3	2	1	25		17	
TJE15	17	15:07	32° 34.388	117° 07.750	TJE15	32 34 23.27933	-117 7 44.89011	1.387	0.025	184.9108	7.2	19	0.4	30	22	3.45	7	77	17	x	x	Pure Spartina foliosa	Low marsh			2	0.25		47			1		12		12	5				5		3	

Supplementary Data 2

85	159	161	32	221	167	92	100	93	164	59	165	98	112	169	136	92	Total live
																	Census dead
																	Ammobaculites spp.
61	38	23	2	7	18	1	1			2	3	1					*Ammonia* sp.
	1				1												*Bolivina* sp.
1																	*Cornuspira involvens*
4	4	6	3	2	5	5			1	2	2						*Elphidium* spp.
56	55	49	44	92	72	184	232	96	312	287	522	560	743	470	440	232	*Jadammina macrescens*
24	12	9	3	1					1								*Miliammina fusca*
										1			8	24	73	35	*Miliammina petila*
10	24	13	4	8			14	17	14	4	3	6	24	208	123	7	Calcareous miliolids
2	1	6															*Scherochorella moniliformis (forma R*
7										1							*Reophax* spp.
7	3	3															Textulariid sp.
4	4	2		1	3	2								4	5		*Trichohyalus aguayoi*
74	33	112	25	98	103	104	248	56	144	81	232	264	112	240	400	248	*Trochammina inflata*
										1	7	5	48	135	40	24	*Trochamminita irregularis*
23	11	11	4	8	1	6	21	9	24	22	54	14	1	32	6	16	juvenile Trochamminids
																1	Unidentified agglutinated miliolid
273	186	234	85	217	203	302	516	178	496	401	823	850	936	1113	1087	563	Total dead
																	Proccessed data
																	Live BF/10 cm^3
0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ammobaculites* spp.
188	94	83	8	164	85	0	0	0	4	20	32	0	0	0	0	0	*Ammonia* sp.
0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Bolivina* sp.
0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	*Cornuspira involvens*
4	11	3	3	8	0	0	0	0	4	4	0	0	0	0	0	0	*Elphidium* spp.
0	19	40	4	208	61	48	108	152	72	112	696	224	504	352	256	192	*Jadammina macrescens*
48	2	24	0	16	0	0	0	0	0	0	0	0	0	0	0	0	*Miliammina fusca*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	32	*Miliammina petila*
48	48	34	5	112	16	0	84	288	356	20	32	48	56	576	448	0	Calcareous miliolids
20	2	8	0	0	8	0	0	0	0	0	0	0	0	0	0	0	*Scherochorella moniliformis (forma R*
0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Reophax* spp.
0	3	3	0	4	0	0	0	0	0	0	0	0	0	0	0	0	Textulariid sp.
0	2	3	0	8	0	24	0	0	0	0	0	0	0	56	0	0	*Trichohyalus aguayoi*
20	40	37	12	356	261	288	188	248	184	60	424	480	288	256	320	392	*Trochammina inflata*
0	0	0	0	0	0	0	0	0	0	0	24	0	0	16	8	48	*Trochamminita irregularis*
12	27	19	0	8	13	8	20	48	36	20	112	32	48	96	32	72	juvenile Trochamminids
0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Unidentified very coarse agglutinated
240	155	123	16	292	101	24	84	296	364	44	64	48	56	632	448	0	Live general Calcareous /10 cm3
340	254.4	257.6	32	884	445	368	400	744	656	236	1320	784	896	1352	1088	736	Live absolute abundances /10 cm3
																	Dead BF/10 cm^3

Supplementary Data 2 continued

Ammobaculites spp.	*Ammonia* sp.	*Bolivina* sp.	*Cornuspira involvens*	*Elphidium* spp.	*Jadammina macrescens*	*Miliammina fusca*	*Miliammina petila*	Calcareous miliolids	*Scherochorella moniliformis* (forma R	*Reophax* spp.	Textulariid sp.	*Trichohyalus aguayoi*	*Trochammina inflata*	*Trochamminita irregularis*	juvenile Trochamminids	Unidentified agglutinated miliolid	Dead general Calcareous /10 cm3	Dead absolute abundances /10 cm3	Live BF %	*Ammobaculites* spp.	*Ammonia* sp.	*Bolivina* sp.	*Cornuspira involvens*	*Elphidium* spp.	*Jadammina macrescens*	*Miliammina fusca*	*Miliammina petila*	Calcareous miliolids	*Scherochorella moniliformis* (forma R	*Reophax* spp.	Textulariid sp.	*Trichohyalus aguayoi*	*Trochammina inflata*	*Trochamminita irregularis*	juvenile Trochamminids	Unidentified very coarse agglutinated	Live general Calcareous %	Dead BF %	*Ammobaculites* spp.	*Ammonia* sp.	*Bolivina* sp.	*Cornuspira involvens*	*Elphidium* spp.	*Jadammina macrescens*	*Miliammina fusca*	*Miliammina petila*	Calcareous miliolids	*Scherochorella moniliformis* (forma R	*Reophax* spp.	Textulariid sp.	*Trichohyalus aguayoi*	*Trochammina inflata*	*Trochamminita irregularis*	juvenile Trochamminids	Unidentified agglutinated miliolid	dead general Calcareous %
0	0	0	0	0	1856	0	280	56	0	0	0	0	1984	192	128	8	56	4504		0	0	0	0	0	26	0	4.3	0	0	0	0	0	53	6.5	10	0	0		0	0	0	0	0	41	0	6	1	0	0	0	0	44	4	3	0	1
0	0	0	0	0	3520	0	584	984	0	0	0	40	3200	320	48	0	1024	8696		0	0	0	0	0	24	0	2.2	41	0	0	0	0	29	0.7	3	0	41		0	0	0	0	0	40	0	7	11	0	0	0	0	37	4	1	0	12
0	0	0	0	0	3760	0	192	1664	0	0	0	32	1920	1080	256	0	1696	8904		0	0	0	0	0	26	0	0	43	0	0	0	4.1	19	1.2	7	0	47		0	0	0	0	0	42	0	2	19	0	0	0	0	22	12	3	0	19
0	0	0	0	0	5944	0	64	192	0	0	0	0	896	384	8	0	192	7488		0	0	0	0	0	56	0	0	6	0	0	0	0	32	0	5	0	6		0	0	0	0	0	79	0	1	3	0	0	0	0	12	5	0	0	3
0	8	0	0	0	4480	0	0	48	0	0	0	0	2112	40	112	0	56	6800		0	0	0	0	0	29	0	0	6	0	0	0	0	61	0	4	0	6		0	0	0	0	0	66	0	0	1	0	0	0	0	31	1	2	0	1
0	24	0	0	16	4176	0	0	24	0	0	0	0	1856	56	432	0	64	6584		0	2	0	0	0	53	0	0	2	0	0	0	0	32	1.8	8	0	5		0	0	0	0	0	63	0	0	0	0	0	0	0	28	1	7	0	1
0	8	0	0	8	1148	0	4	16	0	4	0	0	324	4	88	0	32	1604		0	8	0	0	2	47	0	0	8	0	0	0	0	25	0	8	0	19		0	0	0	0	0	72	0	0	1	0	0	0	0	20	0	5	0	2
0	0	0	0	4	1248	4	0	56	0	0	0	0	576	0	96	0	60	1984		0	1	0	0	1	11	0	0	54	0	0	0	0	28	0	5	0	55		0	0	0	0	0	63	0	0	3	0	0	0	0	29	0	5	0	3
0	0	0	0	0	768	0	0	136	0	0	0	0	448	0	72	0	136	1424		0	0	0	1.1	0	20	0	0	39	0	0	0	0	33	0	6	0	40		0	0	0	0	0	54	0	0	10	0	0	0	0	31	0	5	0	10
0	4	0	0	0	928	0	0	56	0	0	0	0	992	0	84	0	60	2064		0	0	0	0	0	27	0	0	21	0	0	0	0	47	0	5	0	21		0	0	0	0	0	45	0	0	3	0	0	0	0	48	0	4	0	3
0	4	0	0	20	736	0	0	0	0	0	0	8	416	0	24	0	32	1208		0	0	0	0	0	13	0	0	0	0	0	0	6.5	78	0	2	0	7		0	0	0	0	2	61	0	0	0	0	0	0	1	34	0	2	0	3
0	48	3	0	13	192	0	0	0	0	0	0	8	275	0	3	0	69	541		0	19	0	0	0	14	0	0	4	1.8	0	0	0	59	0	3	0	23		0	9	0	0	2	35	0	0	0	0	0	0	1	51	0	0	0	13
0	28	0	0	8	368	4	0	32	0	0	0	4	392	0	32	0	72	868		0	19	0	0	1	24	1.8	0	13	0	0	0	0.9	40	0	1	0	33		0	3	0	0	1	42	0	0	4	0	0	0	0	45	0	4	0	8
0	2	0	0	3	44	3	0	4	0	0	0	0	25	0	4	0	9	85		0	25	0	0	9	13	0	0	16	0	0	0	0	38	0	0	0	50		0	2	0	0	4	52	4	0	5	0	0	0	0	29	0	5	0	11
0	37	0	0	10	78	14	0	21	10	0	5	3	179	0	18	0	70	374		1	32	0	0	1	16	9.3	0	13	3.1	0	1	1.2	14	0	7	1	48		0	10	0	0	3	21	4	0	6	3	0	1	1	48	0	5	0	19
0	61	2	0	6	88	19	0	38	2	0	5	6	53	0	18	0	112	298		0	37	1	0	4	7.5	0.6	0	19	0.6	2	1	0.6	16	0	11	0	61		0	20	1	0	2	30	6	0	13	1	0	2	2	18	0	6	0	38
0	244	0	4	16	224	96	0	40	8	28	28	16	296	0	92	0	320	1092		0	55	0	0	1	0	14	0	14	5.9	0	0	0	5.9	0	4	0	71		0	22	0	0	1	21	9	0	4	1	3	3	1	27	0	8	0	29

Supplementary Data 2 continued

Taxonomic reference list of species presented in text and in Supplementary data 1 and 2

Ammobaculites spp. Wright et al., 2011, p. 59, Fig. A2/4

Ammonia spp. Murray, 1979, p. 57, Figs. 18a–l; Horton and Edwards, 2006; p. 73, P3, Figs. 10a–c, Figs. 11a–c, Fig. 12a–c.

Cornuspira spp. Loeblich & Tappan, 1988, p. 322, Pl. 51, Figs. 7–8

Trichohyalus aguayoi (Bermúdez, 1935). Bermudez, 1935, p. 204, pl. 15, Figs. 10–14.

Elphidium spp. Murray, 1979, p. 53, Figs. 16a–d; Hayward et al., 1999, p. 219, P17, Figs. 1–28; Murray, 2006, p. 65, Fig. 4.2, 11; Horton and Edwards, 2006; p. 75, P4, figs. 15–20.

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

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

Miliammina petila Saunders, 1958. Saunders, 1958, p. 87, pl. 1, figs. 10, 11; Milker et al., 2015, p. 5, Pl. 1, Figs. 3–4.

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

Scherochorella moniliformis Siddall, 1886. Murray, 1979, p. 24, Fig. 5b; Horton and Edwards, 2006; p. 67, P1, Figs. 6a–c; Wright et al., 2011, p. 58, Fig. A1/6.

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

Trochamminita irregularis Cushman & Bro¨nnimann, 1948. Loeblich & Tappan, 1988, p. 67, Pl. 51, Figs. 1–5; Hawkes et al. 2010, p. 18, Pl. 1, Figs. 3a–b; Milker et al., 2015, p. 5, Pl. 1, Fig. 11.

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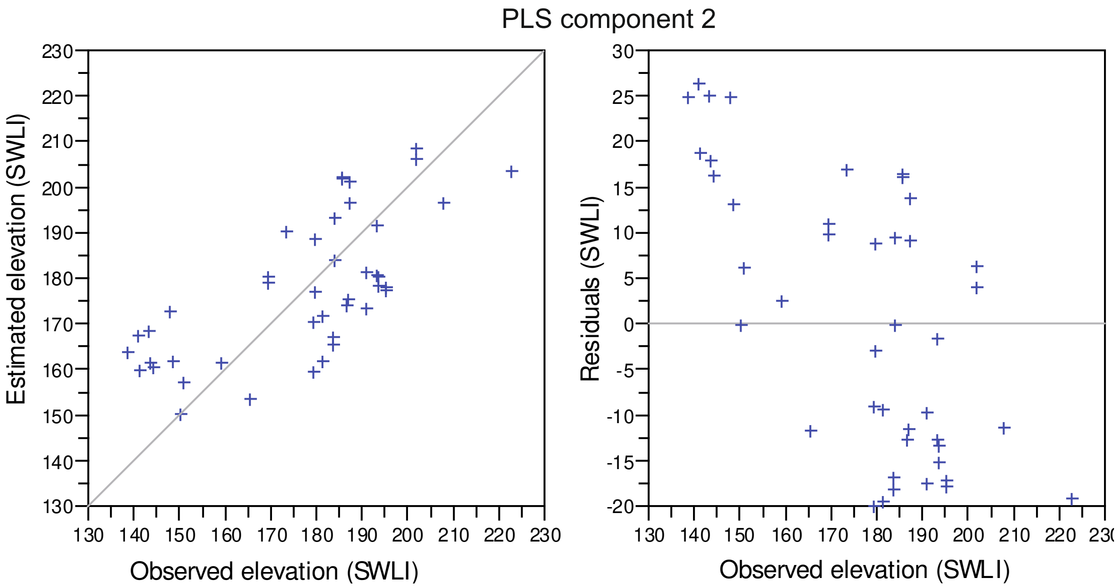

Supplementary data 4