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

Simona Avnaim-Katav[a,b] *, W. Roland Gehrels[c], Lauren N. Brown[b], Elizabeth Fard[b], Glen M. MacDonald [a,b]

[a] University of California, Los Angeles, Institute of the Environment and Sustainability, La Kretz Hall, Suite 300, Box 951496, Los Angeles, CA 90095-1496, USA.
[b] University of California, Los Angeles, Department of Geography, 1255 Bunche Hall, Box 951524, Los Angeles, CA 90095, USA.
[c] Environment Department, University of York, Heslington, York, YO10 5NG, United Kingdom.

*Corresponding author: Telephone: +909-734-9661, Email: Simona100@ucla.edu

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 ($r^2_{Jack} = 0.72$), 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.

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

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

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

179   Natural hydrologic disturbances at Tijuana include extreme flood events which can
180   deposit up to 8 or 9 cm of sediment in low marsh areas near channels (Cahoon et al.,
181   1996; Wallace et al., 2005). In the past century, some reduction in streamflow has
182   been observed due to damming upstream in the watershed. Even so, hydrologic
183   extremes of flood and drought at Tijuana have been known to cause periods of tidal
184   closure and hypersalinity leading to vegetation die-off (Zedler, 2010).

186   The most significant natural hydrologic change at the salt marsh at Seal Beach
187   occurred about 300 years before present with the isolation of the marsh due to
188   changes in the flow of the Santa Ana River (Leeper III, 2015). Historically
189   sedimentation at Seal Beach appears to have kept pace with sea-level rise in the recent
190   past, but the lack of terrestrial sediment input makes the marsh at Seal Beach all the
191   more vulnerable to accelerated sea-level rise (Kirwan and Megonigal, 2013). This
192   danger is compounded by the fact that Seal Beach lies directly along the San Andreas
193   Fault and is suspected to have suffered elevation loss due to tectonic subsidence
194   (Leeper III, 2015). Additionally, the region surrounding Seal Beach has observed a
195   4.13 mm/yr average lowering in surface elevation from 1994 to 2012 (Takekawa et
196   al., 2013) due to oil extraction.

198   Marsh vegetation in Southern California is often classified into zones based on
199   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).

347 A Q-mode CA was processed by PRIMER version 6 software (Plymouth Routines In
348 Multivariate Ecological Research, UK). The data of the common benthic species
349 (>1% relative abundance) were double-root transformed in order to down-weight the
350 relative contribution of highly abundant species. These transformed abundances were
351 used to build a similarity matrix calculated between every pair of samples comprising
352 a Bray–Curtis similarity (Bray and Curtis, 1957) as the distance metric, and used to
353 reconstruct a dendrogram for hierarchical clustering (group average linkage).
354 'Similarity profile' (SIMPROF) permutation tests were used to identify significant
355 groupings, such that the group being subdivided had a significant ($p < 0.05$) internal
356 structure. A 'similarity percentages' (SIMPER) routine was used in order to identify
357 species that contributed most to the similarity within each sample cluster, as well as to
358 dissimilarities with other clusters.

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

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

393 DCA results were also used as an initial step for choosing an appropriate unimodal or
394 linear-based transfer function. In order to develop transfer functions ('ecological
395 response functions') for predicting marsh surface elevations, the relationship between
396 water depth and the relative abundances of foraminiferal taxa within the combined

397 training data set was empirically modeled in the C2 program (version 1.7.4; Juggins,
398 2011). Although the difference in tidal range between the two sites is small, sample
399 elevations were normalized using the Standardised Water Level Index (SWLI),
400 commonly applied in salt-marsh sea-level studies (Gehrels, 1999; Horton et al., 1999;
401 Wright et al., 2011; Barlow et al., 2013; Kemp and Telford, 2015). The SWLI value is
402 calculated as: (100 × (sample elevation − local mean tidal level) / (high water
403 reference level − local mean tidal level)) + 100. We used the mean higher high water
404 as the high water reference level (Kemp and Telford, 2015). Although Wright et al.
405 (2011) recommend to use the highest occurrence of foraminifera as the high water
406 reference level in SWLI calculations, we could not establish this datum because our
407 highest samples still contained foraminifera. All elevations are expressed relative to
408 the same datum and a SWLI of 100 is MTL and 200 is MHHW.
409
410 Model performance was evaluated based on the cross-validated (leave-one-out/ jack-
411 knifed) correlation between model prediction elevation and measured elevation (r^2
412 jack), the root mean squared error of prediction (RMSEP) and the tendency of the
413 model to overestimate (underestimate) parts of the training set gradient, as mean and
414 maximum bias (Birks, 1998; Juggins and Birks, 2012; Kemp and Telford, 2015). The
415 observed residual scatter and observed and predicted values after model prediction in
416 the produced scatterplots were also taken in consideration as complementing the
417 evaluated model performance (Telford et al., 2004).
418 Sampling of the modern analogue along transects (e.g., evenly stratified by elevation
419 and or within one site/marsh) may lead to spatial autocorrelation (increased
420 resemblance of samples) and thus might negatively impact the transfer function model
421 performance (Legendre and Fortin, 1989; Telford and Birks, 2009). The issue of
422 spatial autocorrelation is reduced by sampling two different salt marshes and
423 combining the results into one modern training set. Consequently, we present a robust
424 foraminifera-based transfer function from a modern analogue potentially suitable for
425 RSL reconstructions in Southern California.
426
427

428 ## 4 Results
429 ### 4.1. The environmental properties of surface sediment
430
431 Water temperature (WT) varies between 24 °C and 32 °C and between 15 °C and 20
432 °C in Seal Beach and Tijuana salt marshes, respectively (Fig. 2; Table 2). Differences
433 in WT between the two marshes are related to differences in sampling months
434 (October vs. December) and differences within each marsh are related to sampling
435 hours during the day, in each transect. The pH values of the pore-water show no
436 observable spatial trend and range commonly from 6.1 to 7.8 in Seal Beach excluding
437 one sample with the lowest pH (4.3) and from 6.4 to 7.3 in Tijuana. Low O_2
438 concentration is measured in the most elevated stations of Seal Beach and thereafter a
439 decreasing trend is observed ranging from 8 to 0.3 mg/l. O_2 concentration were rather
440 low, <1.6 3 mg/l, at all stations in Tijuana excluding two stations with values of 6.6
441 and 3.3 mg/l. Salinity values in Seal Beach show a decreasing trend from the high
442 marsh samples (~40 ‰) to the low marsh samples (~34 ‰) whereas in Tijuana the
443 values varies between 27 ‰ and 38 ‰ in all stations apart of one high marsh sample
444 with 20 ‰. The organic matter content is fluctuating in both transects and ranges from
445 67 to 1% and from 12 to 75% in Seal Beach and Tijuana salt marshes, respectively.
446 The organic matter content in both transects was the highest in the mid marsh

447 sediments (apart from two samples in Seal Beach in which sparse vegetation occurs)
448 and it decreases somewhat towards the low marsh edge due to the decrease in
449 vegetation cover. The carbonate content varied between 1% and 22% and between 1%
450 and 11% in Seal Beach and Tijuana salt marshes, respectively, with the higher values
451 occurring in the mid marsh samples in both transects (apart from two samples in Seal
452 Beach which had also low organic matter content). There was no clear trend in the
453 grain-size distribution along the intertidal zone of both transects. Tijuana salt marsh is
454 dominated generally by silty sediment (62-77%), except in two sandy high marsh
455 stations (TJE1, TJE2; Fig. 2; Table 2). Seal Beach stations are characterized by silty
456 to sandy sediments with low concentrations of clay (<14%). Increasing sand
457 concentrations in the lower salt-marsh stations of Seal Beach (SB8-SB17) are
458 probably related to a tidal velocity gradient.

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

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

474 The live species exhibit observable zonation relative to elevation. At both sites, the
475 relative abundance of *M. fusca* is larger at lowest elevations. The tidal flat sediments
476 at Seal Beach (St. 16) are dominated by this species with general abundances between
477 92 and 496 specimens/10 cm^3 sediment volume and *S. moniliformis* with 108 and
478 216/10 cm^3 (Fig. 3). In the low marsh sediments at Seal Beach (St. SB8-SB17) and at
479 Tijuana (St. TJE10-TJE 15) these two species occur in decreasing numbers (Figs. 3
480 and 4). In the middle marsh these species are replaced by high concentrations of *J.*
481 *macrescens* and *T. inflata* (St. TJE7-TJE 9 and TJE 16), while at Seal Beach (St. SB3-
482 SB7) *Ammobaculites* spp. also occur. The highest stations (St. SB1 and SB18-SB20
483 and St. TJE1-TJE 3 and TJE17) are characterized by higher numbers of *J. macrescens*
484 and *T. inflata* and occurrence of *T. irregularis* and *M. petila* (Figs. 3 and 4,
485 Supplementary data 1 and 2).

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

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

497

498   At Seal Beach, cluster 1 contains samples from the low marsh (St. SB17 and SB8-
499   SB15 and their replicates) with elevations between 1.37-1.67 m NAVD88 designated
500   as cluster 1b and samples from tidal flat (St. SB16, 2SB16) with only one elevation of
501   0.98 m NAVD88 labeled as cluster 1a. Both sub-clusters are characterized by *J.
502   macrescens* (7-68%), *T. inflata* (18-57%), calcareous species (1-25%) and *M. fusca*
503   (1-29%). The latter species is more abundant in cluster 3a where it is also
504   accompanied by *S. moniliformis* (5-11%). Cluster 2 consists entirely of mid marsh
505   stations (St. SB2-SB7 and their replicates) with elevations between 1.48 and 1.58 m
506   NAVD88 (Fig. 5, Table 2, Supplementary data 1). This cluster is divided into two
507   sub-clusters 2a and 2b. Sub cluster 2a is characterized by *J. macrescens* (21-75%),
508   *Ammobaculites* spp. (12-62%) and *T. inflata* (<20%). Sub cluster 2b is dominated by
509   *J. macrescens* (57-89%) and accompanied by *T. inflata* (<29%) and calcareous
510   species (<5%). Cluster 3 includes stations from the high marsh (St. SB1, SB18-SB20
511   and their replicates) with elevations between 1.56 and 1.79 m NAVD88. The most
512   significant species contributing to this cluster are *J. macrescens* (>46%), *T. inflata*
513   (<38%) and *T. irregularis* (<7%).

514

515   At Tijuana, cluster 1 consists in part of the low marsh stations (St. TJE12-TJE15) with
516   the lowest elevations between 1.39 and 1.48 m NAVD88 (Fig. 6, Table 2,
517   Supplementary data 2). This cluster is dominated by *J. macrescens* (21-52%),
518   *Trochammina inflata* (18-48%), calcareous species (11-38%), *M. fusca* (4-9%) and by
519   *S. moniliformis* (1-3%). Cluster 2 contains samples from the mid to low marsh (St.
520   TJE4 – TJE11and TJE16) with elevations between 1.42-1.59 m NAVD88. Samples in
521   this cluster are dominated by *J. macrescens* (35-72%), *T. inflata* (20-51%) and
522   calcareous species (1-13%). Cluster 3 encompasses the high marsh samples (St. TJE1-
523   3 and TJE17) with elevations between 1.57- 1.93 m NAVD88. The dominant species
524   in this cluster are similar to those occurring in cluster 3 at Seal Beach including *J.
525   macrescens* (>40%), *T. inflata* (12-44%), *T. irregularis* (4-12%) and *M. petila* (<7%)
526   (Fig. 6).

527

528

529   **4.4. Surface and infaunal foraminiferal distribution in the short cores**

530

531   The infaunal foraminiferal distributions in the short cores are shown in Fig. 7. The
532   down core distribution of dead foraminifera is given in Supplementary data 1 and 2.
533   Similar foraminiferal species are currently living (rose Bengal stained) at the surface
534   (0-1 cm depth) of the transition from mid to low marsh (St. SB5) of Seal Beach and of
535   the mid marsh (St. TJE8) of Tijuana with general abundances of 872/10 cm^3 and
536   340/10 cm^3, respectively. The living assemblage at the surface of Seal Beach is
537   dominated by *J. macrescens* (624/10 cm^3), calcareous species (192/10 cm^3) and *T.
538   inflata* (56/10 cm^3). The living assemblage at the surface of Tijuana is dominated by
539   *T. inflata* (188/10 cm^3), *J. macrescens* (108/10 cm^3), and calcareous species (24/10
540   cm^3). Living infaunal specimens of the same surface living species are observed
541   between 1 cm and maximum down to 6 cm, showing general decreasing numbers with
542   core depth. In the shallowest depths (1-2 cm), the total highest numbers of infaunal
543   specimens representing 16% and 10% out of the total assemblages, in Seal Beach and
544   Tijuana, respectively, are observed. The most abundant infaunal species is *T. inflata*
545   (672/10 cm^3 or 80/10 cm^3 at 1-2 cm in Seal Beach and Tijuana, respectively) which
546   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 $r^2_{Jack} = 0.49$, and the lowest root-mean squared-error of prediction (RMSEP $_{Jack}$) 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 RMSEP $_{Jack}$ of 11.9 SWLI, higher $r^2_{Jack} = 0.72$ 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

647 elevation predictions are underestimated especially from the landward upper edge of
648 the gradient (high marsh).
649
650
5 Discussion

5.1. Environmental controls on modern foraminiferal distribution

655 Among the environmental variables controlling the spatial foraminiferal distribution
656 across salt marshes (e.g., salinity, organic carbon concentration, grain-size, pH) (e.g.,
657 Patterson, 1990; de Rijk and Troelstra, 1997; Scott et al., 1998; Woodroffe et al.,
658 2005; Milker et al., 2015a; Barnett et al., 2016), elevation which is associated with
659 tidal inundation (or subaerial exposure) is frequently identified as the primary control,
660 at least indirectly, responsible for their zonation (Gehrels, 2000; Horton et al., 2003;
661 Edwards et al., 2004; Horton and Edwards, 2005; Barlow et al., 2013; Milker et al.,
662 2015a). Consequently, these organisms have been extensively used as proxies for sea-
663 level reconstruction (e.g., Scott and Medioli,1980; Patterson et al., 2004; Barlow et
664 al., 2013).
665
666 The results of the Q-mode CA and the RDA from Southern California further support
667 the hypothesis that foraminiferal assemblages are strongly related to elevation and
668 hence tidal submergence. At Tijuana elevation explains 43% of the total variance in
669 the foraminiferal assemblages whereas at Seal Beach, 16% of the variance of the
670 species data is explained by elevation (Fig. 8, Table 4a-b). Despite the difference in
671 the elevational control between marshes, the combined RDA results of both data sets
672 still show that elevation is the primary factor influencing the foraminiferal zonation,
673 explaining 17.1% of the variance in the data set (Fig. 9, Table 4c) similar to studies in
674 the Magdalen Islands in the Gulf of St. Lawrence, Canada (Barnett et al., 2016),
675 Oregon, USA (Hawkes et al., 2010) and the UK (Horton and Edwards, 2006).
676 Elevation is followed by four additional environmental variables explaining lower
677 variance in the data set including O_2 (12.2%), temperature (7.6), salinity (10.9), pH
678 (2.1) and with the remainder (50%) consisting of inter-correlations between variables
679 (Table 4c). Inter-correlations between environmental variables and foraminifera are
680 known from other intertidal studies since varied factors also may be governed by the
681 frequency and duration of tidal exposure as controlled by elevation (Horton et al.,
682 2003; Horton and Edwards, 2005). For example in Seal Beach a significant ($p < 0.05$,
683 $r = 0.36$) correlation between elevation and salinity was observed (Fig. 8b).
684 Pore-water salinity is an additional key factor (after elevation) known to control
685 marsh foraminiferal distributions (Murray, 2006), for example in tidal marshes with
686 extremely low gradients having complex topography such as of the Great Marshes of
687 eastern Massachusetts (e.g., de Rijk and Troelstra, 1997). Salinity of the sediment
688 pore-water generally varies considerably due to the combined influence of the tidal
689 cycle and infiltration of seawater, desiccation, precipitation and seepage of fresh
690 ground water. The Southern California marshes experience frequent droughts under
691 dry climate conditions. Pore-water salinity decreases from the high marsh (~40 ‰) to
692 the low marsh (~34 ‰) at Seal Beach marsh (Fig. 2). This trend is also measured by
693 the RDA results where salinity explains 16.8% of the variance in the species data and
694 it has a positive correlation with elevation (Fig. 8b, Table 4b). On the other hand,
695 salinity values at Tijuana were more variable and thus had no significant influence on
696 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

747   al., 2010; Engelhart et al., 2013, Milker et al., 2015a) and the North America's
748   Atlantic coast (e.g., Edwards et al., 2004). In the middle marsh the dominant dead
749   species include *J. macrescens*, *T. inflata* and *Ammobaculites* spp. *Trochammina*
750   *inflata* and more prominently *J. macrescens* are also dominating higher elevations of
751   the high marshes at both sites where they are accompanied by *T. irregularis* and *M.*
752   *petila. Jadammina macrescens* and *T. inflata* have frequently been reported from
753   middle marsh (Guilbault et al., 1996; Jennings and Nelson, 1992; Nelson et al., 2008;
754   Hawkes et al., 2010; Engelhart et al., 2013, Milker et al., 2015a ,b) and the highest
755   marsh environments (e.g., Patterson, 1990; de Rijk and Troelstra, 1997; Horton et al.,
756   1999; Wang and Chappell, 2001; Hippensteel et al., 2002; Horton et al., 2003;
757   Edwards et al., 2004a; Franceschini et al., 2005; Woodroffe et al., 2005).
758   *Trochamminita irregularis* (often grouped with *T. salsa*) has commonly been detected
759   as a dominant species in the high and highest marsh in North American Pacific
760   marshes (Hawkes et al., 2010; Engelhart et al., 2013; Milker et al., 2015a, b) and in
761   New Zealand (e.g., Hayward et al., 2004; Southall et al., 2006) and Tasmania (Callard
762   et al., 2011). Similarly *M. petila* has been also observed in the middle and high
763   marshes from Oregon (Engelhart et al., 2013). The agglutinant *Balticammina*
764   *pseudomacrescens* is an important sea-level indicator (Gehrels and van de Plassche,
765   1999) dominating higher elevation of mid to highest marsh zones in North American
766   Pacific marshes, for example in Oregon salt marshes (Hawkes et al., 2010, 2011;
767   Engelhart et al., 2013; Milker et al., 2015a, b) but is absent in the studied salt marshes
768   in California.
769
770
771   **5.2. The influence of taphonomic processes**
772
773   Processes as sub-surface foraminiferal production (infauna) and taphonomic changes
774   vary temporally and spatially, from one intertidal system to another, and may
775   influence the fossil assemblages (e.g., Martin, 1999; Berkeley et al., 2007).
776   Accordingly there is a clear need to explore these processes in each depositional
777   environment, as a base for employing an adequate surface sampling strategy aiming at
778   accurate paleoenvironmental interpretations based on the microfossil record. At Seal
779   Beach and Tijuana, test production mirrors rather proportionally the standing crop
780   numbers, a principle discussed in Berkeley et al. (2007) (Figs. 3 and 4). Samples with
781   high numbers of standing crops yielded high total numbers (per 10 cm^3 sediment
782   volume) of dead foraminifera though exceeding the living ones, often by over an
783   order of magnitude. This observation applies to most species excluding *S.*
784   *moniliformis* and calcareous species in both marshes which showed opposite trends
785   with higher numbers of live specimens compare to the dead numbers. This is probably
786   due to taphonomic processes and low preservation potential (Figs. 3 and 4). Dead
787   agglutinant specimens of *S. moniliformis* were found only in lower elevations. These
788   are very fragile and tend to break easily due to the loss of organic cement by oxidation
789   (Berkeley et al., 2007). On the low marsh and tidal flat lower numbers of dead
790   calcareous species were observed compared to the live foraminifera (Figs. 3 and 4,
791   Supplementary data 1 and 2). This difference along with apparent dissolution (Plate 2,
792   Fig. 6b) is probably associated with reduced mean pH values of 6.5 and 6.9 in Seal
793   Beach and in Tijuana, respectively, causing carbonate dissolution and lower
794   preservation of the calcareous tests. Early diagenetic dissolution and loss of
795   calcareous tests related to a pH <~7, which results in a carbonate undersaturation is a
796   known process from intertidal environments along the North-West American coastal

797 marshes (e.g., Hawkes et al., 2010; Milker et al., 2015a), salt marshes in the
798 Mediterranean region (Cundy et al., 2000; Shaw et al 2016) as well as from other
799 temperate and tropical coasts (Wang and Chappell, 2001; Edwards and Horton, 2000;
800 Horton and Murray, 2006; Berkeley et al., 2009). Moreover, a general spatial trend of
801 better preservation at higher elevations was observed at Tijuana (Fig. 4), possibly
802 associated with diagenetic controls on the preservation potential of calcareous and
803 agglutinated tests.
804
805 **5.3. Surficial vs. subsurface foraminifera**
806
807 Most paleoenvironmental studies of intertidal marshes use the foraminiferal
808 assemblages in surface sediment (upper 1 to 2 cm) as a modern counterpart assuming
809 that they are characterized primarily by epifaunal production (e.g., Scott and Medioli,
810 1980; Gehrels, 1994; de Rijk, 1995; Horton, 1999; Patterson et al., 2004; Woodroffe
811 et al., 2005; Horton and Edwards 2006; Kemp et al., 2009a) or shallow infaunal
812 (Buzas et al., 1993). However, several studies have shown that intertidal foraminifera
813 can live infaunally as deep as several decimeters in some marsh settings (e.g.,
814 Goldstein et al., 1995; Ozarko et al., 1997; Goldstein and Watkins, 1998; Saffert and
815 Thomas, 1998; Goldstein and Watkins, 1999; Patterson et al., 1999; Hippensteel et al.,
816 2002; Culver and Horton, 2005; Duchemin et al., 2005; Tobin et al., 2005; Berkeley et
817 al., 2007; Leorri and Martin, 2009; Milker et al., 2015a). In such cases sampling the
818 uppermost surface sediment (0-1 cm) would produce poor modern analogues
819 (Duchemin et al., 2005). For example Ozarko et al. (1997) and Patterson et al. (1999)
820 relied on a deeper surface sampling (to 10 cm), covering the entire distribution of the
821 living infauna. Relying on such thick intervals may be misleading as they might
822 represent a longer time span, in some cases a decade or longer, in some salt marsh
823 settings (Milker et al., 2015a).
824
825 At Seal Beach and Tijuana the highest numbers of living specimens at the transition to
826 middle marsh (St. SB5) and middle marsh (St. TJE8) are found in the surface samples
827 (Fig. 7). The numbers of infaunal specimens, restricted to the first six cm of the cores,
828 are low compared to the total foraminiferal assemblage and show a decreasing trend
829 from 16% and 10% between 1 and 2 cm at Seal Beach and Tijuana, respectively, to
830 nil (Fig. 7). These results are in accordance with other salt-marsh studies reporting
831 living species predominantly in the top few centimeters of salt marsh in North
832 Carolina (Culver and Horton, 2005), New Brunswick, Canada (Patterson et al., 2004)
833 and the UK (Horton, 1997; Horton and Edwards, 2006).
834
835 Furthermore, the same infaunal species are presently living in the surface samples
836 indicating that none of them are exclusively infaunal. Additionally the dominant
837 infaunal species *T. inflata*, *J. macrescens* and calcareous miliolids are also dominating
838 the dead surface and fossil assemblages in both marshes. Consequently, our results
839 show that the influence of infaunal species on the dead assemblage is minor since
840 most reproduction is concentrated near the sediment surface and that the same post-
841 depositional processes influence fossil assemblages as the dead surface assemblages.
842 These observations enable us to use the dead assemblages in the upper surface
843 sediments as an adequate modern analogue for accurate quantitative
844 paleoenvironmental interpretations.
845

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 (RMSEP $_{Jack}$) 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 ($r^2_{Jack} = 0.72$), the lower maximum bias values in the training set and by a precision of the reconstructions of 0.09 m NAVD88 ($RMSEP_{Jack}$) 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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1331

Table captions

1333
1334 Table 1. The nearest tide gauge station for each site with observations of Mean Higher
1335 High Water (MHHW), Mean Tide Level (MTL) and Mean Sea-Level (MSL). Tidal
1336 water level heights (m), above North American vertical datum (NAVD88), are
1337 measured over the period from 1983 to 2001 at the National Oceanic and Atmospheric
1338 Administration (NOAA).

1340 Table 2. Sample locations, elevation, pore-water and sediment properties of the
1341 surface marsh samples collected at Seal Beach (denoted with the initials SB) and
1342 Tijuana (denoted with the initials TJE) during spring tide on mid-October, and early
1343 December 2015, respectively. TOM (total organic matter) and carbonate content were
1344 determined by Loss-on-Ignition at 550 and 950 °C, respectively. Detailed
1345 granulometric data detailed in Supplementary data No. 1 and 2. (nd = no data; asterisk
1346 denote stations in which a mini core was collected in addition to the surface sample).

1348 Table 3. Statistical results of Detrended Correspondence Analysis (DCA) for Seal
1349 Beach (a), Tijuana (b) and the combined surface assemblage of both marshes (c).

1351 Table 4. Statistical results of Redundancy Analysis (RDA) for Seal Beach (a), Tijuana
1352 (b) and the combined surface assemblage of both marshes (c).

1354 Table 5. Results of the transfer functions performance criteria for foraminifera
1355 training set using two regression models: Partial Least Squares and Weighted
1356 Averaging-Partial Least Squares (see text for details). Given are the cross-validated
1357 (jack-knifed) correlation (r^2) between observed and estimated elevation in the modern
1358 data, the mean and maximum bias, the Root Mean Squared Error of Prediction
1359 (RMSEP) and the change of the RMSEP (in %) from one component to the next.

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1361

Figure captions

1363
1364 Fig. 1. Location of the study area on the North American Pacific coast, southern
1365 California (A), and sites mentioned in the text including Seal Beach salt-marsh (B)
1366 and Tijuana salt-marsh (C) with transects highlighted showing the surface station

1367 locations (asterisk denote stations in which a mini core was collected in addition to
1368 the surface sample). See also Tables 1 and 2.

1369 Fig. 2. Environmental variables from sampled transects in Seal Beach and Tijuana salt
1370 marshes including: temperature, pH, O_2, salinity, organic matter, carbonate content,
1371 sand, silt and clay content and vertical profile relative to the North American vertical
1372 datum (NAVD88). Sample elevation profiles with the tidal datum for MHHW (mean
1373 highest high water). See also Tables 1 and 2.

1374 Fig. 3. Absolute abundances of the most abundant live (rose Bengal stained) (A) and
1375 dead foraminifera B) and their counts in the Seal Beach salt-marsh surface
1376 samples collected during mid-and late October, 2015. Sample elevation profiles are
1377 shown.

1378 Fig. 4. Absolute abundances of the most abundant live (rose Bengal stained) (A) and
1379 dead foraminifera (B) and their counts in the Tijuana salt- marsh surface samples
1380 collected during December, 2015. Sample elevation profiles are shown

1381 Fig. 5. Dendrogram of Q-mode cluster analysis of the dead foraminifera from Seal
1382 Beach salt-marsh. The most significant species contributing to each cluster, based on
1383 the 'similarity percentages' (SIMPER) routine, are shown on top of each cluster (*J.m.*
1384 *– J. macrescens*; *A.*spp. *– Ammobaculites* spp.; *T.in. – T. inflata*; Cal. – Calcareous
1385 species; *T.ir. – T. irregularis*; *M.f. – M. fusca*; *S.m – S. moniliformis*. The percentages
1386 of the most common dead species are given below the dendrogram.

1387 Fig. 6. Dendrogram of Q-mode cluster analysis of the dead foraminifera from Tijuana
1388 salt-marsh. Taxa that make significant contributions to the similarity within each
1389 cluster, based on SIMPER routine, are shown on top of each cluster (abbreviations are
1390 given in Fig. 5) and the percentages of the most common dead species are given
1391 below the dendrogram.

1392 Fig. 7. Total and individual live (rose Bengal stained) foraminiferal numbers (per
1393 $10cm^3$ sediment volume), and total percentages of live (rose Bengal stained)
1394 specimens relative to the total populations in each mini core (10cm deep) taken from
1395 the middle marshes of Seal Beach and Tijuana, St. 5 and St. 8, respectively.

1396 Fig. 8. Redundancy Analysis (RDA) ordination triplots with forward selected
1397 significant environmental variables (Table 4) showing retrospective projection of the
1398 surface samples—species—environmental variables for Seal Beach (A) and Tijuana
1399 (B). Clusters sample distinguished in the Q-mode CA (Figs. 5 and 6) were
1400 incorporated into the RDA results.

1401 Fig. 9. Redundancy Analysis (RDA) ordination triplot with forward selected
1402 significant environmental variables (Table 4) showing retrospective projection of the
1403 surface samples—species—environmental variables for the combined data sets of
1404 Seal Beach and Tijuana. Clusters sample distinguished in the Q-mode CA (Figs. 5 and
1405 6) were incorporated into the RDA results.

1406

1407 Fig. 10. Scatterplots showing the relationship between observed standardized water
1408 level index (SWLI) against model predicted SWLI and residuals versus observed

1409   SWLI using WA-PLS (component 3) transfer function in the modern data set derived
1410   from the southern California salt marshes.
1411

1412

1413   **Plate captions**

1414

1415   Plate 1. Agglutinant foraminifera from surface sediments collected in Seal Beach and
1416   Tijuana salt marches, along the coast of southern California.
1417   The scale bars of Figs. 2c, 3b equal 20 μm, of Figs. 2a-b equal 50 μm, of Figs. 1a-c,
1418   4a-b, 5b, 6a-c, 7c, 8, 9c, 10b-e equal 100 μm, of Figs. 3a, 5a, 7a-b, 9a-b, 10a equal
1419   200 μm.

1420

1421   (1a-b) *Miliammina fusca* (Brady, 1870), side view. (1c) *M. fusca*, aperture view. (2a-
1422   b) *Miliammina petila* Saunders, 1958, side view. (2c) *M. petila*, aperture view. (3a)
1423   *Scherochorella moniliformis* (Siddall, 1886), side view. (3b) *S. moniliformis*, aperture
1424   view. (4a) *Trochamminita irregularis* Cushman & Brönnimann, 1948 , side view. (4b)
1425   *T. irregularis*, side and aperture view. (5a) *Ammobaculites dilatatus* Cushman &
1426   Brönnimann, 1948 , side view. (5b) *A.dilatatus*, aperture view. (6a-b) *Ammobaculites*
1427   sp., side view. (6c) *Ammobaculites* sp., aperture view. (7a-b) *Ammobaculites* spp.,
1428   side view. (7c) *Ammobaculites* spp., aperture view. (8) *Ammobaculites* spp., side
1429   view. (9a) *Trochammina inflata* (Montagu, 1808), spiral view. (9b) *T. inflata,*
1430   umbilical view. (9c) *T. inflata*, aperture view. (10a-b) *Jadammina macrescens* (Brady,
1431   1870), spiral view. (10c) *J. macrescens*, umbilical view. (10d) *J. macrescens*,
1432   umbilical view showing collapsed chambers occurred soon after the specimen was
1433   dried. (10e) *J .macrescens*, aperture view with secondary apertures.

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1436   Plate 2. Calcareous intertidal taxa from surface sediments collected in Seal Beach and
1437   Tijuana salt marches, along the coast of southern California.
1438   The scale bars of Figs. 1, 3 and 5c equal 50 μm, of Figs. 2, 4a-b, 5a-b and 6a-b equal
1439   100 μm.

1440

1441   (1) *Cornuspira* sp., side view. (2) *Quinqueloculina* sp. side view. (3) miliolid, side
1442   view. (4a) *Trichohyalus aguayoi* (Bermúdez), spiral view. (4b) *T. aguayoi,* umbilical
1443   view. (5a) *Ammonia* sp. spiral view. (5b) *Ammonia* sp. umbilical view. (5c) *Ammonia*
1444   sp. aperture view. (6a) *Elphidium* sp side view. (6b) *Elphidium* sp. aperture view.

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1448   **Supplementary data captions**

1449

1450   Supplementary data 1. Seal Beach salt-marsh: general data and census foraminiferal
1451   data.

1452

1453   Supplementary data 2. Tijuana salt-marsh: general data and census foraminiferal data.

1454

1455   Supplementary data 3. Taxonomic reference list of species presented in text and in
1456   Supplementary data 1 and 2.

1457
1458   Supplementary data 4. Scatterplots showing the relationship between observed
1459   standardized water level index (SWLI) against model predicted SWLI and residuals
1460   versus observed SWLI using PLS (component 2) transfer function in the modern data
1461   set derived from the southern California salt marshes.
1462
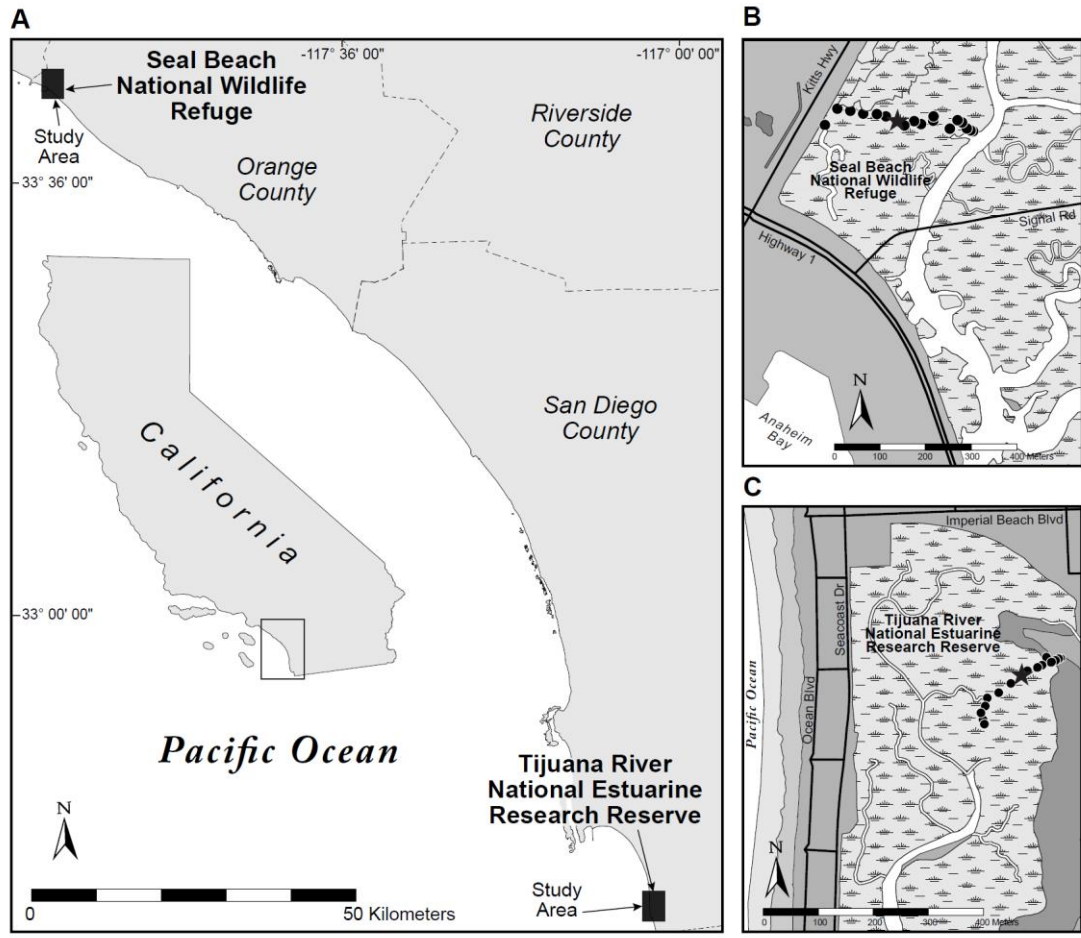
1463

1464   Figure 1

1465

Environmental properties

Seal Beach salt marsh   Tijuana salt marsh
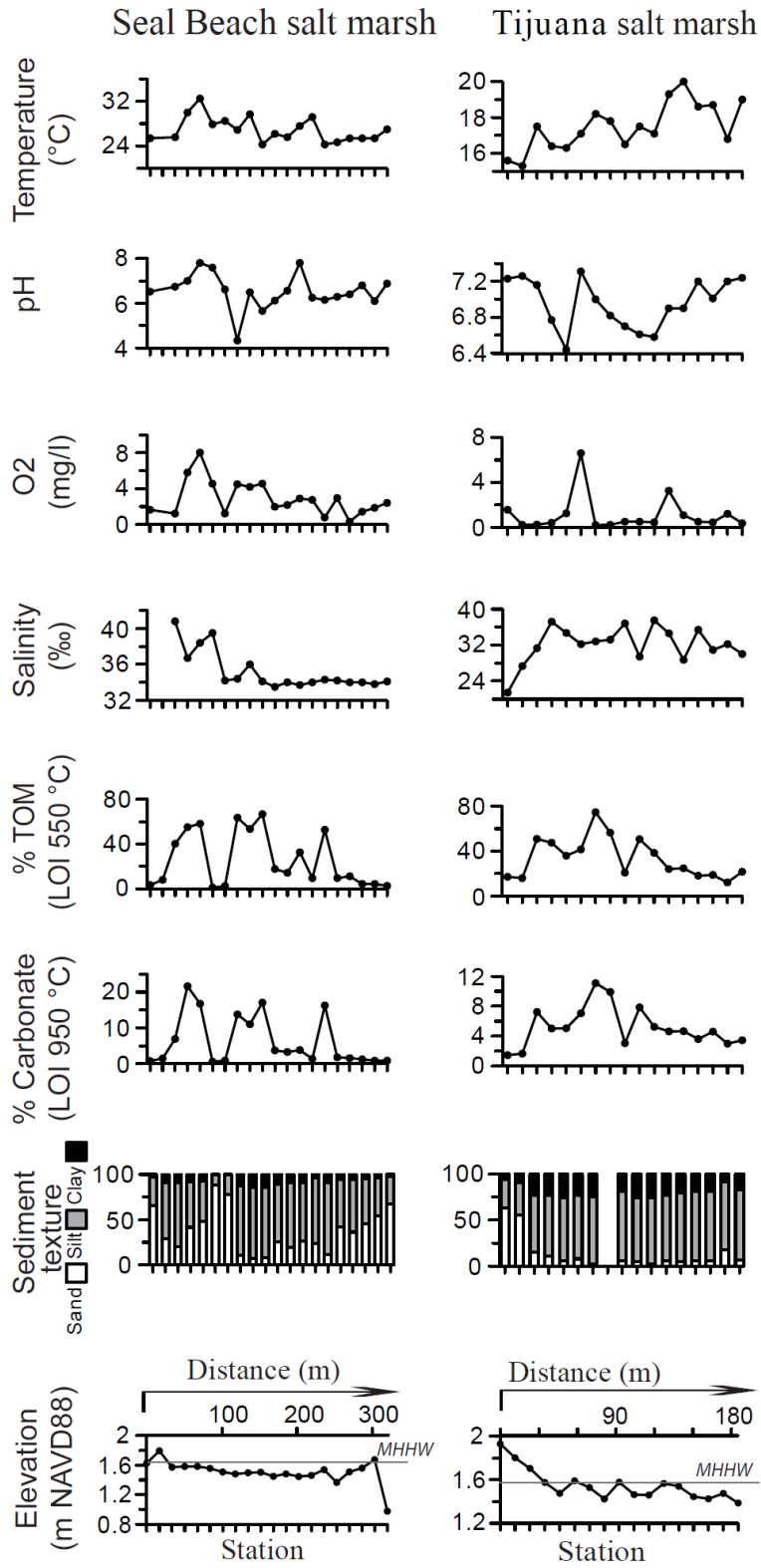
1466

1467   Figure 2

Seal Beach salt marsh
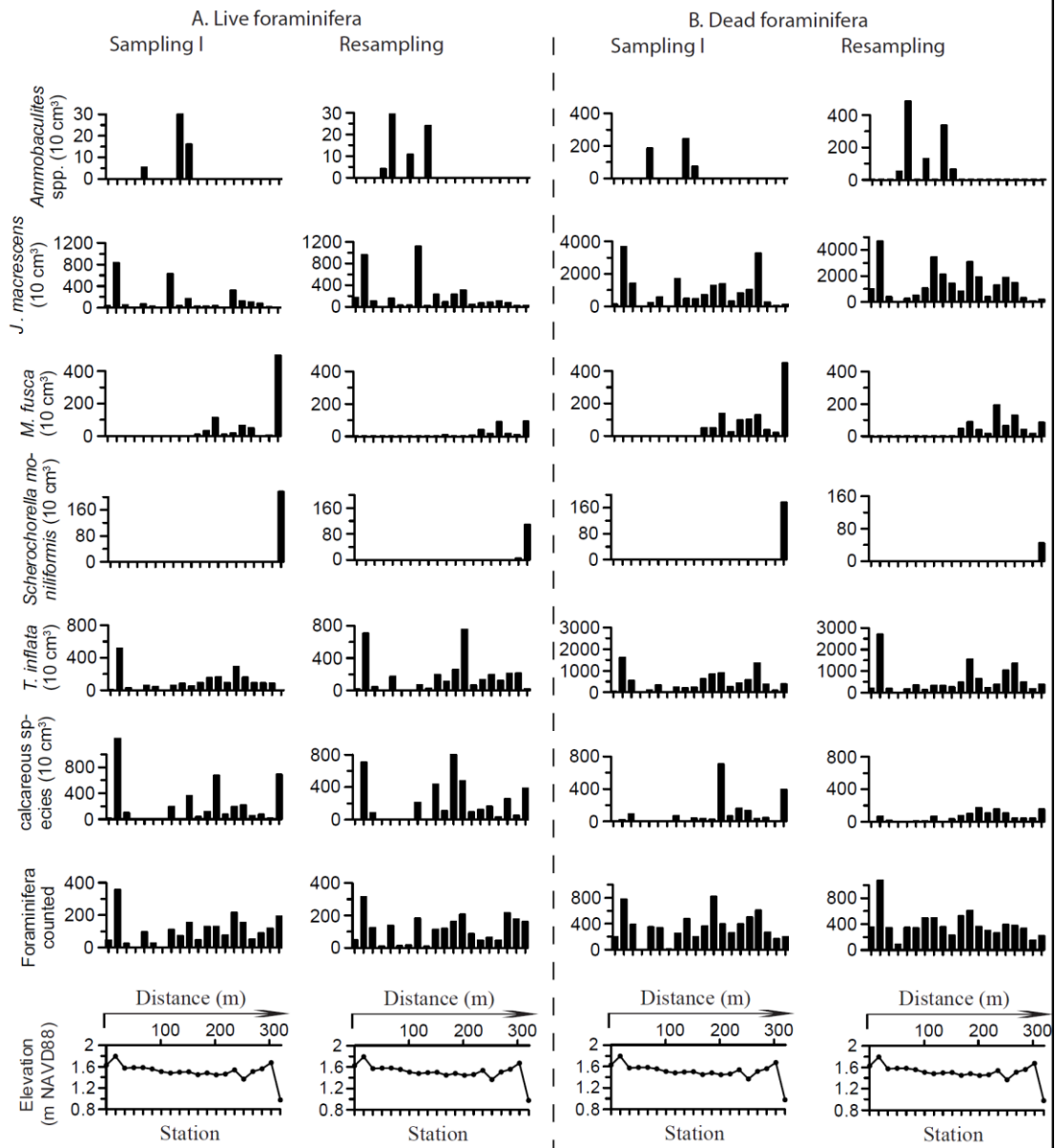
1468

1469 Figure 3

Tijuana salt marsh

A. Live foraminifera   B. Dead foraminifera
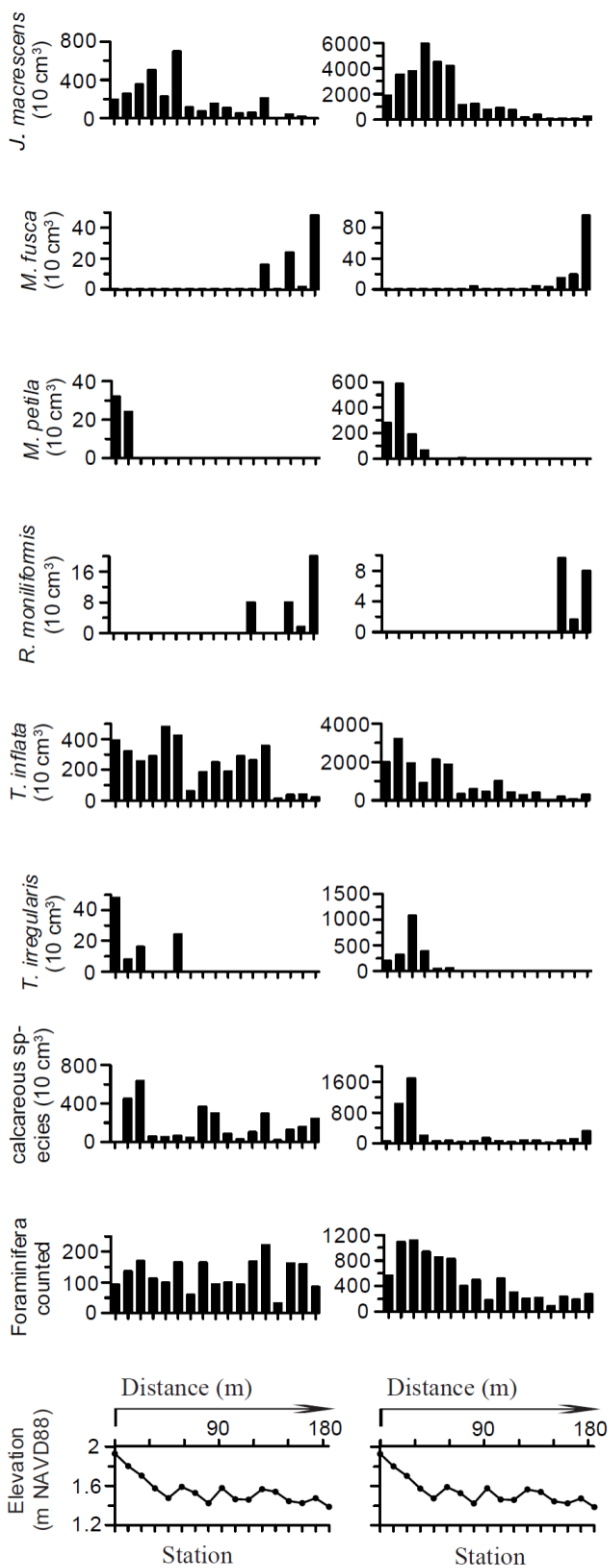
1470

1471   Figure 4
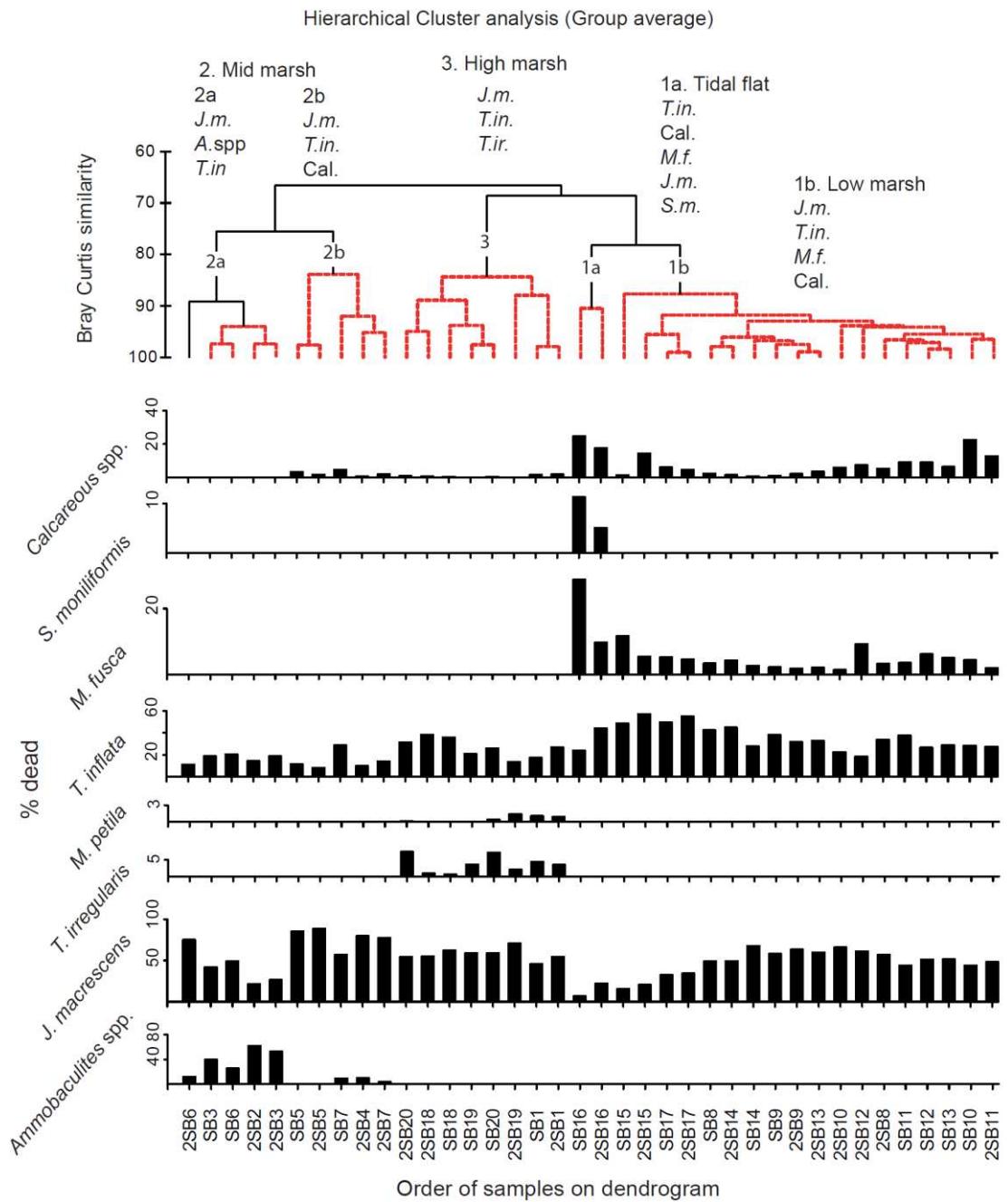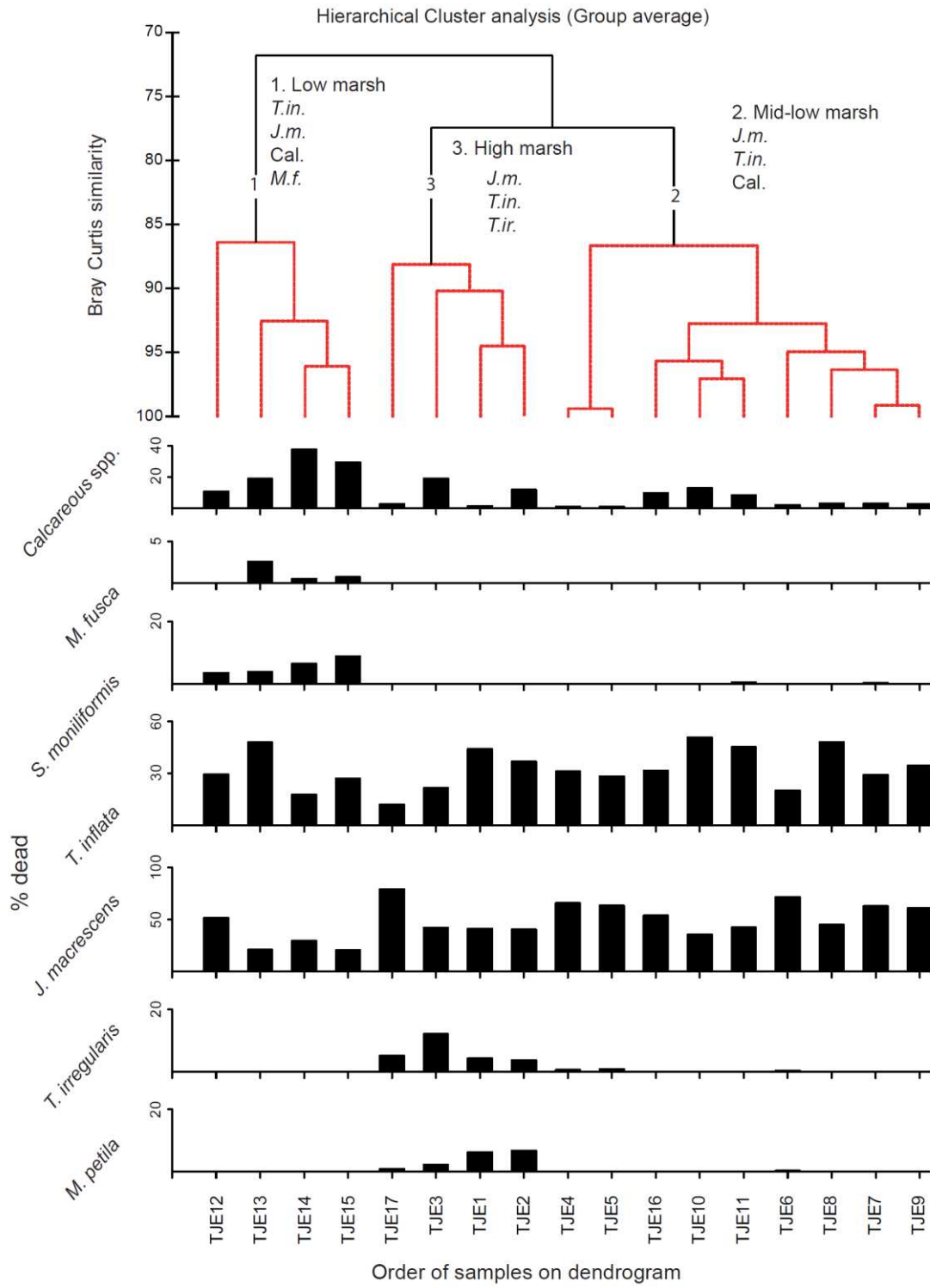
Figure 5

Figure 6

A. Live foraminifera in Tijuana salt marsh
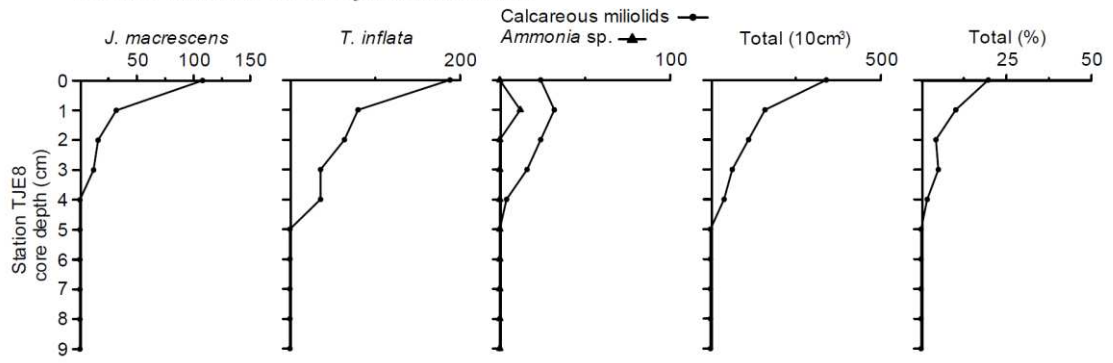
B. Live foraminifera in Seal Beach salt marsh
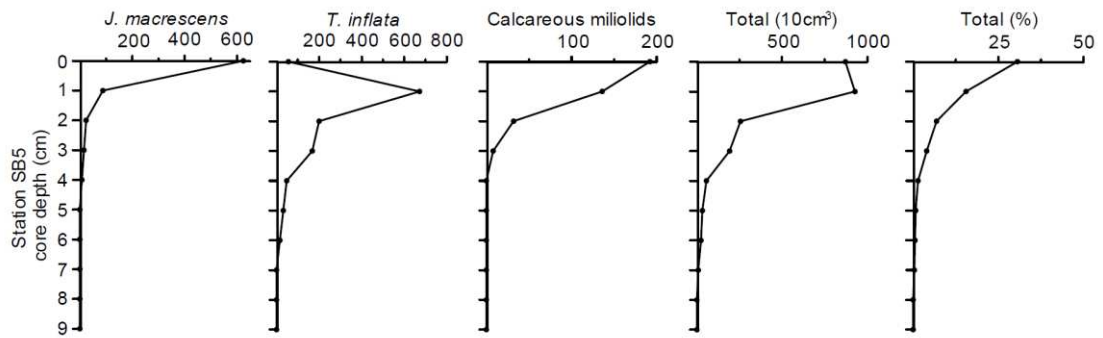
1476

1477 Figure 7
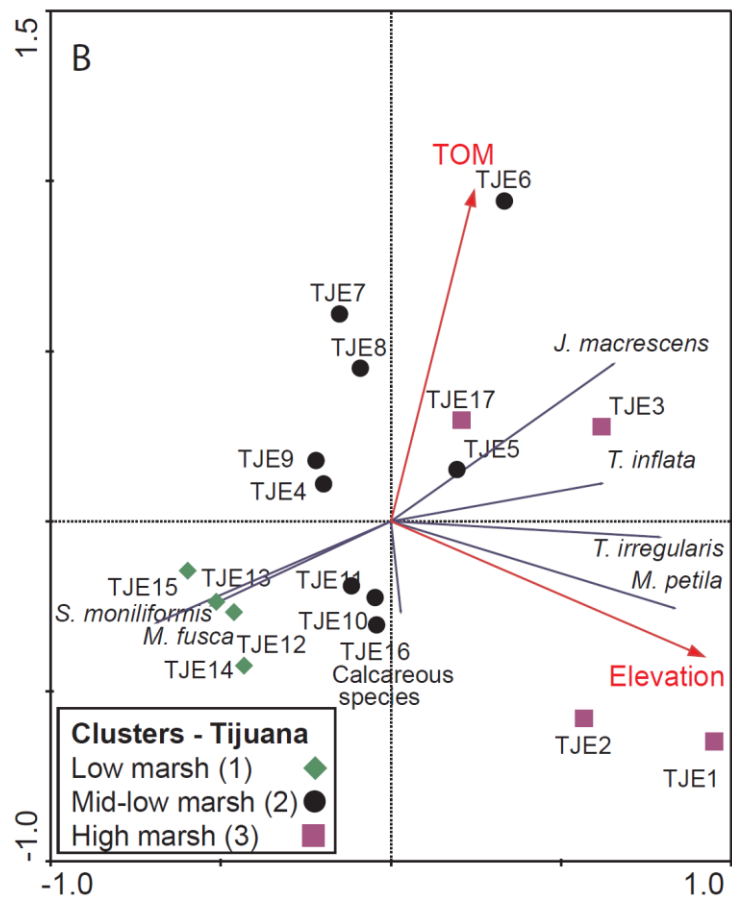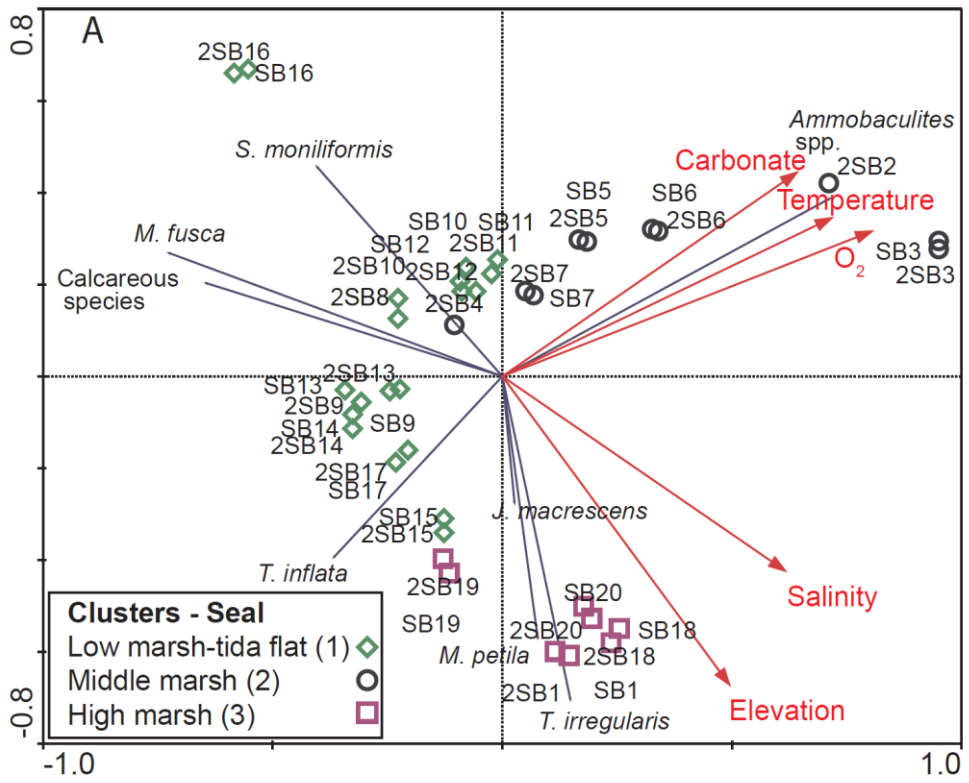
1478

1479   Figure 8
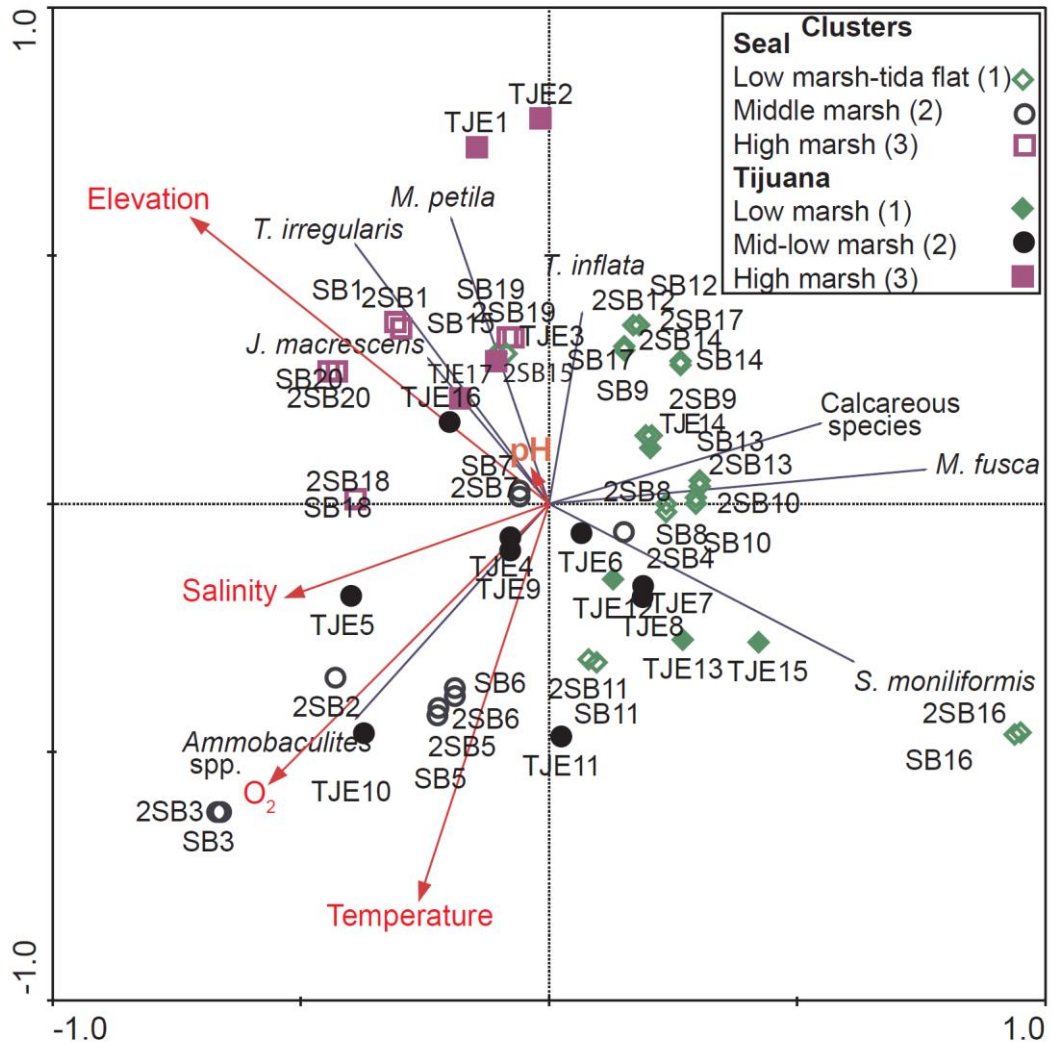
1480

1481   Figure 9
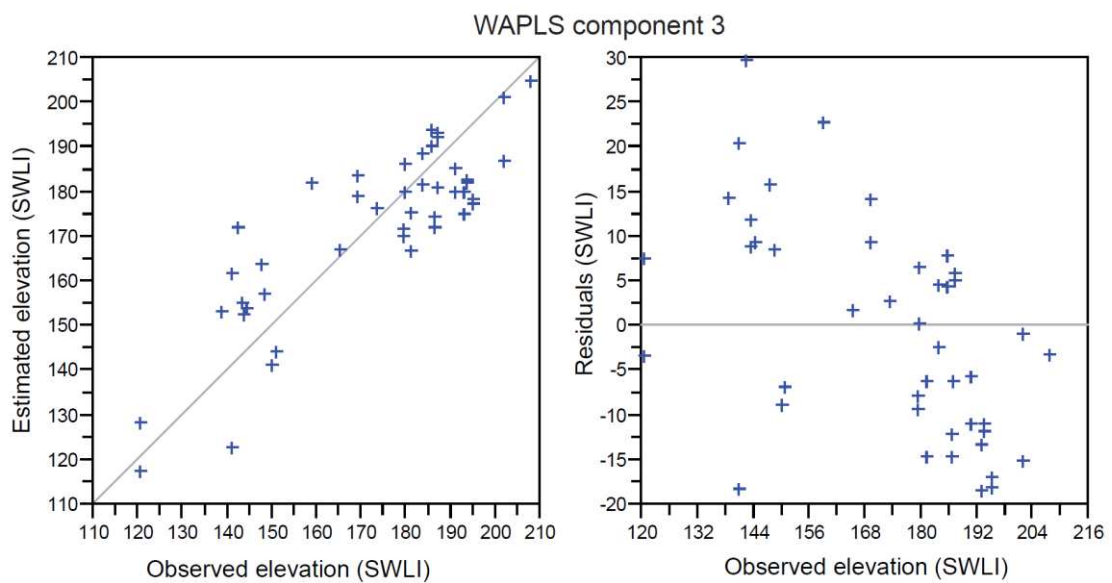
1482

1483   Figure 10
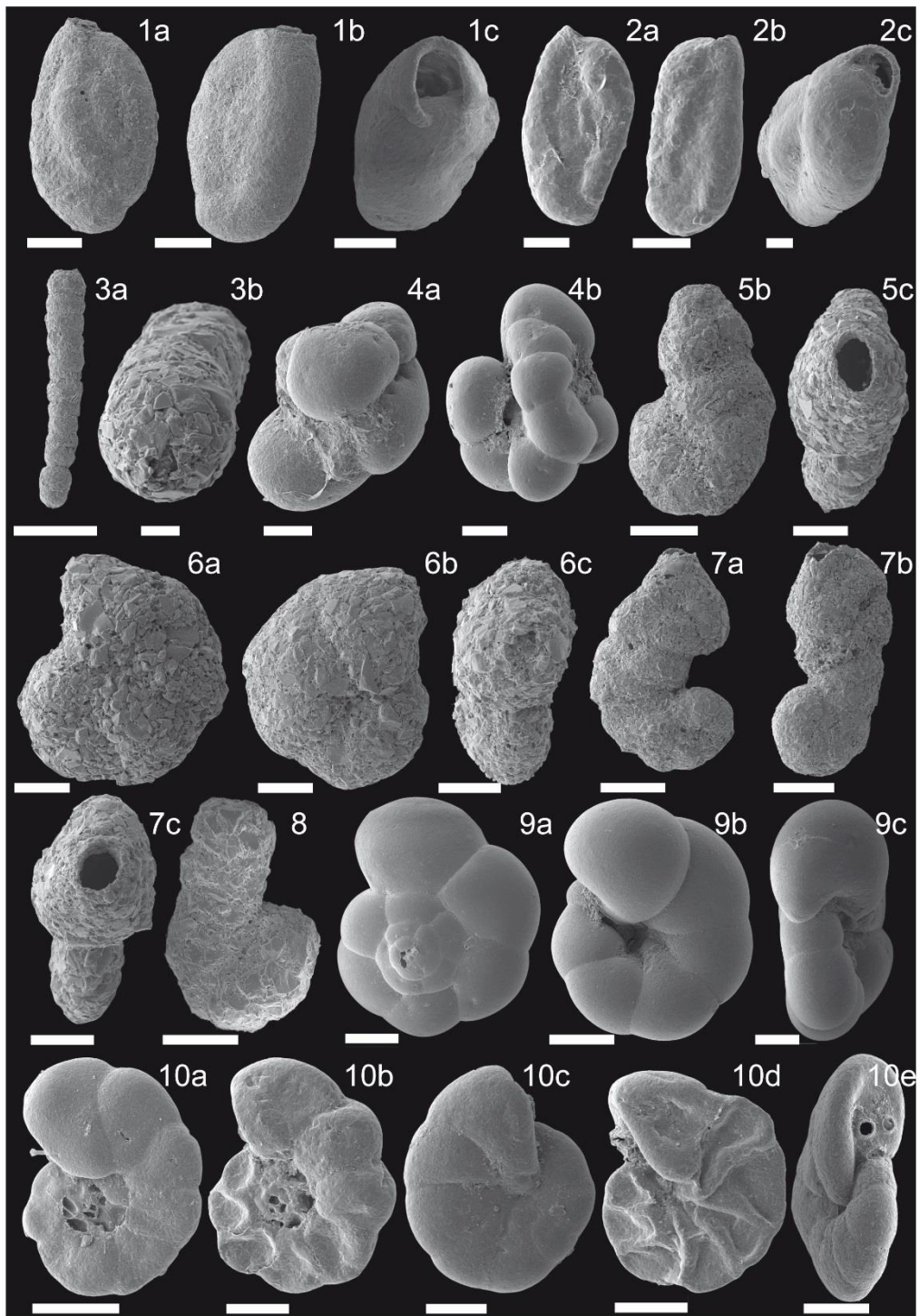
1485   Plate 1
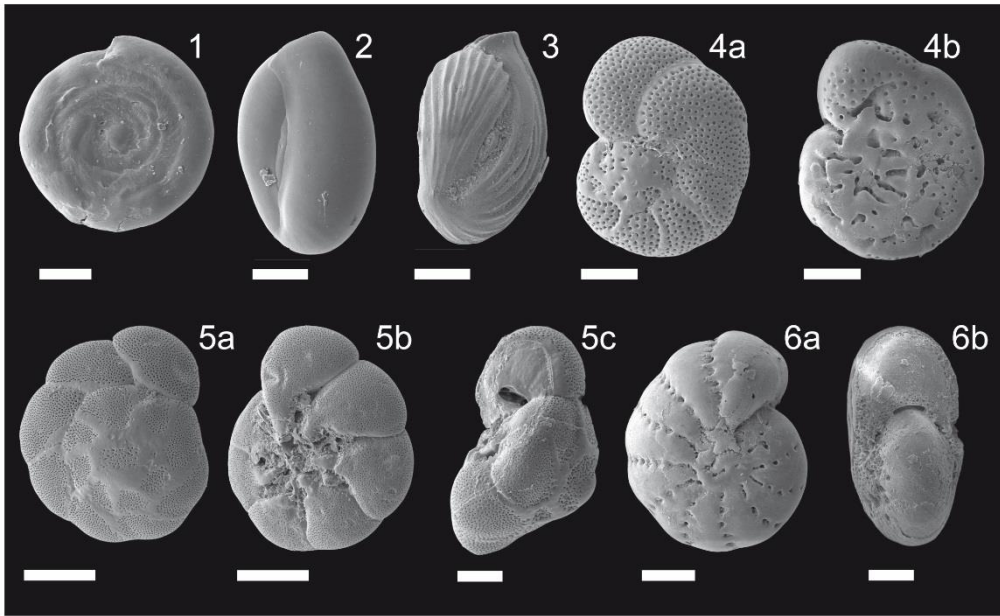
1486

1487   Plate 2

1488

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

1490   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	Carbonate	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

1491
1492   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

1493

1494   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

1495
1496   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

1497

1498   Table 5

1499

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

1500

1501 Supplementary Data 1

1502

Sample Name	#	Hour	HGPS Latitude	HGPS Longitude	Name	DGPS Latitude	DGPS Longitude	Elevation	Error	Distrance between srations 01 as ref.	pH	Temp. C	O₂ (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	0.027	46.8188	6.8	18	0.2	33	56	9.91					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; *Sarcocor*	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		52	1		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	

1503

1504

Supplementary Data 2

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

1505

1506   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
2	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	16	0	4176	0	24	0	0	0	0	0	1856	56	432	0	64	6584		0	2	0	0	0	53	0	2	0	0	0	0	0	32	1.8	8	0	5		0	0	0	0	0	63	0	0	1	0	0	0	0	28	1	7	0	1
0	8	0	8	0	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	4	0	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	20	0	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	2	0	61	0	0	0	0	0	0	1	34	0	2	0	3
0	48	3	13	0	192	0	0	0	0	0	0	8	275	0	3	0	69	541		0	19	0	0	0	14	0	4	1.8	0	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	8	0	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	3	0	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	10	0	78	14	0	21	10	0	5	3	179	0	18	0	70	374	1	0	32	0	0	0	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	6	0	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

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1509 Taxonomic reference list of species presented in text and in Supplementary data 1 and
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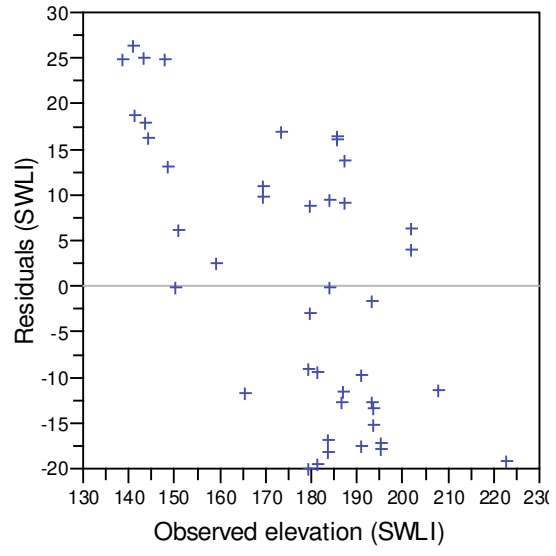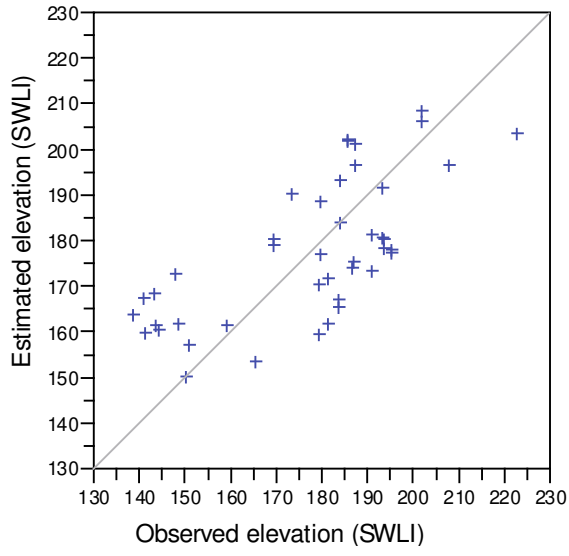1612
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