

Benthic foraminiferal community changes and their relationship to environmental dynamics in intertidal muddy sediments (Bay of Cádiz, SW Spain)

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ABSTRACT: The temporal and vertical variability of live intertidal benthic foraminifera was studied in parallel to environmental variables such as porewater and overlying water nutrients, salinity, temperature, sedimentary pigments and organic carbon. About 80 % of benthic foraminifera were concentrated in the upper 0–4 mm sediment layer, which was also the maximum oxygen penetration depth under light conditions as determined by oxygen microsensor measurements. Significant changes in the composition of the foraminiferal community over the course of the study were found in the surface layer (0–2 mm), whereas no differences were detected in the deepest sediment layers (10–30 mm). Univariate measures, such as abundance, species richness and diversity showed few differences over time and little relation to environmental variables. On the other hand, multivariate regression analysis for the whole community assemblage showed that the significant community composition changes over time in the surface layer could be related to fluctuations of several environmental variables, mainly those related to sediment food availability. The macroalgal bloom that occurred during the winter months had no detectable effect on benthic foraminiferal abundance or community patterns. Overall, the intertidal foraminiferal community in the Bay of Cádiz showed a highly dynamic character and a clear vertical distribution which could be effectively captured by studying the uppermost sediment layer at sub-centimetric vertical resolution.

KEY WORDS: Benthic foraminifera · Intertidal sediment · Microelectrodes · Microphytobenthos · Macroalgal bloom

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INTRODUCTION

Benthic foraminifera are abundant and ubiquitous members of marine and freshwater communities (Holzmann & Pawłowski 2002, Murray 2006). Foraminifera are increasingly being studied with the aim to establish links between modern day assemblages and environmental gradients that could be used as paleoenvironmental proxies (Berkeley et al. 2007).

Apart from their paleoecological interest, foraminifera have been found to play a more important role than previously thought in modern day environments in the sediment carbon and, in particular, the nitrogen cycle (Moodley et al. 2000, van Oevelen et al. 2006), as benthic foraminifera can store nitrate intracellularly and perform denitrification contributing between 8 and 50 % of the measured marine denitrification (Piña-Ochoa et al. 2010).

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Intertidal environments from temperate areas are subject to large temporal environmental fluctuations over the course of a year, as seasonal cycles overlap with cycles of a much higher frequency. Tidal (emersion–immersion) and diel (night–day) cycles create a high degree of temporal and spatial heterogeneity in the physico-chemical (e.g. temperature, salinity, oxygen and nutrient concentrations) and biological variables (e.g. macroalgal cover, microalgal and bacterial abundance, predation pressure), which in turn may influence the abundance and species composition of the benthic foraminifera community. High spatial variability in the living benthic foraminiferal faunas is a common phenomenon in marsh (Swallow 2000), intertidal (Morvan et al. 2006) and shallow subtidal environments (Murray & Alve 2000, Buzas et al. 2002, Diz et al. 2009). Temporal variability is also a common feature of benthic foraminiferal assemblages (Morvan et al. 2006). Simple seasonal cycles are common for some species in certain localities (Erskian & Lipps 1987, Cearreta 1988) but not for others, for which continuous or nearly continuous reproduction throughout the year seems common (Murray 1983, Basson & Murray 1995). The relationship between environmental variables and benthic foraminiferal abundance or reproduction does not always reveal simple patterns (Murray & Alve 2000). These observations indicate that it is still largely unknown what the key ecological factors influencing the population dynamics of intertidal benthic foraminifera are and how foraminifera might vary from one region to another or seasonally.

To date, few studies have actually tried to relate important sediment variables such as sediment organic matter quality (labile versus refractory) and quantity, sediment oxygen and porewater nutrients with changes of foraminiferal community at high vertical resolution. In many cases, studies combining sediment and porewater variables with high vertical resolution of abundance patterns in either shallow (Bouchet et al. 2007b) or deep (Fontanier et al. 2005, Langezaal et al. 2006, Staines-Urías & Douglas 2009, Contreras-Rosales et al. 2012) water environments lack temporal resolution. On the other hand, those including long temporal series and small-scale spatial variability lack high vertical resolution (Debenay et al. 2006, Morvan et al. 2006) or a characterisation of potentially relevant sediment or water column variables (e.g. Alve & Murray 2001).

In this study, we analysed the sub-centimetric scale vertical distribution of living benthic foraminiferal populations and related these to the changes in water column and sediment variables. Samples for benthic

foraminiferal analysis were collected monthly (from July 2008 to June 2009) in an intertidal muddy sediment area of the Bay of Cádiz (Spain). At the same time, overlying and porewater nutrient concentrations, oxygen microporfiles, sedimentary organic carbon (C_{org}) and pigment contents were measured. Accordingly, the present study was designed to explore the potential relationship of the benthic foraminifera community structural changes with those observed in the measured environmental variables. Understanding the factors triggering the dynamics of benthic foraminiferal populations in intertidal environments is essential for increasing our general knowledge of the ecology of these organisms, their role in intertidal food webs as well as to establish relationships between foraminiferal species and environmental parameters that could be potentially applied to interpret past environmental changes.

MATERIALS AND METHODS

Study area

The Bay of Cádiz (SW Spain), a marine protected area, occupies 38 km² (Fig. 1). It is divided into 2 basins, a smaller and deeper outer bay with a mean depth of 12 m and a very shallow inner bay, where 92 % of area is shallower than 1.5 m during low tides (Muñoz-Pérez & Sanchez de Lamadrid Rey 1994).

The inner bay receives no direct discharge from rivers, but non-point sources or other unauthorised outlets exist in the bay (Morris et al. 2009). The main water inputs into the inner bay are the tidal exchange with the outer bay via the narrow Puntales channel and a number of smaller creeks and channels that connect to the surrounding salt marshes (Fig. 1). The inner bay is protected from the action of large waves; however, it is subject to frequent strong winds that mix the water column. In addition, the bay is affected by semidiurnal co-oscillating tides with a mean amplitude of 1.5 m that result in average water turnover rates ranging from 50 to 75 % per tidal cycle (Alvarez et al. 1997). Maximum tidal height in the area is 3.4 m (mean water level is 2.1 m) above hydrographic zero. The sediment of the inner Bay of Cádiz is clayed-silt (96.3 % fraction <63 µm) with an organic matter content ranging from 1.6 to 4.5 % (Carrasco et al. 2003). The intertidal zone represents the largest areal fraction (59 %) of the inner bay. Extensive beds of rooted macrophytes (i.e. *Caulerpa prolifera*, *Cymodocea nodosa*, *Zostera marina* and *Z. noltii*) cover the subtidal and lower intertidal area,

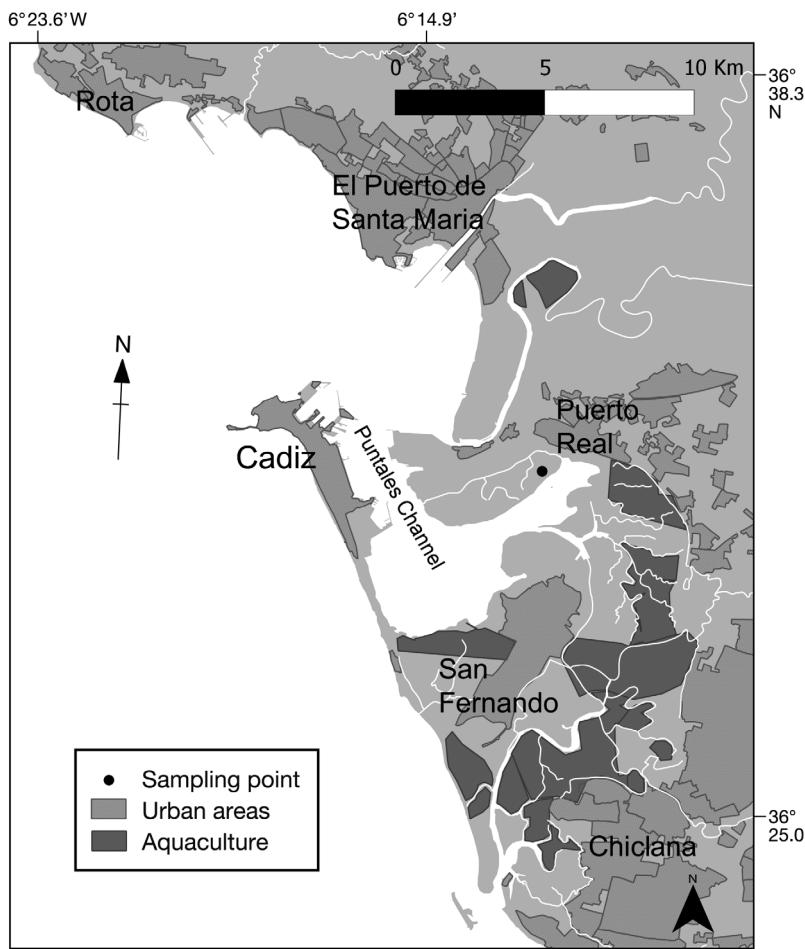


Fig. 1. Study area at low tide indicating position of the sampling station (●)

whereas the rest of the intertidal area is characterised by bare sediment. Green macroalgal blooms also occur in the area mainly during the winter months when large parts of the bare sediment intertidal zone are covered.

Air temperature in the study area during the sampling period showed the typical seasonal pattern of low temperatures in winter (4 to 12°C in January 2009) and highest in summer (24 to 31°C in July 2008) (see Fig. 2). Mean annual precipitation from 1971 to 2000 was ~600 mm, but it was ~900 mm in 2008–09, the year of the present study (data collected from the nearest weather station located at El Puerto de Santa María, Consejería de Agricultura y Pesca, Junta de Andalucía). Water temperature in the bay showed a seasonal trend with high values in August (25°C) and low values in December (13°C) (J. I. Gómez-Gordillo unpubl. data). Seawater salinity ranged from 34 in some winter months (wet season) to 39 in summer (dry season).

Sampling

Samples for benthic foraminifera, water column, porewater and sedimentary organic geochemistry analyses were collected from Trocadero Island (36° 31' 09" N, 6° 12' 01" W; inner Bay of Cádiz) on a monthly basis from July 2008 to June 2009 during low tide (no samples were available for August 2008 and April 2009). Samples were always collected when the sediments were exposed during low tide. The sampling area is at a tidal height of 1.5 to 1.7 m above the hydrographic zero. For each sampling, 3 random 1 m² plots were selected at a distance of 10 to 15 m from each other. For benthic foraminiferal analyses, 3 cores (1.6 cm internal diameter, i.d.) were used per plot. In addition, 14 sediment cores were taken in each plot: three 2.9 cm i.d. cores were collected for C_{org} and nitrogen measurements, three 1.6 cm i.d. cores for pigments, three 1.6 cm i.d. cores for the determination of porewater nutrient concentrations and two 5.4 cm i.d. cores for the determination of oxygen concentration and penetration depth. All cores within each plot were first pushed into the sediment down to a depth of at least 3 cm and then slowly removed from the sediment. Cores were collected at sufficient distance from each other so as not to disturb sample collection of adjacent cores. For the analysis of nutrient content of the overlying seawater,

samples were filtered through a glass fibre Whatman GF/F filters (nominal pore size 0.7 µm). All cores and samples were placed upright on ice and transported immediately to the laboratory always taking care to minimise vertical sediment disturbance. Macroalgae proliferated extensively over the study area between December 2008 and February 2009. During this period, additional sediment cores were collected in 3 randomly selected areas covered with macroalgae just underneath the mat. Sample collection followed the same sampling procedure described above.

Sample processing

Benthic foraminiferal analysis

In the laboratory, samples for benthic foraminiferal analyses were sliced at 0–2, 2–4, 4–10 and 10–30 mm intervals using a surgical blade and callipers. The

sediment slices at the same depth were pooled together from the 3 cores taken within a plot, and fixed with ethanol containing 1 g l⁻¹ Rose Bengal stain. Thus, for each plot, we had a sample from a total surface area of 6 cm². Although this surface area is smaller than the recommended 50 cm² (Schönfeld et al. 2012), the obtained population densities were generally larger than 100 individuals, which ensures statistically significant abundance numbers per sample. Samples were wet sieved into 63 to 150 µm and >150 µm size classes. Immediately after sieving, all hard shelled benthic foraminifera considered alive at the time of collection (i.e. individuals that had all their chambers stained red/pink except for the last 2 chambers) were sorted from wet samples from both fractions and stored on micropaleontological slides. The generic assignments follow those of Loeblich & Tappan (1987). The reference faunal list (Table S1) and SEM pictures of the most characteristic species (Figs. S1 to S8) are shown in the Supplement at www.int-res.com/articles/suppl/m490p121_supp.pdf. Faunal densities are expressed per 6.0 cm² surface area (total number of foraminifera in the 0–30 mm interval) or per cm³ volume (for layers of different thickness). In order to describe the vertical distribution of benthic foraminifera, the average living depth (ALD) (Jorissen et al. 1995) was calculated from 0–2 mm to the deepest studied interval (10–30 mm) for the total community (ALD_{30mm}) in the >63 µm fraction.

Porewater and overlying water nutrient analysis

Upon returning to the laboratory, cores for pore-water nutrients determination were sliced at every mm down to 10 mm. Slices from the same depth from different cores from each plot were pooled and homogenized to obtain a sufficiently large sample for subsequent analyses. Sediment samples were centrifuged at 8000 × g for 20 min at 4°C to extract pore-water. Nutrient concentrations in the extracted pore-water (NH₄⁺, NO₃⁻, NO₂⁻, PO₄³⁻ and Si(OH)₄) and in the overlying water column were measured on a Techicon autoanalyzer after appropriate dilutions following standard protocols (Grasshoff 1976).

Oxygen concentration and oxygen penetration depth

Once in the laboratory, sediment cores used for the determination of oxygen penetration depth were maintained in an aquarium with recirculating *in situ*

seawater, a photon flux density (PFD) of 800 µmol m⁻² s⁻¹ and under a 12 h light:12 h dark photoperiod cycle until the next day. Oxygen profiles (n = 3 to 4 per core) were measured in the light (800 µmol photons m⁻² s⁻¹) and in the dark at the sediment–water interface in each of the 6 sediment cores using an O₂ microelectrode with a tip diameter of 20 to 30 µm and at a depth resolution of 100 µm (Unisense) (Corzo et al. 2009).

Sediment characteristics

Sediment cores for the determination of sediment C_{org} and total nitrogen were sliced every 2 mm down to 10 mm depth, and samples were analysed on a CHN elemental analyser according to Kristensen & Andersen (1987). Pigment extraction was carried out on the 0–4 mm layer. Chlorophyll a (chl a) and chlorophyll c (chl c) were extracted in 100% methanol overnight at 4°C in the dark (Thompson et al. 1999). Extracts were centrifuged at 2200 × g for 10 min and measured using a spectrophotometer (Unicam UV/Vis UV2®). Chl a and chl c content were estimated after Ritchie (2008).

Statistical analysis

All analyses were completed at the level of replicate plot unit (n = 3) at each sampling. Total number of individuals (N 6.0 cm⁻²), and species number (S 6.0 cm⁻²) were calculated for each plot of each month using the whole depth interval (0–30 mm). In addition, in order to evaluate differences with depth, individuals (N cm⁻³), species number (S 6.0 cm⁻²) and species diversity (Shannon-Wiener H') were calculated for each depth layer after normalising abundances for the volume sampled.

The Pearson product moment correlation coefficients were calculated between abundance, species numbers and diversity and the environmental variables using the monthly means. Environmental variables that did not conform to normality, namely nutrients, oxygen, pigments and precipitation data were ln-(x + 1)-transformed.

Significant differences over time and with depth were tested using a permutational analysis of variance (PERMANOVA) (Anderson 2001, McArdle & Anderson 2001) on a Euclidean distance resemblance matrix followed by post hoc pairwise test where appropriate. As depth intervals within cores were not independent, core identity was introduced as a new random factor, nested within time. A total of 10000

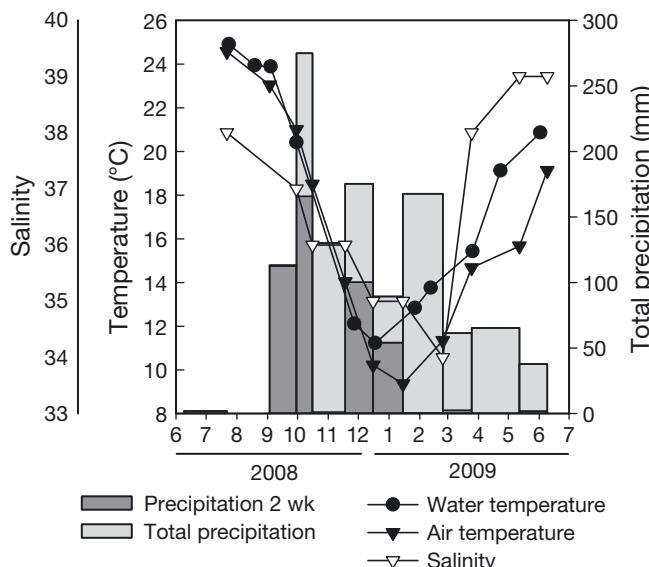


Fig. 2. Average monthly air and water column temperature, salinity, precipitation during the 2 wk prior to sampling and total precipitation since the previous sampling at the sampling station Trocadero Island, Bay of Cádiz. Horizontal axis is linear and ticks correspond to the first day of each month

unrestricted permutations of raw data were used in all tests. When the number of permutations was small (<100), p-values were obtained through Monte Carlo random draws from the asymptotic permutation distribution (Anderson & Robinson 2003). Separate PERMANOVA tests were performed in the months with macroalgal presence using macroalgal presence as an additional factor.

Significant changes of the multivariate species data set were determined by applying PERMANOVA on square root transformed abundance data using the Bray-Curtis similarity measure. Community patterns were then visualised by non-metric multi-dimensional scaling (NMDS).

The relationship between multivariate species data and environmental variables was explored by distance-based multivariate multiple regression (DISTLM) (McArdle & Anderson 2001). As this analysis is intended for exploratory purposes, in order to avoid an over-parameterised model, replicate plot within each sampling time were kept separate. Environmental variables were checked for collinearity (Table S2 in the Supplement at www.int-res.com/articles/suppl/m490p121_supp.pdf) and removed when a correlation >0.51 was found. The variables tested were porewater NO_x^- ($\text{NO}_3^- + \text{NO}_2^-$), salinity, precipitation, sediment C_{org} , chl *c*, $\text{C}_{\text{org}}\text{N}$, water column NH_4^+ and Si(OH)_4 . Estimates of the analyses were obtained by a forward selection procedure using Akaike's information criterion (AIC). The

model in multi-dimensional space was visualised using the dbRDA routine. All statistical analyses were run using the programs PRIMER 6.0 and PERMANOVA+ (PRIMER-e).

RESULTS

Environmental variables

Water temperature in the bay ranged from 12 (January 2009) to 25°C (July 2008) and salinity from 33 (February 2009) to 38 (June 2009) (Fig. 2). The concentration of nutrients in the water column was generally low (below 5 μM) showing, however, a significant temporal variation (Fig. 3A). Ammonium concentrations (NH_4^+) showed 2 peaks (2.0 μM), one in October 2008 and one in April-May 2009. Concentrations of NO_x^- were higher than those of NH_4^+ , showing lowest values in summer (0.3 μM) and highest in January 2009 (6.7 μM). Phosphate (PO_4^{3-}) concentrations ranged from 0.3 μM (July 2008 and June 2009) to 2.7 μM (September 08). Silicate (Si(OH)_4) concentrations showed much larger variations than the other nutrients with minimum values in January 2009 and 2 peaks, one in October 2008 (21.1 μM) and the other one in March 2009 (16.7 μM).

Porewater nutrients showed a temporal trend as well, with higher concentrations in autumn and winter (Fig. 3B). Porewater NH_4^+ in the upper 0–2 mm layer showed the highest values in winter (78.7 nmol cm^{-3} , December 2008) and the lowest towards the end of summer (5.9 nmol cm^{-3} , September 2008) (Fig. 3B). NO_x^- showed a highly similar pattern to that of NH_4^+ with highest values in December 2008 (23.1 nmol cm^{-3}). Phosphate and Si(OH)_4 presented a similar pattern with highest values in autumn (8.7 and 32.0 nmol cm^{-3} for PO_4^{3-} and Si(OH)_4 , respectively) and lowest in summer.

C_{org} content in the upper sediment layer (0–2 mm) ranged from 9.9 (June 2009) to 16.7 mg cm^{-3} (December 2008), with maximum rates in winter (Fig. 3C). Chl *a* content was highest during the winter months showing a peak in December 2008 (24.9 $\mu\text{g cm}^{-3}$) and lowest during the summer months (5.9 $\mu\text{g cm}^{-3}$, June 2009). Phaeopigments showed a pattern similar to that of chl *a*, with highest values in winter (42.8 $\mu\text{g cm}^{-3}$, December 2008) and lowest in summer (11.3 $\mu\text{g cm}^{-3}$, June 2009) (results not shown).

Oxygen profiles at the sediment–water interface showed the typical consumption and production shapes in dark and in light respectively (Fig. 4A). Maximum oxygen penetration depth in light (z_{oxL})

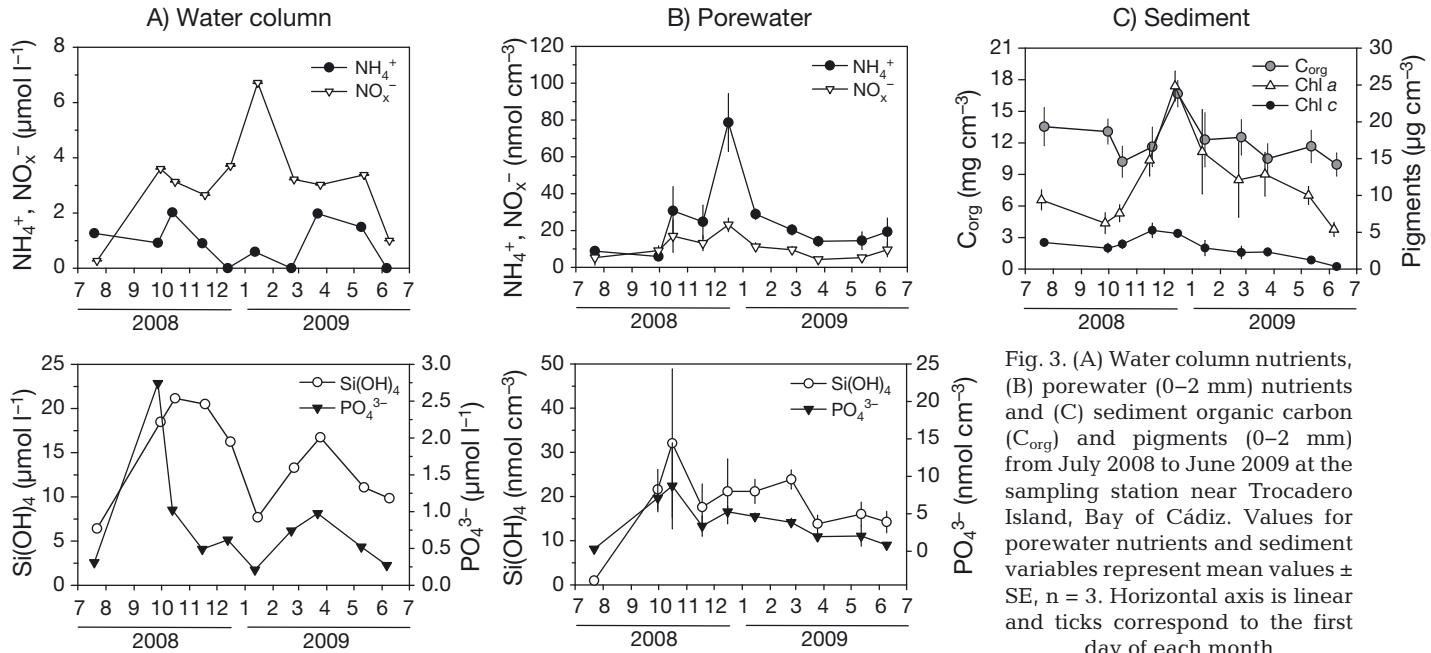


Fig. 3. (A) Water column nutrients, (B) porewater ($0-2 \text{ mm}$) nutrients and (C) sediment organic carbon (C_{org}) and pigments ($0-2 \text{ mm}$) from July 2008 to June 2009 at the sampling station near Trocadero Island, Bay of Cádiz. Values for porewater nutrients and sediment variables represent mean values \pm SE, $n = 3$. Horizontal axis is linear and ticks correspond to the first day of each month

was deeper by $\sim 1500 \mu\text{m}$ than in darkness (z_{oxD}). Whilst z_{oxD} changed little during the annual cycle ($1.35 \pm 0.07 \text{ mm}$), z_{oxL} displayed a higher seasonal variability ($3.10 \pm 0.22 \text{ mm}$) with the highest values during winter (4.67 mm, November 2008). Accordingly, the higher oxygen production and deeper penetration within the sediment under light conditions resulted in higher oxygen availability during the winter months. Oxygen concentrations in darkness were an order of magnitude lower and showed less variation with time.

Benthic foraminiferal community

The abundance of benthic foraminifera presented a clear vertical pattern, highly correlated with sediment oxygen concentration in dark and light conditions (Fig. 4B), with $68 \pm 10\%$ of the total foraminifera assemblage found in the $0-2 \text{ mm}$ layer of the sediment or $79 \pm 9\%$ when considering the $0-4 \text{ mm}$ layer. Over the sampling period, the average living depth ($\text{ALD}_{30\text{mm}}$), on the other hand, ranged from 2.9 to 6.0 mm of depth (Fig. 4C).

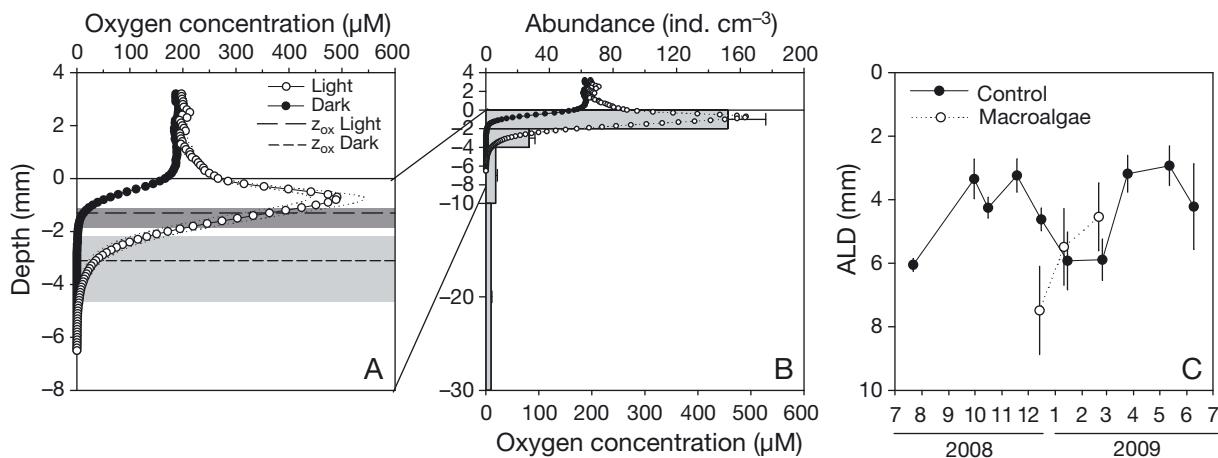


Fig. 4. (A) Mean vertical oxygen concentration profiles (dots), mean oxygen penetration depth (dashed horizontal lines) and min. and max. oxygen penetration depth (z_{ox} , shaded areas) in light and in darkness; (B) vertical distribution of foraminiferal abundance (solid bars) over the whole sampling period (mean \pm SE, $n = 10$) plotted together with oxygen concentrations. Note the difference in scale on the vertical axis; (C) average living depth of the total assemblage ($\text{ALD}_{30\text{mm}}$) from July 2008 to June 2009 at the sampling station on Trocadero Island, Bay of Cádiz (mean \pm SE, $n = 3$). Horizontal axis is linear and ticks correspond to the first day of each month

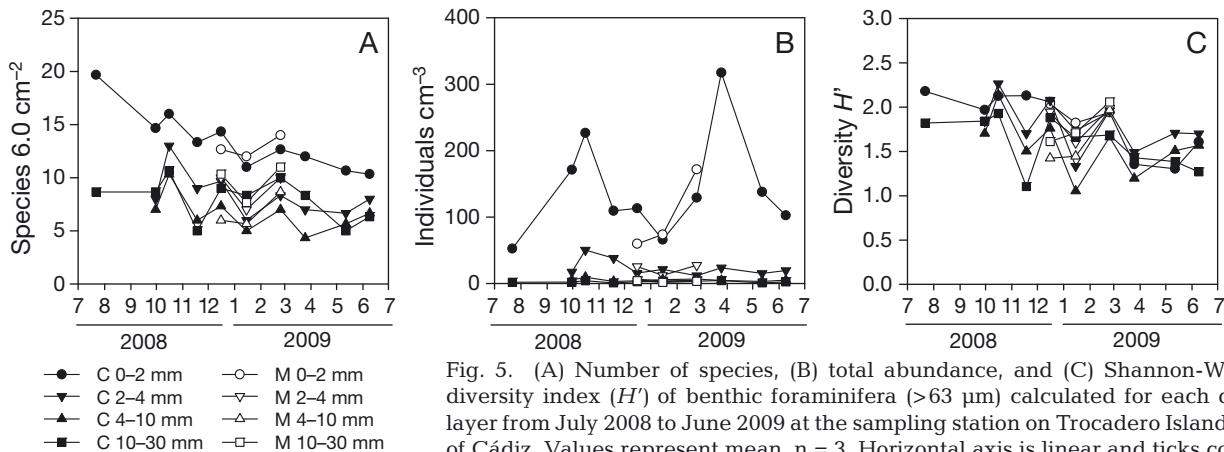


Fig. 5. (A) Number of species, (B) total abundance, and (C) Shannon-Wiener diversity index (H') of benthic foraminifera ($>63 \mu\text{m}$) calculated for each depth layer from July 2008 to June 2009 at the sampling station on Trocadero Island, Bay of Cádiz. Values represent mean, $n = 3$. Horizontal axis is linear and ticks correspond to the first day of each month. C: control; M: macroalgae

Total numbers of species per plot (i.e. 6.0 cm^2) ranged from 12 (May 2009 and June 2009) to 25 (December 2008 and February 2009), whereas total abundance of living benthic foraminifera varied between $150 \pm 120 \text{ ind. } 6.0 \text{ cm}^{-2}$ (January 2009) to $430 \pm 220 \text{ ind. } 6.0 \text{ cm}^{-2}$ (March 2009). Benthic foraminifera mainly belonged to the small size fraction (63 to 150 μm), with small foraminifera representing between 62 and 89% of the total community.

The number of species (S) was significantly higher in the first 0–2 mm layer ($p < 0.05$; Table S3 in the Supplement) and showed no differences in time (Fig. 5A). The number of individuals per sediment layer was significantly higher in the surface sediment compared to deeper sediment layers for most of the study period ($p < 0.05$; Table S3), with the exception of winter months when no significant differences were observed with depth (Fig. 5B). Over time, only the surface sediment showed significant differences in number of individuals. Diversity index H' showed significant differences between the 0–2 and 2–4 mm layers and the bottom 2 layers and between autumn and spring ($p < 0.05$; Table S3).

The presence of macroalgae on the sediment did not influence the foraminiferal community in any appreciable way (Fig. 5), with no significant differences found between samples taken under macroalgae mats and bare sediment for number of species, abundance or diversity index ($p > 0.05$).

Surface foraminifera abundance, number of species and diversity index H' showed correlations with some environmental data. Abundance correlated with water column Si(OH)_4 ($r = 0.637$, $p < 0.05$, $n = 10$) and diversity index significantly correlated with sediment chl c ($r = 0.695$, $p < 0.05$, $n = 10$) and oxygen concentration during light treatment ($r = 0.719$, $p < 0.05$, $n = 10$).

The community of living benthic foraminifera in the Bay of Cádiz was dominated by individuals belonging to the suborders Rotalina and Miliolina. Agglutinated foraminifera were only relatively important in November 2008 and February 2009, with *Eggerelloides scaber* (Williamson) being the only representative species of this suborder (Fig. 6D). Rotalids were represented by the relatively common species *Haynesina germanica* (Ehrenberg) ($21 \pm 11\%$; Fig. 6F), and some other species with high relative and absolute abundances in particular periods such as *Ammonia tepida* (Cushman) peaking in July 2008 (Fig. 6A), *Cribroelphidium excavatum* (Terquem) with high abundance in autumn 2008 (Fig. 6C) and *Fissurina lucida* (Williamson) peaking in February and March 2009 (Fig. 6E). The main representative of suborder Miliolina was *Pseudotriloculina* sp., which was relatively common over the whole sampling period ($19 \pm 12\%$; Fig. 6G). From the end of winter to spring-early summer, another representative of the suborder Miliolina, *Cornuspira involvens* (Reuss), dominated the living assemblage (40 to 60%; Fig. 6B). Other, subsidiary species of this suborder were also present, such as *Quinqueloculina seminula* (Linnaeus), *Q. canariatastrata* (Wiesner), *Quinqueloculina* spp. 1., and *Quinqueloculina* spp. 2., all of which were grouped together in *Quinqueloculina* spp. (Fig. 6H).

Multivariate analyses of benthic foraminifera

The ordination NMDS plot of the normalised foraminiferal abundance at each depth revealed few but significant changes in the community composition from the surface layer to the deepest part of the sediment (Fig. 7, Table S3 in the Supplement). Signif-

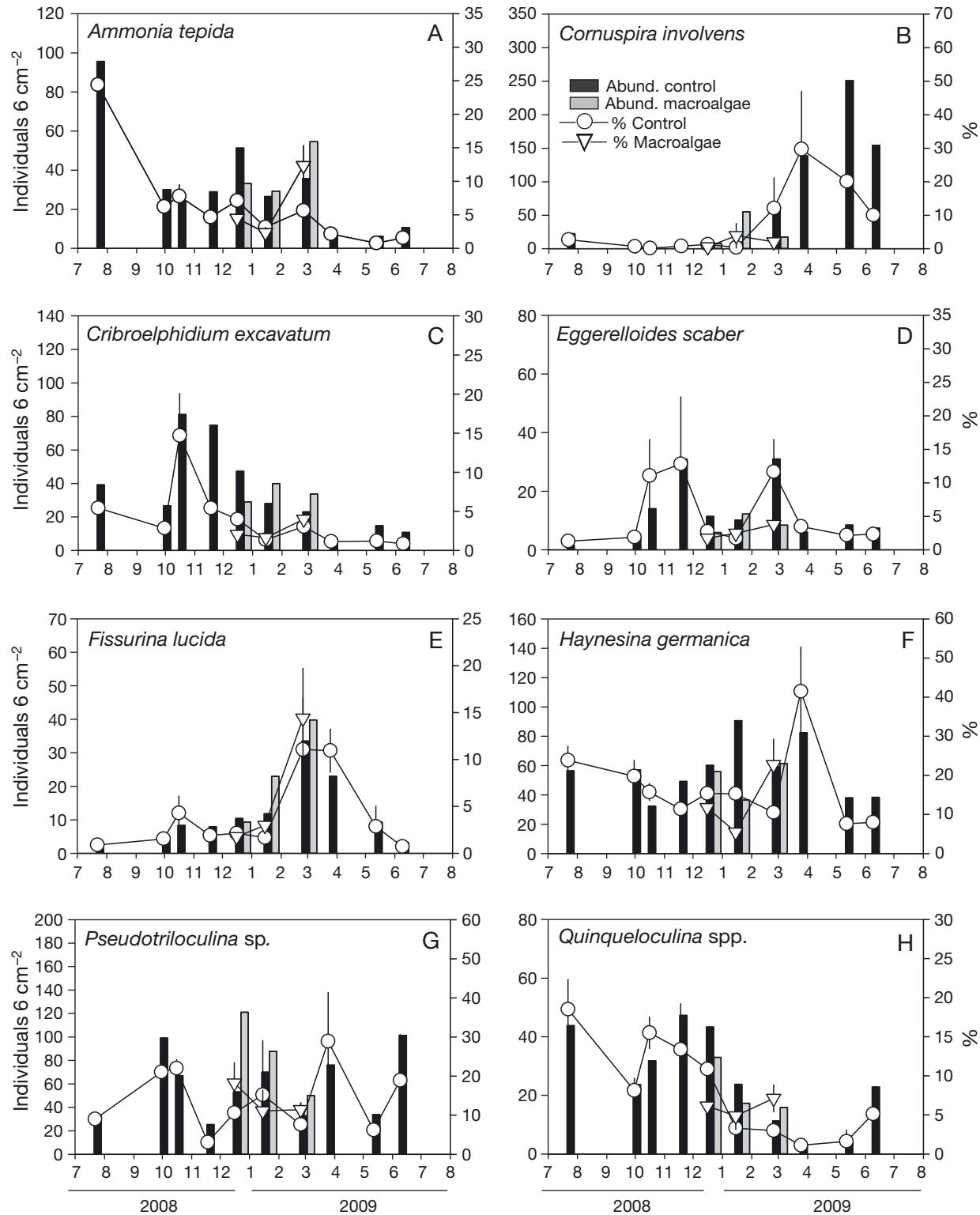


Fig. 6. Mean absolute abundance (bars) and relative abundance and standard error (lines) of the most characteristic foraminiferal species ($>63 \mu\text{m}$, 0–30 mm interval) from July 2008 to June 2009 at the sampling station Trocadero Island in the Bay of Cádiz. (A) *Ammonia tepida*, (B) *Cornuspira involvens*, (C) *Criboelphidium excavatum*, (D) *Eggerelloides scaber*, (E) *Fissurina lucida*, (F) *Haynesina germanica*, (G) *Pseudotriloculina sp.*, (H) *Quinqueloculina spp.* Control: black bars and circles; macroalgae: grey bars and triangles

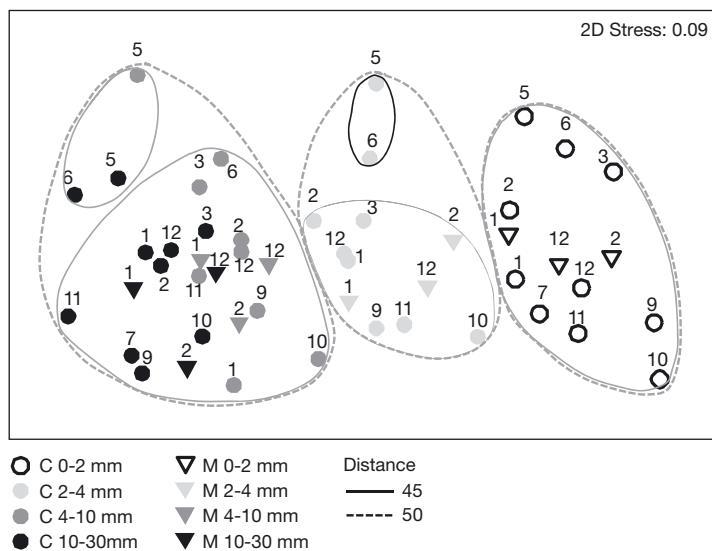


Fig. 7. NMDS ordination diagram on 2 axes of Bray-Curtis similarities from square root transformed abundance data of the foraminiferal community from the different sediment layers (0–2, 2–4, 4–10 & 10–30 mm) from July 2008 to June 2009 at the sampling station in Trocadero Island, Bay of Cádiz. Months of sampling are indicated on plot by corresponding numbers. Best plot was obtained after 100 random restarts. Groups at 45 and 50% distance are shown after applying a group average clustering. C: control; M: macroalgae

ificant differences with time were almost exclusively observed at the sediment surface (0–2 mm).

DISTLM showed that, of the variables tested, the ones that individually explained the greatest amount of variation of the surface foraminiferal community (0–2 mm) were porewater NO_x^- (7.06%), C_{org} (11.55%), salinity (12.66%), water column Si(OH)_4 (14.17%), precipitation (15.53%) and chl c (17.75%) (Table 1). The forward selection procedure using AIC selected 5 variables, chl c, water column Si(OH)_4 and NH_4^+ , salinity and precipitation, which together explained 47% of species data variation during the study (Table 1).

The first 2 axes on the projection biplot explained 39% of the total variance of the species data (Fig. 8). The first axis was highly correlated with precipitation, chl c and salinity, whereas the second axis was related primarily to changes in water column Si(OH)_4 and NH_4^+ and secondarily to chl c. Of the species that showed the highest correlation with the plot axes, *Cornuspira involvens* showed a high

variance and showed the highest values towards spring-summer 09, characterised by high salinity and low chl c values. In contrast, *Ammonia tepida* and *Quinqueloculina carinatastriata* among others showed the highest values in late autumn-winter when the higher values of precipitation and chl c also occurred. *Pseudotriloculina* sp. also showed high variance and was correlated with *Fissurina lucida* and negatively correlated with *Quinqueloculina seminula*. These species showed a high covariance with water column nutrients concentrations. On the other hand, *Quinqueloculina* spp. 1, *Brizalina spathulata* and *Cribroelphidium excavatum* and a number of other secondary species showed higher abundances in early autumn, when high values of water column nutrients and precipitation occurred.

DISCUSSION

The response of the community of benthic foraminifera differed between sediment layers. The composition of the live benthic foraminiferal assemblage changed significantly over the course of the year in the surface layer and these changes could be linked to fluctuations of several environmental variables, directly or indirectly related

Table 1. Results of non-parametric multiple regression of Bray Curtis dissimilarities of square root foraminiferal community abundance data on individual environmental variables for (a) each variable taken individually (ignoring other variables) and (b) forward selection model using the Akaike's information criterion (AIC). % Var and Cumul. (%): percentage of variance in species data explained by that variable or the model, respectively

Variable	pseudo-F	p	Var (%)	Cumul. (%)	AIC	df
(a) Variables taken individually						
C:N_{org}	0.646	0.729	2.25			
Water column NH_4^+	1.880	0.074	6.29			
Porewater NO_x^-	2.128	0.042	7.06			
Organic carbon	3.656	0.004	11.55			
Salinity	4.059	0.002	12.66			
Water column Si(OH)_4	4.624	0.002	14.17			
Precipitation	5.146	0.002	15.53			
Chlorophyll c	6.042	0.001	17.75			
(b) Forward selection model						
+ Chlorophyll c	6.042	0.001	17.75	17.75	211.94	28
+ Water column Si(OH)_4	4.752	0.001	12.31	30.06	209.08	27
+ Precipitation	3.176	0.003	7.61	37.67	207.62	26
+ Water column NH_4^+	2.301	0.013	5.25	42.93	206.98	25
+ Salinity	1.666	0.099	3.70	46.63	206.97	24

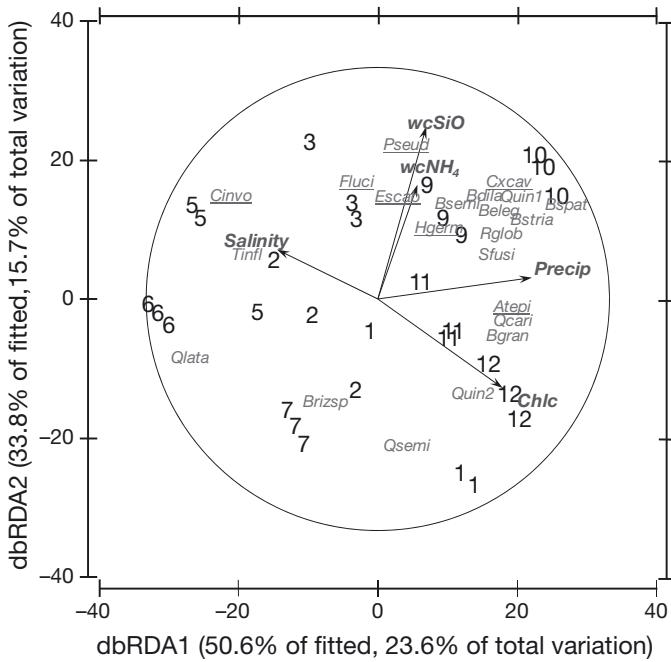


Fig. 8. RDA projection triplot based on Bray-Curtis dissimilarities of square root taxa abundances. Numbers indicate month of sampling starting from July 2008 (7) to June 2009 (6). Lines indicate direction and relative magnitude of influence. The covariance matrix was used. The first 2 axes explain 84% of the total sum of all canonical eigenvalues which corresponds to 39% of the variation in the species data. Only significant explanatory variables selected by the forward selection model were used. Precip: precipitation during the 2 previous weeks; wcNH₄: water column NH₄⁺; wcSiO: water column Si(OH)₄; Chl c: chlorophyll c. Species with a correlation >0.4 with the axes or a high abundance overall are shown. Species showing a high abundance during the study are underlined. Atepi: *Ammonia tepida*; Bdila: *Brizalina dilatata*; Beleg: *Buliminella elegantissima*; Brizsp: *Brizalina* sp.; Bsem1: *Brizalina* cf. *seminuda*; Bspat: *Brizalina spathulata*; Bstria: *Brizalina striatula*; Bgran: *Bucella granulata*; Cinvo: *Cornuspira involvens*; Cxav: *Cribroelphidium excavatum*; Escab: *Eggerelloides scaber*; Fluci: *Fissurina lucida*; Hgerm: *Haynesina germanica*; Pseud: *Pseudotrilobulina* sp.; Quin1: *Quinqueloculina* spp.1; Quin2: *Quinqueloculina* spp.2; Qcari: *Quinqueloculina carinatostriata*; Qlata: *Quinqueloculina lata*; Qsemi: *Quinqueloculina seminuda*; Rglob: *Rosalina globularis*; Sfusi: *Stainforthia fusiformis*; Tinfl: *Trochammina inflata*.

to food availability. In contrast, in deeper layers, temporal changes of the community assemblage were not significant. No effect of the presence of the macroalgal bloom could be detected on foraminiferal assemblages.

Distribution of benthic foraminifera

The standing stock of benthic foraminifera was mainly concentrated (68% on average) in the upper

sediment layer (0–2 mm) over the whole studied period, in agreement with the few previous studies describing the vertical distribution of intertidal foraminifera at sub-centimetric scale (Murray & Alve 2000). Most published studies of foraminifera normally focus on the uppermost centimetre, likely missing the fine scale changes occurring near the sediment-water interface (Debenay et al. 2006, Horton & Murray 2007, Berkeley et al. 2009). The use of oxygen microsensors and the positive correlation found between both species number and abundance and oxygen concentration with depth (Fig. 4) clearly showed that the vertical distribution of living benthic foraminifera was responding to oxygen distribution. In addition to oxygen levels, food quantity and quality are additional variables potentially influencing vertical distributions. Bacteria and microalgae are known food resources for benthic foraminifera inhabiting intertidal environments (Goldstein & Corliss 1994, Moodley et al. 2000, Langezaal et al. 2005, Topping et al. 2006, Pascal et al. 2008). Microalgae, mainly diatoms, are often visible in the study area as a brown layer on the sediment surface. These microalgae are not only responsible for the increased oxygen penetration depth under light conditions (García-Robledo et al. 2010), but also act as a direct food resource for benthic foraminifera. Furthermore, diatoms produce colloidal carbohydrates (exopolymeric substances) (Smith & Underwood 1998), an additional energy source for bacteria and possibly also for foraminifera in the upper sediment layers. The lack of a relationship between the vertical distribution of foraminiferal abundance and C_{org} or chlorophyll could simply indicate that total C_{org} is not a good indicator of labile or easily accessible organic matter (Dell'Anno et al. 2000).

The benthic foraminiferal community below 2 mm (i.e. well below the average depth where oxygen penetrates in darkness) differed from the one living at the sediment surface, suggesting that this community is probably adapted to suboxic or anoxic conditions and food resources of lower quality. Some species of benthic foraminifera are able to sustain hypoxia or even anoxia for long periods of time (Moodley & Hess 1992, Geslin et al. 2004, Pucci et al. 2009). Bacterial symbiosis has been proposed as a potential mechanism used for some species of benthic foraminifera to sustain hypoxia or anoxia (Bernhard & Sen Gupta 1999). Another mechanism used by benthic foraminifera to survive temporarily in the absence of oxygen is to store nitrate intracellularly and perform denitrification (Risgaard-Petersen et al. 2006, Piña-Ochoa et al. 2010). Among the species in

the Bay of Cádiz, only a few are known to survive anoxia for short periods of time (*Cribroelphidium excavatum*, *Quinqueloculina seminula*, *Eggerelloides scaber*) or to perform denitrification (*Bulimina* sp., *Globobulimina* sp. and *Stainforthia* sp.) (Moodley & Hess 1992, Piña-Ochoa et al. 2010). The abundance of denitrifying species was, however, too low to reliably test for a relationship with porewater or water column NO_x^- levels. Alternatively, the presence of benthic foraminifera in the deep sediment layers could be the result of particle reworking and bioirrigation (Berkeley et al. 2007).

The abundance, species richness and assemblage composition of living benthic foraminifera in our study area are comparable to communities observed in other Atlantic and Mediterranean intertidal environments (Basson & Murray 1995, Debenay et al. 2006, Morvan et al. 2006). Thus, high abundance of species such as *Ammonia tepida*, *Haynesina germanica* and *Cribroelphidium excavatum* characterise temperate European intertidal areas (Alve & Murray 1994, 2001, Debenay et al. 2006, Morvan et al. 2006) including that of the Iberian Peninsula (Cearreta 1988, González-Regalado et al. 2001). Miliolids, in particular species of the genus *Quinqueloculina*, *Triloculina* and *Pseudotriloculina*, are frequently present and occasionally dominate in low marsh, lagoon and mudflat environments. For example, *Quinqueloculina* spp. together with *Ammonia beccarii* characterise the marginal marine assemblage of the SW Spanish estuaries (González-Regalado et al. 2001), the mid-intertidal areas of French estuaries (Debenay et al. Morvan et al. 2006) and can also be found in low marshes and tidal flat habitats of Atlantic Europe (Swallow 2000, Horton & Edwards 2006, Horton & Murray 2007, Leorri et al. 2010). Species of the genus *Pseudotriloculina* (*P. oblonga*) and *Triloculina* (*T. oblonga*) have been described as abundant in tropical hypersaline lagoons (Debenay et al. 2001, Debenay & Guillou 2002) and hypo- and mesohaline shallow bays (*T. oblonga*; Buzas-Stephens et al. 2011). Also, in our intertidal setting, we found species (e.g. *Brizalina* spp., *Eggerelloides scaber*) generally considered typical of subtidal deeper marine environments, which are characterised by less variable environmental conditions (e.g. light, temperature, tides) than intertidal areas. The observation of such species is not uncommon in shallow environments, such as estuaries (Alve & Murray 1994, Diz & Francés 2008), and is generally explained by the transport of adult individual propagules or embryonic juveniles by currents (Alve 1999, Goldstein & Alve 2011).

Benthic foraminifera and environmental variables

The environmental variables measured in the present study showed significant variation over time. With the exception of NO_x^- , water column nutrients showed their highest values in autumn and spring coinciding with periods of increased precipitation. The availability of the nutrients induced a response by microphytobenthos, evident as an increase first in chl c, a proxy of benthic diatoms' abundance, and later as an increase in sediment chl a persisting over a longer period. This increase also translated in an increase in both the maximum oxygen penetration depth and oxygen concentration in the sediment (Figs. 2, 3 & 4).

With the exception of diversity, the temporal evolution of benthic foraminiferal abundance or species richness showed few significant differences which, in addition, were confined to the surface sediment layer. Moreover, these measures did not follow the trend of variables generally used as proxies of increased food supply or high food quality in the sediment, such as C_{org} and chl a content, similar to what was observed in a long-term study in the Hamble estuary (e.g. Murray & Alve 2000). In fact, the high C_{org} and chl a values in the sediment occurring in December (Fig. 3C) coincided with one of the lowest foraminiferal abundance values registered during the sampling period (Fig. 5B). This lack of a relationship between abundance and chl a might be due to the existence of a time lag between the fluctuation of a variable, in this case C_{org} or chl a, and the response of the foraminiferal assemblage (Debenay et al. 2006). However, in our study, the interval between the highest C_{org} and chl a contents (December 2008) and the peak in abundance (April 2009) seems too long (~4 mo) to be explained by such a time lagged response (compare Figs. 3 & 5). On the other hand, a significant correlation was found between diversity index and chl c, suggesting a more specific relationship between foraminifera and benthic diatoms, similar to what has been suggested previously between foraminifera and bacteria (Haynes et al. 2007).

The DISTLM analysis using the surface foraminiferal community showed that a number of environmental factors, i.e. rainfall and salinity patterns, water column nutrients and sediment variables such as chl c, could explain a significant part of the variation of the foraminiferal community over time (Fig. 8). Salinity, which shows an inverse relation with rainfall patterns over long periods of time in the area (authors' unpubl. data), is considered one of the most important factors affecting the distribution of brackish to

subtidal foraminifera along with other related variables such as calcium carbonate and pH (Debenay et al. 2006, Horton & Murray 2007). The remaining factors that best explained the variation in the foraminiferal community assemblage in our study area are directly or indirectly related to food availability either in the water column or in the sediment. Thus, water column nutrients are linked to phytoplankton productivity and abundance in the water column, whereas chl *c*, which correlated with C_{org}, chl *a* and other sediment variables, indicates the importance of microphytobenthos as a food source for foraminifera.

Relatively frequent species (*Pseudotriloculina* spp., *Fissurina lucida*, *Cribroelphidium excavatum*) and some subsidiary species (*Brizalina spathulata*, *Quinqueloculina lata* (Terquem), *Eggelleroides scaber*) showed significant covariance with water column nutrients (Fig. 8). Such a relationship is likely the result of increased phytoplankton availability in the overlying water or increased remineralisation of C_{org} in the sediment. Reproduction of *C. excavatum* has been related to increased food supply in subtidal environments of Swedish fjords (Gustafsson & Nordberg 1999). Also, Schönfeld & Numberger (2007) reported high pigment concentration in the protoplasm of *Elphidium excavatum clavatum* (closely related species to *C. excavatum*) and reproduction peaks related to high sedimentary chl *a* and phytoplankton blooms, suggesting a 'bloom-feeding behaviour' of this species in the subtidal brackish environment of Kiel Fjord. On the other hand, *Quinqueloculina canariastriata* is a typical Mediterranean species, although it has been found in high abundance in intertidal areas of the French Atlantic coast during summer (Bouchet et al. 2007a). *Ammoa tepida* and *Q. canariastriata* are some of the species that show a positive relation to chl *c* in the sediment, suggesting a possible preference of these species for microphytobenthos. This is supported by laboratory experiments showing that although *A. tepida* is able to feed on bacteria, it prefers microalgae as a food source (Pascal et al. 2009).

Of particular interest is the pattern of *Cornuspira involvens*. This species first appeared in the assemblage in March 2009, right after the macroalgal bloom collapsed, and remained present until June 2009 (Fig. 6B). The high abundance of *C. involvens* coincided with low sedimentary C_{org} or chl *c* content. The cause that triggered this rapid increase in *C. involvens* is unclear, but our data suggest that this species might benefit from macroalgae degradation or an increase in temperature and salinity that occurred in the area from late winter to spring.

Exceptionally high abundances of this species, comparable to the ones observed in our study area, have also been reported in other non-intertidal areas, for instance the continental shelf of Scotland (Murray 2003). Further studies are needed to identify a direct link between *C. involvens* and post-macroalgal bloom conditions.

Macroalgal blooms consisting mainly of the tubular form of *Ulva* sp. are a common phenomenon in the Bay of Cádiz. Previous experimental studies have shown a significant effect of the macroalgal bloom on benthic fluxes across the sediment–water interface, as well as on the microphytobenthic community. However, in shallow systems, the effect depends on the bloom stage (García-Robledo et al. 2008, Corzo et al. 2009, García-Robledo & Corzo 2011). Actively growing macroalgae cover the sediment surface, reducing the light and inhibiting microphytobenthic photosynthesis. As a result, heterotrophic activity consumes the organic material contained in the sediment (García-Robledo & Corzo 2011). Over time, decomposition of macroalgal detritus increases the C_{org} and nitrogen content of the sediment, oxygen is rapidly consumed inside the mat and the sediment becomes anoxic (García-Robledo et al. 2008, Corzo et al. 2009). Once the bloom collapses, remineralisation of macroalgae fertilizes the microphytobenthic community, increasing oxygen production and microalgal biomass (García-Robledo et al. 2008). Despite the aforementioned effects, comparison of plots covered with macroalgal mats and plots with no visible macroalgae did not reveal differences in the abundance, species number, diversity or community structure of benthic foraminifera. A similar result was suggested (even though it was not tested with samples collected outside macroalgal mats) by Murray & Alve (2000). This may suggest that the benthic foraminifera community is adapted to the changes imposed by the macroalgal bloom or that other factors exert a stronger influence on the foraminiferal community. It should be noted, however, that macroalgal mats were not analyzed separately for their foraminiferal content; therefore, there is no information at present of any association between a particular benthic foraminiferal species and macroalgae as indicated by other authors (Atkinson 1969, Ribes et al. 2000).

CONCLUSIONS

We simultaneously studied the response of the living intertidal benthic foraminiferal community and several environmental variables in the water column

and the sediments in the Bay of Cádiz over a year. The analysis of the community parameters at sub-centimetric vertical resolution allowed us to identify relationships explaining the foraminiferal patterns in this muddy intertidal area. Benthic foraminiferal community changes were mainly recorded in the upper 0–2 mm. This layer also had the highest benthic foraminiferal abundance and oxygen concentrations. Therefore, sampling at sub-centimetric or millimetre scale is recommended in order to better characterise the ecology of intertidal benthic living foraminifera. Multivariate regression analysis of the community assemblage, on the other hand, showed significant temporal community composition changes which could be related to fluctuations of environmental variables, mainly those of water column nutrients and sediment food availability (e.g. chl c). However, univariate whole community descriptors such as abundance, diversity or species richness showed few differences during the study period and weak relationships to environmental variables. Therefore, differences in the species-specific response to environmental changes seem to be balanced to produce rather constant seasonal values of species richness and diversity of foraminiferal community in the Bay of Cádiz. Studies including other components of the benthic community (e.g. bacteria, other meiofauna) are warranted in order to evaluate the role of factors such as predation and competition controlling modern day foraminiferal community assemblages in the Bay of Cádiz.

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