

RESEARCH PAPER



Relationship between substrate, physico-chemical parameters and foraminiferal tests in the Doñana National Park, a Biosphere Reserve in SW Spain

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Abstract

A multidisciplinary analysis of sediments collected in different environments of the Doñana National Park (Guadalquivir estuary, SW Spain) provides an overview of the textural, mineralogical and physico-chemical parameters that control the distribution of benthic foraminiferal tests in this Biosphere Reserve. These microorganisms are absent in the fine quartzitic sands that constitute the substrate of temporary ponds with brief hydroperiods located in the dune systems and spits, as well as in other ponds with low conductivities or hypersaline conditions located in the inner marshlands or near the Guadalquivir river banks. Dead benthic foraminifera are mainly found on phyllosilicate-rich, silty-clayey substrates. The taphonomic analysis of the main species (*Ammonia tepida*, *Haynesina germanica*, *Trochammina inflata*, *Entzia macrescens*) points to its deposit in situ. Cluster analysis permits to delimitate six foraminiferal assemblages. Cluster II (*A. tepida* + *H. germanica*) is the dominant assemblage in the central ponds and the margins of the main channels, while cluster IV (*T. inflata* + *E. macrescens*) is restricted to some ponds located on the high marsh and cluster VI (*Ammonia beccarii* + *Quinqueloculina* spp.) is abundant on external beaches. Tidal fluxes cause the transport of these last marine benthic species and some planktonic forms both to the inner areas of the estuary and to these beaches.

Keywords Texture · Mineralogy · Physico-chemical parameters · Foraminiferal test · Doñana National Park · SW Spain

Resumen

El análisis multidisciplinar de sedimentos obtenidos en diferentes medios del Parque Nacional de Doñana (estuario del río Guadalquivir, S. O. de España) proporciona una visión general de los parámetros texturales, mineralógicos y físico-químicos

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que controlan la distribución de los foraminíferos bentónicos muertos en esta Reserva de la Biosfera. Estos microorganismos están ausentes en las arenas finas cuarcíticas que constituyen el sustrato de lagunas temporales con breves hidroperiodos situadas en los sistemas de dunas y flechas litorales, así como en otras lagunas con bajas conductividades o condiciones hipersalinas localizadas en las marismas internas o cerca de las riberas del río Guadalquivir. Los caparazones de los foraminíferos se han encontrado principalmente en sustratos limo-arcillosos, ricos en filosilicatos. El análisis tafonómico de las principales (*Ammonia tepida*, *Haynesina germanica*, *Trochammina inflata*, *Entzia macrescens*) apunta a su depósito in situ. El análisis clúster permite diferenciar seis asociaciones. El clúster II (*Ammonia inflata* + *Haynesina germanica*) es la asociación dominante en las lagunas centrales del Parque y los márgenes de los canales principales, en tanto que el clúster IV (*Trochammina inflata* + *Entzia macrescens*) se restringe a algunas lagunas situadas sobre las marismas más elevadas y el clúster VI (*Ammonia beccarii* + *Quinqueloculina spp.*) es abundante en las playas externas. Los flujos mareales provocan el transporte de estas últimas especies marinas y de algunas formas planctónicas tanto hacia las zonas internas del estuario como a estas playas.

Palabras clave Textura · Mineralogía · Parámetros físico-químicos · Caparazones de foraminíferos · Parque Nacional de Doñana · S.O. España

1 Introduction

Benthic foraminifera are among the main environmental indicators in coastal and marine areas, due to their small size (< 100 µm-2 cm in most cases), abundance, high preservation potential within the sediment record after death and distinctly diagnostic test shape (Murray 2006; Sreenivasulu et al. 2019). Assemblage composition is influenced by both abiotic (temperature, salinity, dissolved oxygen availability, nutrient flux, sedimentology, current flow, etc.) and biotic (food, predation, inter- and intra-specific competition) conditions of an area (Diz et al. 2000; Alves et al. 2019).

They have an ubiquitous distribution, found throughout all the marine and littoral regions, but individual taxa are extremely restricted to specific ecological niches. This advantage is especially interesting in estuaries, where there is a great variability of sedimentary environments, such as ebb-tide channels, marshes, beaches or spits, which can be differentiated by their assemblage (or absence) of benthic foraminifera (e.g. Debenay et al. 2000; Ballesteros and Bernasconi 2019). In these estuarine areas, changes in the composition of the foraminiferal assemblages can reflect their occupation and the elimination of original ecosystems (Cearreta et al. 2008), sea-level variations (Helfensdorfer et al. 2019), an increasing pollution (Martins et al. 2011)

In the southwestern Spanish littoral, several investigations have analyzed the distribution and main assemblages of benthic foraminifera in the different sedimentary environments of most of its estuaries (González-Regalado et al. 2001; Camacho et al. 2015). However, this group remains almost unknown in the Guadalquivir River estuary, the most important in the region. Only a recently published study has analyzed the benthic foraminifera present in the main channel of this river (González-Regalado et al. 2019).

In this paper, we analyze the benthic foraminifera of the Doñana National Park, one of the most important Biosphere Reserves in southwestern Europe, located near the Guadalquivir River mouth. Their abundance and diversity are related to different physico-chemical factors and to the substrate, and we thus aim to determine which of them are those that are responsible for the benthic foraminiferal distribution in this area.

2 Study area

The Guadalquivir River is the fifth longest river in Spain (680 km) and drains an area of about 64,000 km². Its estuary has a length of 110 km, with the main hydrodynamic processes controlled by tides, waves and fluvial inputs. The

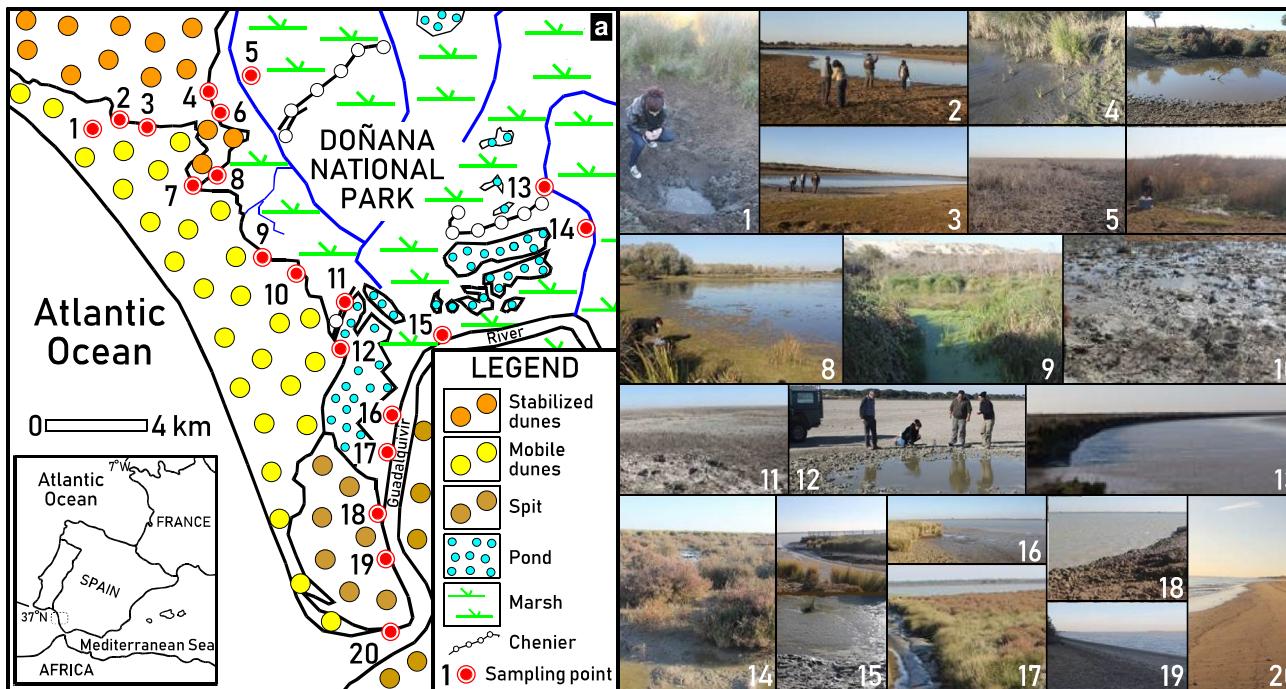


Fig. 1 a Geomorphological map of the Doñana National Park and sampling points. 1: Temporary pond; 2: Margin of temporary pond (Santa Eulalia); 3: Margin of temporary pond (Dulce); 4: Temporary pond (Palacio de Doñiana); 5: Temporary pond (Marismas de Hinojos); 6: Partially filled stream (Caño del Peral); 7: Temporary pond (Lucio del Caballero); 8: Temporary pond (Lucio Saperón); 9: Very eutrophicated pond; 10: Temporary pond in a very dry marsh; 11:

Temporary pond (Vetelenga); 12: Bubbling waterhole in marsh plain; 13: Margin of partially filled stream (Caño del Buen Tiro); 14: Temporary pond (Lucio de Tío Oreja); 15: Partially filled stream (Caño de Breñas); 16: Margin of the Guadalquivir River; 17: Small pond; 18: Ancient marsh covered by sand; 19: Mouth of the Guadalquivir River; 20: Punta Malandar beach

Near the mouth, this estuary includes the Doñana National Park (Fig. 1), one of the largest wetlands in Europe (55,000 ha). Due to the convergence of natural and cultural values, this park was successively recognized as Biosphere Reserve (1981), Certificate of the Council of Europe to the Management and Preservation (given in 1985 and renewed every 5 years since then) and Human Heritage (1994), among others.

This protected zone is a very complex system (see review in García Novo et al. 2007), mainly formed by extensive low fluvio-tidal marshes (Fig. 1, A-14: ~35,000 ha) that are drained by numerous partially filled ebb-tide channels so-called 'caños' (Fig. 1, 15–17). This clayey-silty ecosystem is very flat and includes some 'hills' (1–3 m m.s.l.) occupied by bioclastic cheniers and sandy ridges (Fig. 1, A-11). These low marshes include the most important habitats for the reproduction of many bird species (Casas and Urdiales 1995).

This area has the characteristic variability of a Mediterranean climate (Siljeström and Clemente 1990), with a temperature range quite regular between years (winter: 0–15 °C; summer: 30–>40 °C) but a very irregular rainfall. In fact, 50% of the total precipitation falls during winter (Siljeström 1985). The accumulated water produces the progressive flooding of the marshes between October to November, reaching its peak in January or February (Casas and Urdiales 1995). Beginning in spring, evaporation losses are not offset by the river inputs, leading to dry the marsh during the summer (Sánchez 2009).

3 Materials and methods

This single sampling took advantage of the fact that the sampled environments were flooded by previous rains, while many of them remain dry during most of the year. Approximately 200 g of sediment were taken in each sampling point from 0 to 5 cm depth and stored in plastic bags.

3.2 Grain size analysis

In the laboratory, each sample was dried in an oven and then passed through a 250 µm sieve, to separate the coarse and fine fractions. The coarse fraction of the samples was then washed through 4 mm-250 µm sieves for grain size analysis. The fine fraction went through a H₂O₂ reaction for removing the organic matter, and was analysed in MALVERN master-size for grain size. GRADISTAT 14.0 program was used to calculate the different grain size distribution of the samples and the sediment type, according to Folk and Ward (1957).

3.3 Mineralogical analysis

Twenty sub-samples were separated from the previous sedimentological samples for this purpose. These sub-samples were dried in an oven at about 40 °C and grinded in a mortar. They were then mixed with alcohol, grinded in Micronising Mill for 10 min, and dried in an oven at 40 °C. Once dried, the samples were grinded once more and read in X'Pert Pro PANalytical and analyzed in Xpowder 2004 Version 0.4.0.2 Pro.

3.4 Physico-chemical analysis

In the sedimentological samples, a multiparameter probe was also used to measure abiotic parameters like ph, temperature, conductivity and Eh, at each site. In a later step, the percentage of water and organic matter in each sample was also calculated by loss of ignition after drying the samples and burning the organic matter at 40 and 500 °C, respectively.

3.5 Benthic foraminifera

Surface samples (10 cm³; 0–1 cm depth) were extracted using marked syringes and remained untouched in the laboratory during 14 days, as it is the minimum time necessary for staining

very low (less than 10 individuals), the distinction between live and dead foraminifera was not made.

In these samples, the faunal density has been calculated (e.g. individuals/gram of sand), as well as the planktonic/benthic ratio (if possible) and diversity indexes (Shannon –H-, species richness, α-Fisher Alpha and equitability). The taxonomic classification of foraminifera is based on Loeblich and Tappan (1987) and the Word Register of Marine Species (WoRMS).

3.6 Statistical analysis

In a first step, the Pearson correlation coefficients were calculated between the different grain sizes and the mineralogical composition of all samples (Figs. 2a, 3a). In a second step, a cluster analysis was applied to both data sets (Figs. 2b, 3b; Ward's method). In addition, data was centralized (e.g. subtracting the mean of each variable) and two discriminant functions were calculated in order to differentiate groups with similar grain size distribution or mineralogy, with a later comparison with the previous cluster results (Figs. 2c, 3c). In the case of mineralogy, this discriminant analysis was only applied to the main five minerals, which constitute more than 90% of the total composition in most samples. Finally, the two discriminant functions obtained were drawn on the same graph (Fig. 4).

A Canonical Correspondence Analysis (CCA) was made to study the relation between texture and physico-chemical variables. This multivariate analysis is preferred rather than other ordination methods such as correspondence analysis (CA) and detrended correspondence analysis (DCA) because it has been tailored to specifically include environmental data (Maddy and Brew 1995). CCA was performed in R software using the Vegan library. CCA was also applied to define relations between the different diversity indexes obtained, texture and physico-chemical variables.

Two types of cluster analyses were used for foraminifera: (a) a Q-mode cluster analysis to produce the differentiation of sample groups, using a paired group algorithm and the Bray–Curtis similarity measure; and (b) a R-mode cluster analysis to differentiate the foraminiferal assemblages in the same way. The data matrix of species was based on abundances > 1% for both Q and R modes.

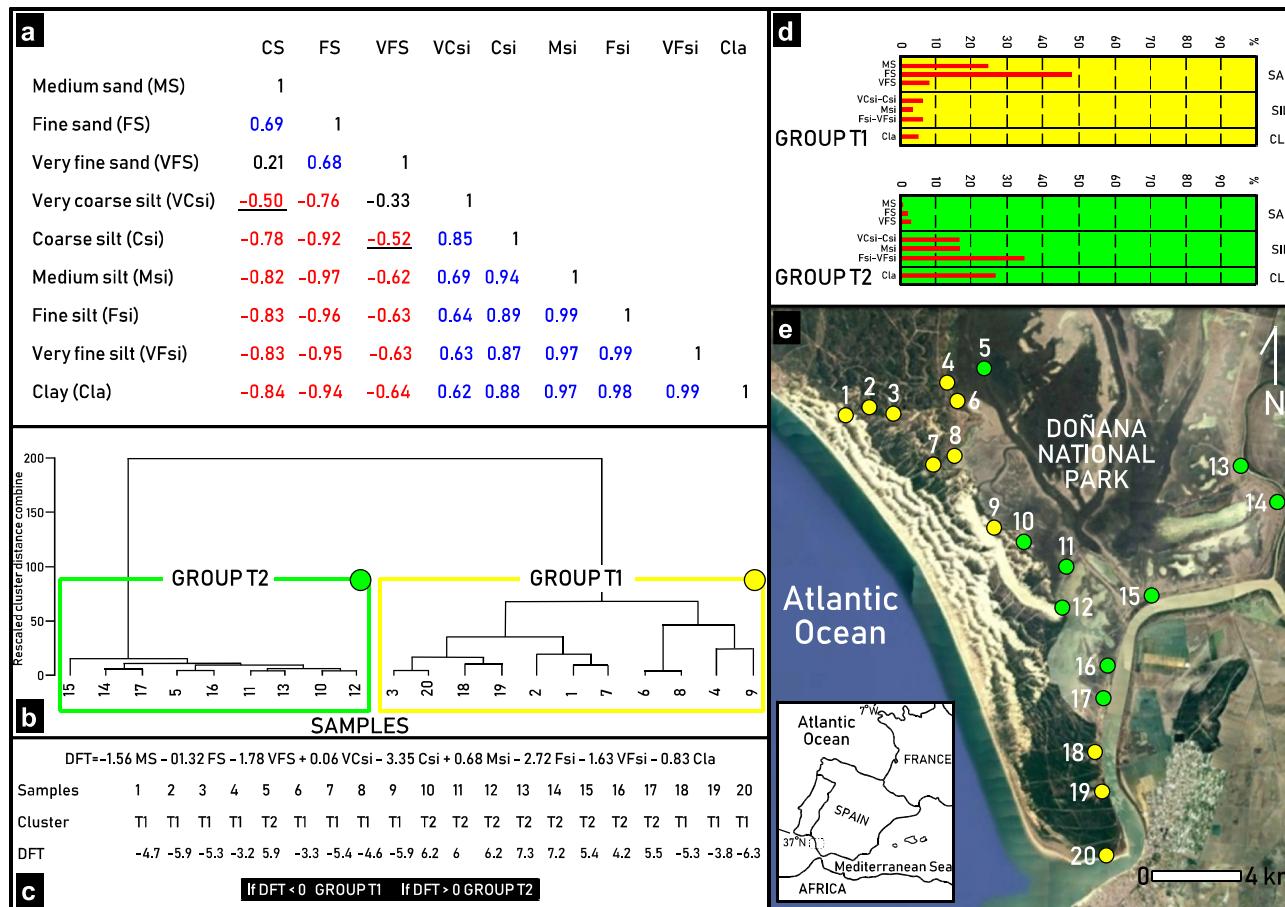


Fig. 2 Grain size analysis. **a** Pearson correlation matrix. Bold (blue or red): $p < 0.01$; underlined (blue or red): $p < 0.05$. **b** Dendrogram (Ward's method); **c** discriminant analysis, with indication of the limit

group (T1) includes nine samples located within the dune systems (samples 1–4) and their transition to the internal marshes (samples 6–9), as well as at the mouth of the Guadalquivir estuary (samples 18–20). In this group, fine sands are dominant (24.7–66.8%; mean-M: 47.85%), with important percentages of medium sands (9.7–47.7%; M: 23.85%) and silts (0–36.6%; M: 15.78%). Sorting is very variable ($\phi = 0.059$ –0.776), as well as kurtosis ($\phi = 0.713$ –3.327). These samples present a symmetrical or very fine skewed grain size distribution in most cases ($\phi = 0.059$ –0.776).

value between the determined groups; **d** average distribution of grain sizes in the two differentiated groups; **e** spatial distribution of the two groups

to very poorly sorted samples ($\phi = 1.833$ –2.285) have a frequent symmetrical grain size distribution ($|\phi| < 0.138$) and a moderate to low concentration of grain sizes around their mean (Table 1: mesokurtic-platykurtic curves).

4.1.2 Statistical analysis

The correlation matrix of grain sizes (Fig. 2a) differentiates two groups of grain sizes: (a) fine sand, highly correlated with both coarse and very fine sands ($r = 0.68$ –0.69;

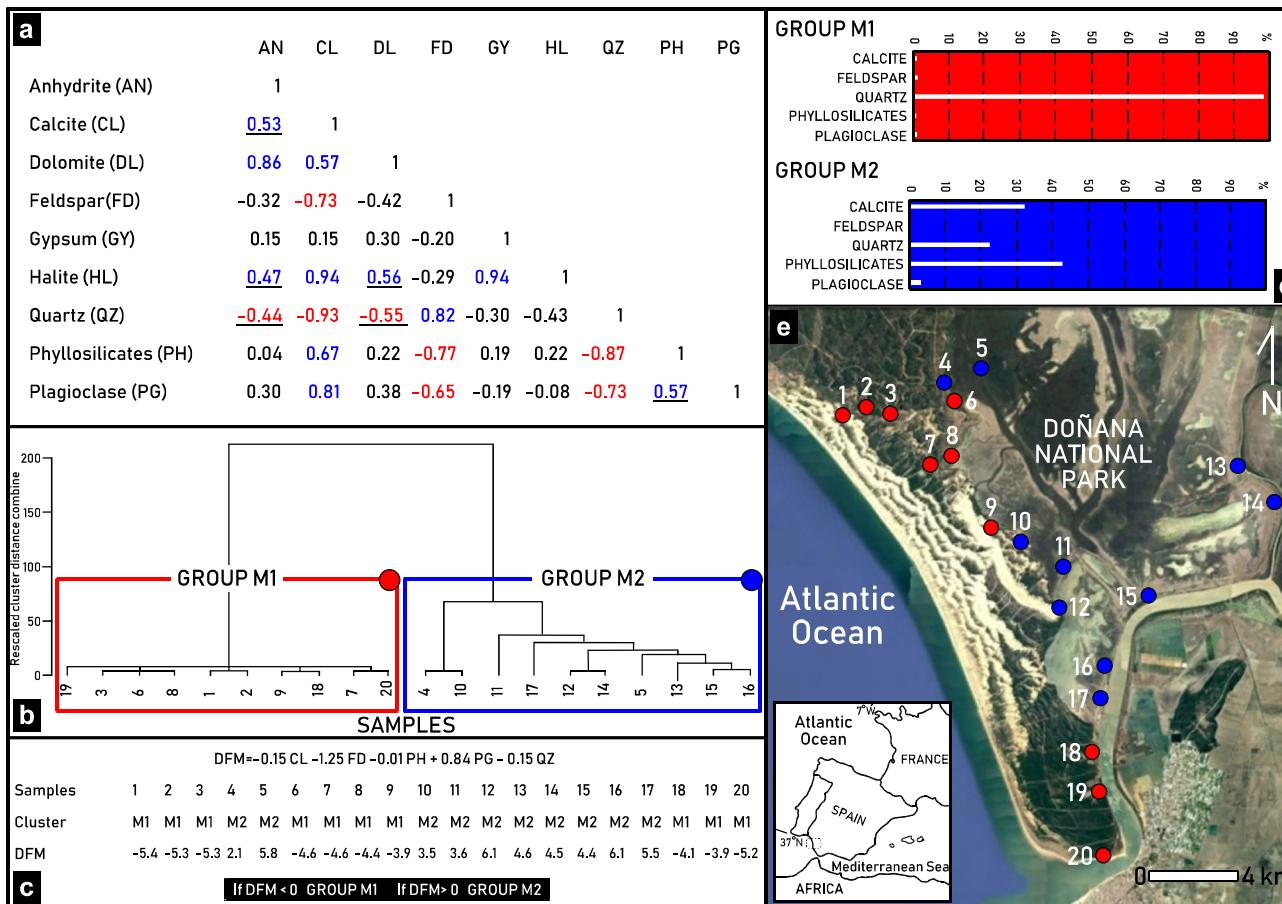
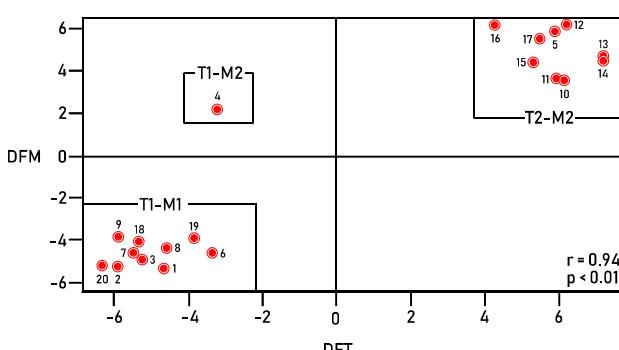


Fig. 3 Mineralogical analysis. **a** Pearson correlation matrix. Bold (blue or red): $p < 0.01$; underlined (blue or red): $p < 0.05$. **b** Dendrogram (Ward's method); **c** discriminant analysis, with indication of the

limit value between the determined groups; **d** average mineralogical composition in the two differentiated groups; **e** spatial distribution of the two groups



is distributed in the innermost areas of the Doñana National Park.

4.2 Mineralogy

4.2.1 Main mineralogical components

An initial analysis of mineralogical composition (Table 2) also allows to differentiate two groups of samples, very similar in mineralogical composition, but with different

Table 1 Grain size distribution and textural parameters of the collected samples

Sample	Sand			Silt			Clay		
	Medium	Fine	Very fine	Very coarse	Coarse	Medium	Fine	Very fine	
1	29.2	47.2	3.3	1.6	2.6	2.6	4.2	4	5.3
2	38.7	53.7	3.7	0.5	1	0.2	0.6	0.4	1.1
3	17.3	66.8	15.9	0	0	0	0	0	0
4	29.2	24.7	3.4	3	5.6	8.6	9.4	6.9	9.1
5	0	0.1	1	4	13.3	20.4	19.6	14.8	26.7
6	9.7	32.9	11.5	5.6	7.5	7.6	8.3	7.6	9.3
7	21.6	48.6	7.1	2	4.5	3.8	3.9	3.1	5.4
8	7.9	34.1	13.9	4.6	8.1	8.1	8.1	5.7	9.4
9	47.7	29.9	5.2	5.4	4.2	2.6	2	1.2	1.9
10	1.6	3.2	2	6.5	11.9	16	16.9	15.1	26.8
11	0	0.8	2.4	4.6	12.1	17.2	17.7	15.4	29.8
12	0.7	3.1	3.3	5.1	9.7	14.9	17.5	16.2	29.6
13	0	0.1	2	6.9	13.9	17.6	17	14	28.5
14	0	0.3	1.5	2.9	9.7	18.6	20.6	16.6	29.9
15	0	1.1	4.9	10.7	15.4	16.9	16	12.8	22.2
16	0	0.8	2.5	5.4	12	18.5	19.9	16	24.8
17	0.3	1.7	2.8	3.8	7.7	15.9	20.6	18.3	29
18	19.4	57.4	8.5	1.2	3.2	1.9	2.4	1.9	4.1
19	24.5	64.4	5.2	1	1.6	0.2	0.8	0.6	1.6
20	17.1	66.7	12.3	0.2	1.6	0.2	0.5	0.4	0.8

Sample	Mean		Median (ϕ)	Sorting		Skewness		Kurtosis	
	ϕ	Description		ϕ	Description	ϕ	Description	ϕ	Description
1	3.377	Very fine sand	2.262	2.229	Very poorly sorted	0.776	Very fine skewed	3.327	Extremely leptokurtic
2	2.175	Fine sand	2.111	0.59	Moderately well sorted	0.066	Symmetrical	1.756	Very leptokurtic
3	2.481	Fine sand	2.446	0.492	Well sorted	0.059	Symmetrical	0.915	Mesokurtic
4	4.160	Very coarse silt	2.705	2.956	Very poorly sorted	0.632	Very fine skewed	0.74	Platykurtic
5	7.764	Fine silt	7.539	1.882	Poorly sorted	0.138	Fine skewed	0.841	Platykurtic
6	4.572	Very coarse silt	3.425	2.686	Very poorly sorted	0.59	Very fine skewed	0.713	Platykurtic
7	3.479	Very fine sand	2.45	2.197	Very poorly sorted	0.751	Very fine skewed	2.502	Very leptokurtic
8	4.497	Very coarse silt	3.361	2.637	Very poorly sorted	0.621	Very fine skewed	0.78	Platykurtic
9	2.534	Fine sand	2.036	1.758	Poorly sorted	0.501	Very fine skewed	2.589	Very leptokurtic
10	7.531	Fine silt	7.512	2.285	Poorly sorted	0.078	Symmetrical	0.985	Mesokurtic
11	7.812	Fine silt	7.718	2	Very poorly sorted	0.021	Symmetrical	0.838	Platykurtic
12	7.723	Fine silt	7.757	2.236	Very poorly sorted	0.107	Coarse skewed	0.973	Mesokurtic
13	7.693	Fine silt	7.543	2.048	Very poorly sorted	0.069	Symmetrical	0.805	Platykurtic
14	7.974	Fine silt	7.818	1.833	Poorly sorted	0.076	Symmetrical	0.85	Platykurtic
15	7.196	Fine silt	7.06	2.181	Very poorly sorted	0.07	Symmetrical	0.866	Platykurtic

Table 2 Mineralogy of the studied samples (in %)

Sample	Halite	Dolomite	Calcite	Plagioclase	Feldspar	Quartz	Anhydrite	Phyllosilicates	Gypsum
1					1.47	98.53			
2					1.42	98.58			
3					1	99			
4				0.95		63.1		35.95	
5		2.21	25.78	2.97		21.2		47.85	
6					0.75	99.25			
7					0.96	97.12		1.92	
8					0.58	99.42			
9				0.69	0.75	98.56			
10			19.8	1.95		37.81		40.44	
11	5.62	3.32	50.09	3.29		15.55	5.16	16.97	
12	6.42	2.2	25.15	1.29		10.2	3.33	51.4	
13			36.08	2.13		14.02		47.77	
14			32.81	0.96		10.94		55.29	
15			34.91	2.75		20.35		41.99	
16			36	4.29		16.36		43.34	
17	23.08	1.78	25.35			7.76	1.38	39.25	1.4
18				0.58	0.86	98.56			
19				0.41		0.14	99.45		
20			1.97		1.29	96.9			

small pond located near the Guadalquivir estuary banks (Fig. 1, 17).

4.2.2 Statistical analysis: grain size vs mineralogy

The correlation matrix defines two main mineralogical assemblages (Fig. 3a): (a) quartz, with feldspar as secondary mineral ($r=0.82$; $p<0.01$); (b) phyllosilicates-calcite, with plagioclase and, to a lesser extent, dolomite as secondary components. Anhydrite and halite show positive coefficients, sometimes significant with this second association.

Cluster analysis presents a strong similarity with that made for the grain size, with two well differentiated groups (Fig. 3b). Group M1 includes the sandy samples of T1 (except sample 4), whereas group M2 is composed of the silty-clayey samples of T2 and sample 4 (Figs. 2e, 3e). These groups are confirmed in the discriminant analysis (Fig. 3c), in which the function obtained groups 100% of the samples belonging to each group.

halite (23.08%) and the only appearance of gypsum (1.4%) in all the samples studied.

A comparison between both discriminant functions (e.g. DFT and DFM) permits to draw a clear statistical distinction ($r=0.94$; $p<0.01$) between two groups of samples according to the substrate (Fig. 4). Quartz (M1) is the main constituent of the sandy samples located both near the Guadalquivir mouth and the northwestern boundary between the dune systems and the adjacents marshes (T1), as well as in a silty-clayey pond located very close to this boundary (sample 4). The remaining silty-clayey samples (T2) are mainly composed of phyllosilicates, calcite and quartz (M2). Some isolated samples of these last samples may present significant values ($>3\%$) of some salts (anhydrite, dolomite, halite).

4.3 Physico-chemical factors

4.3.1 Spatial distribution

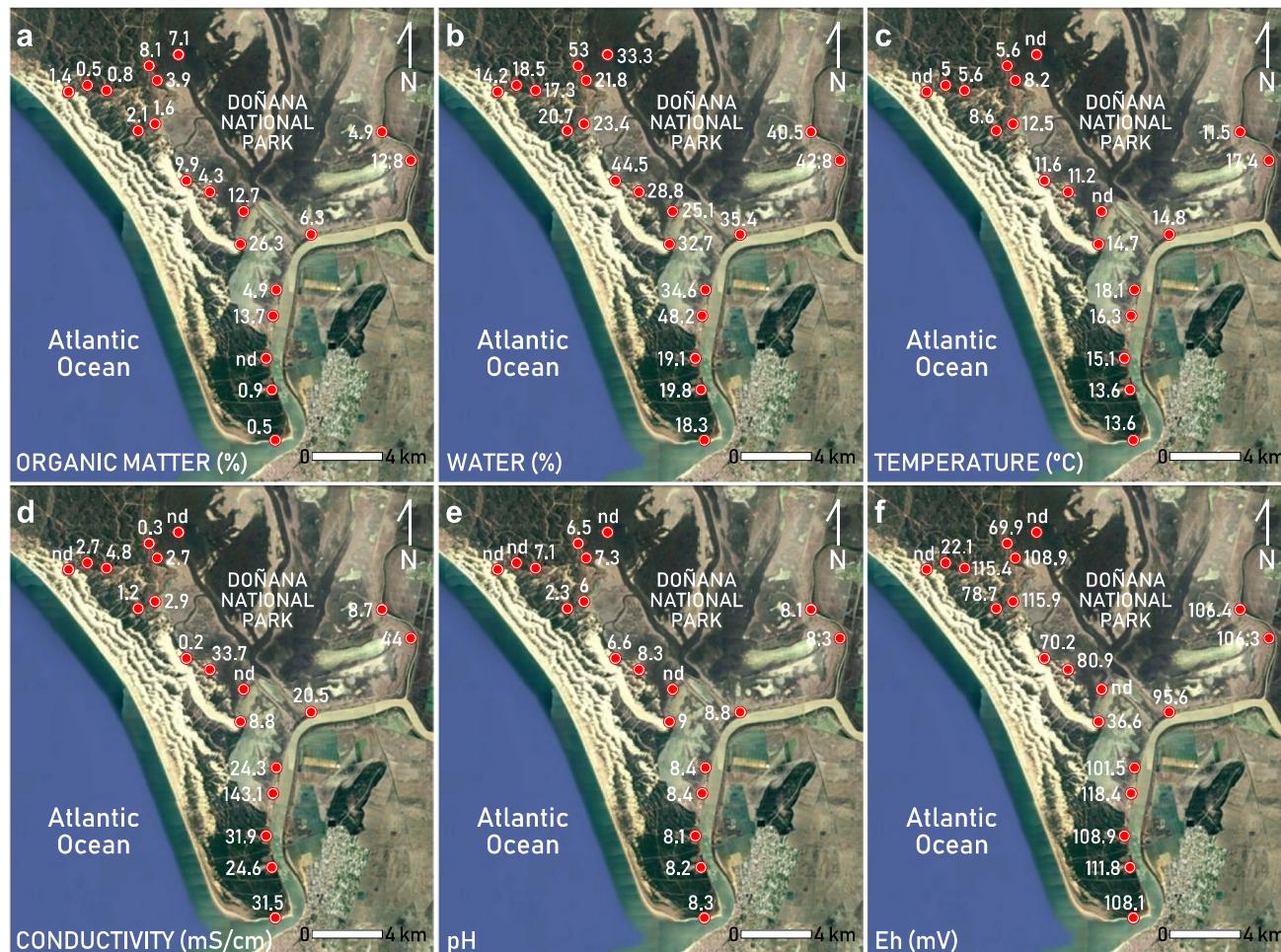


Fig. 5 Spatial distribution of physico-chemical parameters in the Doñana National Park

to that observed for water content (Fig. 5b: 14.2–48.2%), with the lowest values measured in the vicinity of the stabilized dunes and the mouth (14.2–20.7%) and the highest (>40%) in some ponds and partially filled channels (Fig. 1a: 9-13-17).

In November, temperature increases from the most protected areas located to the northwest of the park (Fig. 5c: 5–8.6 °C) towards the southern banks of the Guadalquivir estuary and its tributary channels (13.6–18.1 °C). Conductivity shows a similar transition (Fig. 5d), with very low values in the interior zones (2.7–3.7 mS/cm) and high values (>100 mS/cm) in the coastal areas.

Guadalquivir estuary have an alkaline range (pH 8.1–8.8). These last environments show high Eh values (95.6–118.4 Mv), whereas the most internal zones (Fig. 1a: samples 1–12) are characterized by a strong variability (Fig. 5f: 22.1–115.4 Mv).

4.3.2 Statistical analysis: texture vs physico-chemical variables

The first two axes of CCA explain more than 91% of the variance (Fig. 6a). The first axis (Fig. 6b) is mainly influenced

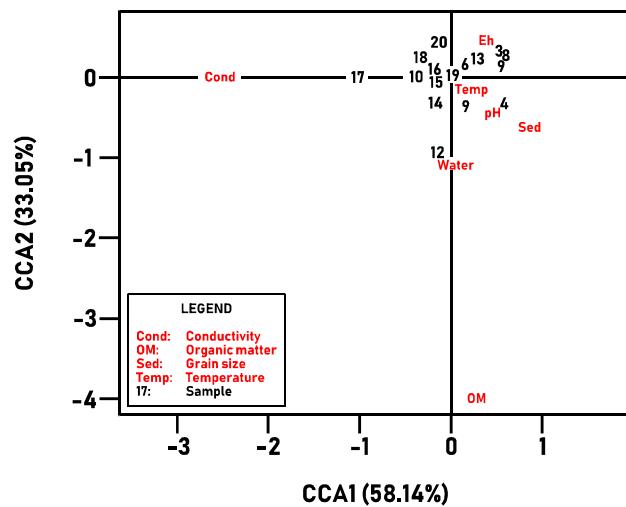


Fig. 6 Canonical correspondence analysis (CCA) between physico-chemical variables, grain size and samples

general overview, most of innermost samples have slightly positive CCA1 values, whereas these values are negative for the samples extracted near the Guadalquivir estuary margins.

4.4 Foraminifera

4.4.1 Abundance and diversity

Benthic foraminifera are only found in eight surface samples (Table 3). No foraminifera were collected in nine samples taken in the north-western sector of the park, within the dune systems or in the ecotone (Table 3: samples 1–9). These microorganisms were not present in three samples located near the margins of the Guadalquivir estuary (samples 17–19). They are moderately abundant on the innermost river banks and adjacent sedimentary environments and Punta Malandar beach (Table 3: > 27 individuals/gram of sand). Density decreases remarkably in some ponds located near the transition between the mobile dunes and marshes (3–7 individuals/gram of sand), as well as in the margins of some tributaries (< 9 individuals/gram of sand).

Thirty-four species belonging to twenty-five genera have been recognized, while nine forms were assigned to genera (Table 3). The main differences between the different environments are the presence of marine planktonic foraminifera in the Guadalquivir estuary and its tributaries, and the absence of benthic foraminifera in the dune systems and the ecotone.

located near the Guadalquivir estuary and its tributaries (1.53–2.02). A similar trend is detected in the Fisher's alpha index, ranging from 0.39 to 0.65 in the marshlands to values up to 5 in Punta Malandar beach (Fig. 1, 20). On the contrary, equitability increases in ponds, marshes and some partially filled channels, due to the dominance of two or three species (Table 3: samples 10–12).

Suborden Rotaliina is dominant in seven samples (54.54–100%), with *Ammonia tepida* (Fig. 7, 15–16: 0–64.1%), *Haynesina germanica* (Fig. 8, 8: 5.86–66.67%) and occasionally *Ammonia beccarii* (Fig. 7, 13–14: 0–33.48%) as main species. The two first species constitute the main foraminiferal assemblage of the Doñana National Park, while the last one is dominant in the more external beaches (Fig. 1, 20). Agglutinated forms (Fig. 7, 3: *Trochammina inflata*; Fig. 7, 4: *Entzia macrescens*) are only dominant in an isolated pond situated near a tributary channel (Fig. 1, 12). Porcellaneous species are mainly represented by several species of *Quinqueloculina* (Fig. 7, 10–12), only collected in some partially filled ebb-tide channels (samples 13–15) and near the mouth.

4.4.2 Taphonomy

In a general overview, the dominant dead species (*A. tepida*, *H. germanica*, *B. ordinaria*, *E. macrescens*, *T. inflata*) have a good state of preservation. They have different shell sizes in all of them without evidence of transport or dissolution and consequently they can be considered as in situ foraminifera. However, a partial break of the opening or the last chambers is frequent in Punta Malandar beach, affecting specimens of *A. beccarii* (Fig. 7, 13–14) or some miliolids (Fig. 7, 12). This break has been also observed in some specimens of *P. mediterranensis* collected in the margins of the Guadalquivir River (Fig. 8, 14; sample 16).

Marine planktonic foraminifera (Table 3: 0–6%) are mainly found on the banks of the Guadalquivir estuary, its tributaries, some partially filled channels and the beach located near the mouth. Some specimens of this group were also collected near a chenier (Fig. 1, 11).

4.4.3 Statistical analysis

Table 3 Abundance and diversity of dead benthic foraminifera (in %), including the different calculated indexes

Suborden	Species/samples	10	11	12	13	14	15	16	20
Textulariina	<i>Ammotium</i> sp.	0	0	0	0	0	0.73	0	0
	<i>Entzia macrescens</i>	0	0	0	0	20.51	0	0	0
	<i>Textularia</i> sp.	0	0	0	0	0	2.2	0	0
	<i>Trochammina inflata</i>	0	0	0	9.09	78.02	2.2	0	0
Lagenina	<i>Cornuloculina</i> sp.	0	0	0	6.06	0	0	0	0
	<i>Fissurina</i> sp.	0	0	0	12.12	0	0.73	1.19	0
	<i>Lagena</i> sp.	0	0	0	0	0	0	0	0.45
	<i>Stilostomella</i> sp.	0	0	0	0	0	0.73	0	0.45
Miliolina	<i>Cornuspira involvens</i>	0	0	0	0	0	0.37	0	0
	<i>Miliammina fusca</i>	0	0	0	0	0	6.23	1.19	0
	<i>Quinqueloculina laevigata</i>	0	0	0	9.09	0	0	0	0
	<i>Quinqueloculina seminula</i>	0	0	0	0	0	0	0	2.68
	<i>Quinqueloculina schlumbergeri</i>	0	0	0	9.09	0	2.2	4.76	4.46
Rotaliina	<i>Quinqueloculina</i> sp.	0	0	0	0	0	0.37	4.76	12.05
	<i>Ammonia beccarii</i>	0	0	0	0	0	0	0	33.48
	<i>Ammonia tepida</i>	50	50	0	21.21	0	64.1	23.81	25.89
	<i>Astigerinata mamilla</i>	0	0	0	3.03	0	0	2.38	0.45
	<i>Bolivina ordinaria</i>	25	0	0	6.06	0	5.49	1.19	0.45
	<i>Brizalina</i> sp.	0	0	0	0	0	2.2	1.19	0.89
	<i>Bulimina elongata</i>	0	0	0	0	0	0	0	0.89
	<i>Buliminella elegantissima</i>	0	0	0	0	0	0.37	0	0
	<i>Cassidulina laevigata</i>	0	0	0	0	0	0.37	0	0
	<i>Elphidium complanatum</i>	0	0	0	0	0	0	0	1.34
	<i>Elphidium crispum</i>	0	0	0	0	0	0	0	10
	<i>Elphidium cuvillieri</i>	0	0	0	0	0	0	1.19	0.89
	<i>Elphidium</i> sp.	0	0	33.33	0	0	1.83	0	0
	<i>Globocassidulina minutula</i>	0	0	0	0	0	0	1.19	0
	<i>Haynesina germanica</i>	25	50	66.67	24.24	1.47	5.86	53.57	6.25
	<i>Hopkinsina atlantica</i>	0	0	0	0	0	2.2	0	0
	<i>Nonion fabum</i>	0	0	0	0	0	0	1.19	0.45
	<i>Nonionella stella</i>	0	0	0	0	0	1.47	0	0
	<i>Porosononion granosum</i>	0	0	0	0	0	0	1.19	0.45
	<i>Planorbulina mediterranensis</i>	0	0	0	0	0	0	1.19	0.89
	<i>Rosalina bradyi</i>	0	0	0	0	0	0.37	0	3.12
Number of individuals picked		64	66	48	33	273	273	84	224
Number of benthic species		3	2	2	9	3	19	14	19
Individuals/gram of sand		6.4	6.6	4.8	3.3	27	88	8.4	52
P/B index (%)		0	0.25	0	6	0.01	2.25	5	0.6
Shannon index		1.04	0.69	0.64	2.02	0.58	1.53	1.53	2.01
Equitability		0.95	1	0.92	0.92	0.53	0.53	0.58	0.67
Fisher's α		0.65	0.29	0.42	4.07	0.47	4.65	4.8	5.21

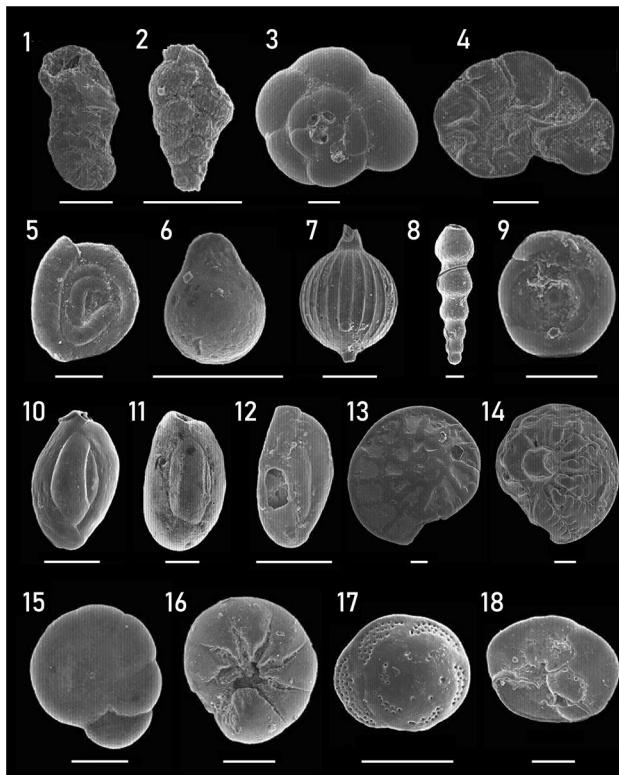


Fig. 7 Dead benthic foraminifera from the Doñana National Park (I). Scale bars: 100 µm. 1. *Ammotium* sp. 2. *Textularia* sp. Side view. 3. *Trochammina inflata* (Montagu). Dorsal side. 4. *Entzia macrescens* (Brady). Dorsal view. 5. *Corniloculina* sp. Dorsal side. 6. *Fissurina* sp. Side view. 7. *Lagena* sp. Side view. 8. *Stilostomella* sp. Side view. 9. *Cornuspira involvens* (Reuss). Side view. 10. *Quinqueloculina laevigata* d'Orbigny. Side view. 11. *Quinqueloculina seminula* (Linnaeus). Side view. 12. *Quinqueloculina schlumbergeri* (Wiesner). Side view. 13. *Ammonia beccarii* (Linnaeus). Dorsal side. 14. *Ammonia beccarii* (Linnaeus). Ventral side. 15. *Ammonia tepida* (Cushman). Dorsal side. 16. *Ammonia tepida* (Cushman). Ventral side. 17. *Astigerinata mamilla* (Williamson). Dorsal side. 18. *Astigerinata mamilla* (Williamson). Ventral side

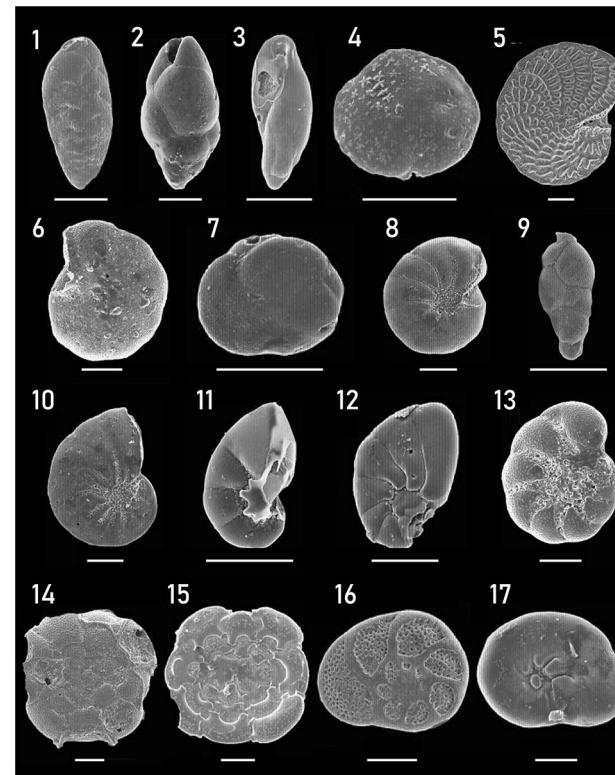


Fig. 8 Dead benthic foraminifera from the Doñana National Park (II). Scale bars: 100 µm. 1. *Bolivina ordinaria* Phleger & Parker. Side view. 2. *Bulimina elongata* d'Orbigny. Side view. 3. *Buliminella elegantissima* (d'Orbigny). Side view. 4. *Cassidulina laevigata* d'Orbigny. Dorsal side. 5. *Elphidium crispum* (Linnaeus). Side view. 6. *Elphidium cuvilli* Levy. Side view. 7. *Globocassidulina minuta* (Cushman). Ventral side. 8. *Haynesina germanica* (Ehrenberg). Side view. 9. *Hopkinsina atlantica* Cushman. Side view. 10. *Nonion fabum* (Fichtel & Moll). Side view. 11. *Nonionella stella* Cushman & Moyer. Dorsal view. 12. *Nonionella stella* Cushman & Moyer. Ventral view. 13. *Porosononion granosum* d'Orbigny. Side view. 14. *Planorbulina mediterranensis* d'Orbigny. Dorsal view. 15. *Planorbulina mediterranensis* d'Orbigny. Ventral view. 16. *Rosalina bradyi* Cushman. Dorsal view. 17. *Rosalina bradyi* Cushman. Ventral view

a dendrogram that allowed the differentiation of six clusters (Fig. 9b). Cluster I includes *T. inflata* and *E. macrescens* (Fig. 6a–d, 7) and is almost restricted to sample 12. Cluster II is the most abundant of the Doñana National Park and is composed of *H. germanica*, *A. tepida* and *B. ordinaria*. Cluster III (5 species) is abundant especially in sample 13

5 Discussion

In the Doñana National Park, the presence/absence and distribution of the dead benthic foraminifera species depend on different physico-chemical factors and, to a lesser extent,

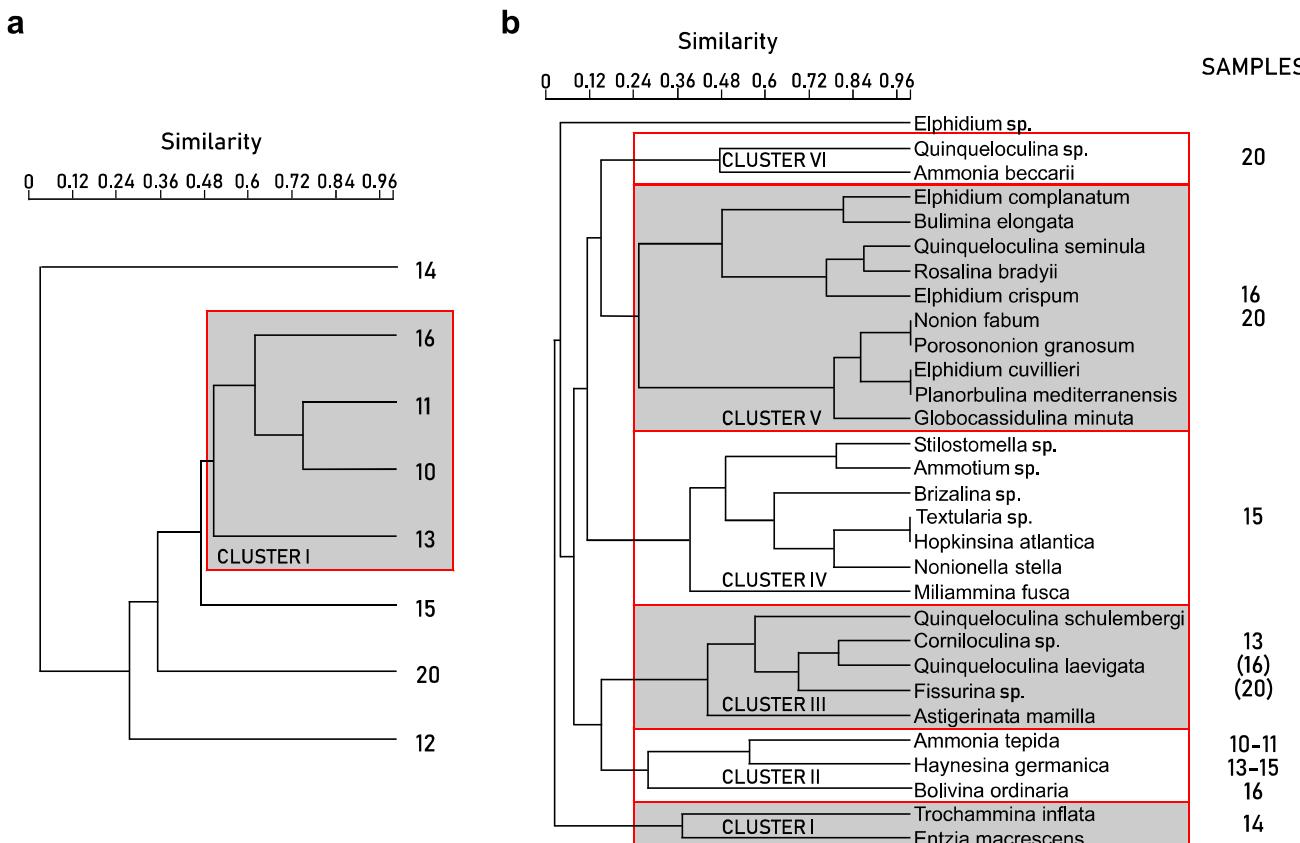


Fig. 9 Foraminifera: statistical analysis. **a** Q-mode cluster analysis; **b** R-mode cluster analysis

(groups T1 and M1), as well as in some silty-clayey ponds located in the nearby marshlands. In these environments, waters are ephemeral, with a hydroperiod (1–6 months) and extension (< 100 m² in most cases) that depend on the annual rainfall (Díaz et al. 2010). Water chemistry of these ponds is very similar to that of the other temporary ponds in the Mediterranean Region (Zacharias et al. 2007; Gómez Rodríguez 2009). These shallow water bodies (< 1 m depth) have a very low conductivity (< 5 mS/cm), but benthic foraminifera could live within this range (Ordiales et al. 2017). pH is slightly alkaline to acidic (2.3–7.3), an acidity that has been occasionally reported when rainfall is deposited on rich organic soils (Serrano et al. 2006). The prolonged subaerial exposure (> 6 months/year in many cases) and local acidity

species of very scarce assemblages (2–3 species/sample; < 7 individuals/gram) obtained in phyllosilicate-rich, silty-clayey sediments (groups T1 and M2). Conductivity varies remarkably between these different water bodies (8.8–33.7 mS/cm), with *A. tepida* as dominant species in temporary ponds with higher conductivities and *H. germanica* in the bubbling waterhole with higher organic matter content and lower Eh. These two species and some additional species of *Elphidium* are widely distributed in numerous marshes, pools, lagoons and estuaries of the Iberian Peninsula (Pascual et al. 2004, 2006; Blázquez and Usera 2010; Alday et al. 2013; Blázquez et al. 2018) and around the world (Debenay et al. 2000; Murray 2006; Calvo and Pratolongo 2009; Saad and Wade 2017) where conductivity, organic matter and Eh are the main controlling variables.

SAMPLES	SUBSTRATE		PHYSICO-CHEMISTRY		DEAD BENTHIC FORAMINIFERA
	TEXTURE	MINERAL.			
1	T1	M1	ORGANIC MATTER Mainly 0.5%-4% WATER Mainly 14%-23.5%	CONDUCTIVITY 0.2-3 mS/cm pH 6-7.3	NO FORAMINIFERA
2	T1	M1			
3	T1	M1			
6	T1	M1			
7	T1	M1			
8	T1	M1			
9	T1	M1			
18	T1	M1		CONDUCTIVITY 24.9-31.9 mS/cm pH 8.08-8.3	NO FORAMINIFERA
19	T1	M1			
20	T1	M1			A. beccarii + A. tepida + Miliol.
4	T1	M2	ORGANIC MATTER 4%->26% WATER 25%-53%	CONDUCTIVITY: 0.26 mS/cm pH: 6.48	NO FORAMINIFERA
5	T2	M2			
12	T2	M2		CONDUCTIVITY 20.5-33.3 mS/cm pH 8.29-9.04	Mainly A. tepida + H. germanica
13	T2	M2			
10	T2	M2			
11	T2	M2			
14	T2	M2			Some ponds
15	T2	M2			T. inflata + E. macrescens
16	T2	M2		CONDUCTIVITY: 143.1 mS/cm pH: 8.4	NO FORAMINIFERA
17	T2	M2			

Fig. 10 Synthetic scheme about relationships between substrate, mineralogy and dead benthic foraminifera in the Doñana National Park

ago and introduced marine species into the ancient lagoon that existed in this area at that time (Ruiz et al. 2010).

A similar substrate (T1-M1) characterizes the margin of an ebb-tide channel located to the northeast of the park (sample 13), but cluster II is accompanied by the miliolids that make up cluster III. Species of genus *Fissurina* are mainly found in marine environments at different depths (Figueroa et al. 2006; Milker and Schmiedl 2012), but some species can live in the outer part of some estuaries under fully marine conditions (conductivity: 60 mS/cm; Strotz 2003). Consequently, the presence of this small genus implies a transport in suspension as dead tests from the adjacent marine areas. Transport of tidal fluxes is also evident through the presence of reworked specimens of *Quinqueloculina laevigata* and *Quinqueloculina stelligera* (Figs. 7, 8, 9, 10) in sample 13, which is located in a fluvio-marine environment.

middle-low marshes, while *E. macrescens* increases in high marshes located up to the mean high water level (González-Regalado et al. 2001).

In the sedimentary environments located near the Guadalquivir estuary banks (samples 15–19), benthic foraminifera were only present in the river margins (sample 16) and some adjacent partially filled channels with tidal connections (sample 15). Both samples are dominated by cluster II and they have similar substrate (T1-M2) and physico-chemical parameters (Fig. 5: e.g. mixed marine-fluvial waters, low organic contents, alkaline pH) but *A. tepida* is dominant in more exposed areas (e.g. sample 15) and *H. germanica* prefers more quiet zones (e.g. sample 16). This difference has been also observed in dead foraminifera assemblages of some Mediterranean lagoons (Ruiz et al. 2012). High tides in the Guadalquivir estuary are associated with strong fluctuations in the water levels, which may explain the presence of marine species in the river margins (samples 15–19).

silty-clayey substrate (T2) that includes high percentages of halite and calcite, as well as a minor but significant presence of gypsum (1.4%). Their joint presence with anhydrite and dolomite (Table 2) implies very brief hydroperiods and an intense evaporation that dominate the hydrological budget (Isla, 2009). Samples 18 and 19 have similar substrate (T1-M1) to those collected in the northwestern part of the Doñana National Park. These samples have been extracted from small water bodies present within the dune systems that make up the Doñana spit, which are only flooded during the highest tides or by rainfall. Consequently, these three samples present too short hydroperiods and unfavourable conditions for the development of these microorganisms.

Punta Malandar beach (sample 20: T1-M1) shows a mixture of marine and estuarine species (cluster II and cluster VI), which is dominant at the mouth of the Guadalquivir (González-Regalado et al. 2019) and the adjacent inner shelf of the Cádiz Gulf (<50 m depth; Villanueva and Canudo 2008). Consequently, the dead foraminiferal assemblage is the result of transport from both marine and estuarine environments. This strong hydrodynamic gradient is reflected in the high number of miliolids with fractures or loss of the last chambers.

6 Conclusions

1. The statistical treatment (cluster analysis + discriminant analysis) of sediments collected in different environments of the Doñana National Park allows to distinguish two groups of samples: (a) fine to very fine sands (T1), the substrate of beaches and numerous temporary ponds widely distributed along the dune systems and spits; and (b) clayey silts (T2), which characterize the inner marshland and its ponds, channel margins and ebb-tide channels.
2. A similar analysis applied to the mineralogical content detects similar groups: a) M1 (quartz > 97%), which characterizes the sandy sediments (T1); and M2 (phyllosilicates + calcite + quartz), closely linked to clayey-silty sediments (T2).
3. The taphonomical analysis of the most abundant spe-

is the most abundant assemblage in the central part of the park (temporary ponds, ebb-tide channels, partially filled channels), while cluster IV (*T. inflata* + *E. macroscens*) is locally abundant in high marshes and cluster VI (*A. beccarii* + miliolids) on the outer beaches of the Guadalquivir River estuary. The remaining three clusters have poor representativity.

5. Benthic foraminifera are absent in numerous ponds with brief hydroperiod, low conductivity, acidic pH, as well as in hypersaline conditions with high evaporation rates.

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Systematic appendix

Ammonia beccarii (Linnaeus, 1758)

Figure 7, 13–14.

1758 *Nautilus beccarii* Linnaeus, p. 710, pl. 1, fig. 1 (in Ellis & Messina, 1940).

Ammonia tepida (Cushman, 1926)

Figure 7, 15–16

1926 *Rotalia beccarii* var. *tepida* Cushman, p. 79, pl. 1 (in Ellis & Messina, 1940).

Astigerinata mamilla (Williamson, 1858)

Figure 7, 17–18

1858 *Rotalina mamilla* Williamson, p. 54, pl. 4, figs. 109–111.

Bolivina ordinaria Phleger & Parker, 1952

Figure 8, 1

1952 *Bolivina ordinaria* Phleger & Parker, pl. 3, figs. 1–3.

1826 *Cassidulina laevigata* d'Orbigny, p. 282, pl. 15, figs. 4–5 (in Ellis & Messina, 1940).

Cornuspira involvens (Reuss, 1850)

Figure 7, 9.

1850 *Operculina involvens* Reuss, p. 370, pl. 46, fig. 30.

Elphidium complanatum (d'Orbigny, 1839)

1839 *Polystomella complanata* d'Orbigny, p. 129, pl. 2, figs. 35–36 (in Ellis & Messina, 1940).

Elphidium crispum (Linnaeus, 1758)

Figure 8, 5

1758 *Nautilus crispus* Linnaeus, p. 709, pl. 19, figs. a–d (in Ellis & Messina, 1940).

Elphidium cuvillieri Levy, 1966

Figure 8, 6

1966 *Elphidium cuvillieri* Levy, p. 5, pl. 1, fig. 6.

Entzia macrescens (Brady, 1870)

Figure 7, 4.

1870 *Trochammina inflata* var. *macrescens* Brady, p. 290.

Globocassidulina minuta (Cushman, 1933)

Figure 8, 7

1933 *Paracassidulina minuta* Cushman, p. 92, pl. 10, fig. 3.

Haynesina germanica (Ehrenberg, 1840)

Figure 8, 8

1840 *Nonionina germanica* Ehrenberg, p. 23, pl. 2, fig. 1 (in Ellis & Messina, 1940).

Hopkinsina atlántica Cushman, 1944

Figure 8, 9

1944 *Hopkinsina pacifica* var. *atlantica* Cushman, p. 30, pl. 4, fig. 1.

Miliammina fusca (Brady & Robertson, 1870)

1870 *Quinqueloculina fusca* Brady & Robertson, p. 286, pl. 11, fig. 2.

Nonion fabum (Fichtel & Moll, 1798)

Figure 8, 10

1798 *Nautilus faba* Fichtel & Moll, p. 103, pl. 19, figs. a–c.

Nonionella stella Cushman & Moyer, 1930

Figure 8, 11–12

1930 *Nonionella miocenica* var. *stella* Cushman & Moyer, p. 56, pl. 17, figs. 17 a–c.

Porosononion granosum (d'Orbigny, 1846)

Figure 8, 13

Figure 7, 10

1839 *Quinqueloculina laevigata* d'Orbigny, p. 134, pl. 4, Fig. 1.

Quinqueloculina seminula (Linnaeus, 1758)

Figure 7

1758 *Serpula seminulum* Linnaeus, p. 786.

Quinqueloculina schlumbergeri (Wiesner, 1923)

Figure 7, 12

1923 *Miliolina schlumbergeri* Wiesner, p. 49, pl. 6, fig. 73.

Rosalina bradyi (Cushman, 1915)

Figure 8, 16–17

1915 *Discorbis globularis* var. *bradyi* Cushman, p. 12, pl. 8, fig. 1 (in Ellis & Messina, 1940).

Trochammina inflata (Montagu, 1808)

Figure 7, 3.

1808 *Trochammina inflata* Montagu, p. 81, pl. 18, fig. 3.

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