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Benthic foraminifera as a proxy of the range of the tidal wave in the Oyambre Estuary (Cantabria, Spain)

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Abstract

Recent benthic foraminifers from the Oyambre estuary (north of Spain) have been studied in order to learn their biological response to drastic anthropic environmental changes that this estuary has undergone within the last centuries. Up to 41 species have been identified and 24 of them showed live specimens during the sampling period. The most abundant species are *Ammonia tepida*, *Balticammina pseudomacrescens*, *Criboelphidium williamsoni*, *Entzia macrescens*, *Haynesina germanica*, *Cibicides lobatulus*, *Miliammina fusca* and *Trochammina inflata*. The statistical analysis (cluster and correspondence analysis) has allowed the differentiation of four groups of samples that are characterized by three assemblages that define the following environments: sandy outer estuary with marine influence (*C. lobatulus*), mid and inner estuary that comprises an euryhaline subtidal environment with silty sediment (*A. tepida* and *H. germanica*), intertidal channels with the lowest salinity levels (*C. williamsoni*), and marshes (*B. pseudomacrescens*, *E. macrescens*, *M. fusca* and *T. inflata*). The great number of species with agglutinated shells reveals the ongoing draining in mud-flat areas, as well as the establishment of the vegetated high marsh, where the invasive exotic plant *Baccharis halimifolia* is removing the reed bed ecosystem and filling, blocking and reducing main and secondary channels. As a result, there is hardly any sandy low marsh left, which in other nearby estuaries of Cantabria is delimited by the species *M. fusca*. Thus, areas with tidal levels between MHWNT (Mean High Water Neap Tide) and MHW (Mean High Waters) are scarce. However, foraminifer species that live in the high marsh above MHW are dominant. *Entzia macrescens* and *T. inflata* mark the interval between MHW and MHWST (Mean High Water Spring Tide), while *B. pseudomacrescens* the one from MHSWST to the barren zone (vegetated high marshes, closest to land). A comparison between the biocoenosis and thanatocoenosis assemblages generally shows a good similarity (Sanders' index > 60%). The few samples with a low similarity reveal the effect of post-mortem processes, specially decantation, and, to a lesser extent, suspended transport, which once again points to the lack of hydrodynamism in the estuary. The percentage of exotic or allochthonous species that are deposited in this estuary is very low (the average ranges from 13.4% in the mouth to 0.7% in the inner area), which reveals that the Oyambre estuary has a mesotidal character in its mouth, while in the mid and inner area it can be considered a microtidal estuary. All these data expose that the works conducted in order to recover the Oyambre estuary between years 2009 and 2010 seem not to have been successful in restoring the marshes to their original hydrodynamic conditions.

Keywords	Benthic foraminifers; ecology; anthropogenic interventions; tidal levels; estuary; S Bay of Biscay
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**Benthic foraminifers as a proxy of the range of the tidal wave in the Oyambre
Estuary (Cantabria, Spain)**

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Abstract

Recent benthic foraminifers from the Oyambre estuary (north of Spain) have been studied in order to learn their biological response to drastic anthropic environmental changes that this estuary has undergone within the last centuries. Up to 41 species have been identified and 24 of them showed live specimens during the sampling period. The most abundant species are *Ammonia tepida*, *Balticammina pseudomacrescens*, *Criboelphidium williamsoni*, *Entzia macrescens*, *Haynesina germanica*, *Cibicidoides lobatulus*, *Miliammina fusca* and *Trochammina inflata*. The statistical analysis (cluster and correspondence analysis) has allowed the differentiation of four groups of samples that are characterized by three assemblages that define the following environments: sandy outer estuary with marine influence (*C. lobatulus*), mid and inner estuary that comprises an euryhaline subtidal environment with silty sediment (*A. tepida* and *H.*

germanica), intertidal channels with the lowest salinity levels (*C. williamsoni*), and marshes (*B. pseudomacrescens*, *E. macrescens*, *M. fusca* and *T. inflata*).

The great number of species with agglutinated shells reveals the ongoing draining in mud-flat areas, as well as the establishment of the vegetated high marsh, where the invasive exotic plant *Baccharis halimifolia* is removing the reed bed ecosystem and filling, blocking and reducing main and secondary channels. As a result, there is hardly any sandy low marsh left, which in other nearby estuaries of Cantabria is delimited by the species *M. fusca*. Thus, areas with tidal levels between MHWNT (Mean High Water Neap Tide) and MHW (Mean High Waters) are scarce. However, foraminifer species that live in the high marsh above MHW are dominant. *Entzia macrescens* and *T. inflata* mark the interval between MHW and MHWST (Mean High Water Spring Tide), while *B. pseudomacrescens* the one from MHSWST to the barren zone (vegetated high marshes, closest to land).

A comparison between the biocoenosis and thanatocoenosis assemblages generally shows a good similarity (Sanders' index > 60%). The few samples with a low similarity reveal the effect of post-mortem processes, specially decantation, and, to a lesser extent, suspended transport, which once again points to the lack of hydrodynamism in the estuary. The percentage of exotic or allochthonous species that are deposited in this estuary is very low (the average ranges from 13.4% in the mouth to 0.7% in the inner area), which reveals that the Oyambre estuary has a mesotidal character in its mouth, while in the mid and inner area it can be considered a microtidal estuary. All these data expose that the works conducted in order to recover the Oyambre estuary between years 2009 and 2010 seem not to have been successful in restoring the marshes to their original hydrodynamic conditions.

Keywords:

Benthic foraminifers, ecology, anthropogenic interventions, tidal levels, estuary, S Bay of Biscay

1. Introduction

Micropalaeontological analyses of recent materials are used on an everyday basis, due to the highly interesting data they provide for palaeoenvironmental reconstructions. The mentioned reconstructions are indeed based on data yielded by particular groups of microfossils. Foraminifers are one of the most commonly used groups in paleoecology due to their sensitiveness towards environmental changes. They also have a wide geographical distribution as they live in all the marine and transitional natural environments (Murray, 1991). Moreover, the understanding of biotic and ecological characteristics of the different species enables to infer the behaviour of the main environmental parameters that ruled past environments.

The marshes are usually the areas where the most important sedimentation processes that occur within the estuarine systems, so that they built up a record of the environmental changes. Foraminifers from these marshes have proved to be a key proxy in studies of sea level changes (Haslett et al., 2001; Horton and Edwards, 2000, 2006; Gehrels et al., 2001; Pascual and Rodríguez-Lázaro, 2006).

Benthic foraminifers can also be used as biological proxies of the reach of the tidal wave in estuaries. This is the cause of the distribution of some species along the estuaries according to the tide level (Scott and Medioli, 1986; Scott and Leckie, 1990; Boomer, 1998; Haslett et al., 1997; Gehrels and Van de Plassche, 1999; Hippensteel et al., 2000; Hayward et al., 2004; Pascual and Rodríguez-Lázaro, 2006; Fatela et al., 2009; Rodríguez-Lázaro et al., 2013). The shell preservation within the sediment allows

for their use as proxies of the reach of the recent tidal processes. Besides, they enable the identification of those sectors that, under natural conditions, should be affected by the tidal wave.

The coastal population has built up walls and dams in the estuary to reduce the frequency of tidal floods (Marquínez et al., 2003). These kinds of interventions result in important changes in the tidal dynamic. The use of the foraminifers helps us to understand the reach of the tidal wave in the past, before the beginning of the anthropic activities. Tidal range and fluvial discharge undergo intense variations in scale through time and, thus, it is difficult to define its reach. However, as foraminifers are part of the sediments that are preserved over long periods, they reflect the processes that have taken place in the recent past of the Oyambre estuary.

In the last 100 years, the anthropogenic interventions that have been conducted in this estuary, in particular several dams, have affected the tidal wave, due to a modification in the natural hydrodynamics, which has reduced the potential flood zone. This fact has caused the blooming of invading species, specially *Baccharis halimifolia*. In 2010, an environmental recovery project of the estuary was implemented. Therefore, several dams and the above mentioned plant were removed, in order to recover the marsh environments.

In order to know the environmental conditions in this estuary, four years after the recovery works, benthic foraminifers from the sediment have been studied. Specifically, the distribution of benthic foraminifers has been analysed for the first time, data about the biodiversity of this Protected Natural Park have been provided and the influence of the physical changes in the microfauna in this Cantabrian coastal area has been interpreted.

2. Study area

The Oyambre estuary is located in the southern Bay of Biscay, west of Santander, in the north of Spain. The Oyambre estuary has two valleys. The eastern branch is called La Rabia estuary and has a north-south direction. The westernmost branch is called El Capitán estuary and flows in an east-west direction (Fig. 1). Both branches converge in the Oyambre Beach, also called Bay of Jerra, that is 2.5 km long and extends as a sand bar towards the mouth of the estuary (Fig. 1). Over this sand bar, there is a 1 km long and 100 m wide dune field that consists of vegetated dunes.

This area is just a fragment of the larger protected “Parque Natural de Oyambre”, which in addition to the estuary, also includes the beaches, dunes and cliffs, with a total surface of 5758 ha. All the territory within this Natural Park conforms a smooth topography with topographic heights no higher than 300 m.

The mouth of La Rabia, where the marshes are settled, is located on the Early Cretaceous Weald facies, that are made up of silty clay, silt and micaceous sand.

Towards the north, there are Aptian (limestones and calcarenites) and Albian (silty lutites and sandstones) outcrops, which are also present southwest of El Capitán estuary. South of this estuary, Late Cretaceous (Cenomanian) calcarenites, siltstone and sandstones can be found. Finally, towards the northwest (Oyambre cape), outcrops Cenozoic (Oligocene) red clays, reef limestones, sandstones and conglomerates. Both of the estuaries, as well as the marshes, are covered by fluvial-marine Holocene sediments (Ramírez del Pozo et al., 1976).

The Oyambre estuary is, thus, the merging of two sediment-filled valleys, where one of them is tributary to the other (Flor-Blanco and Flor, 2012). It is a mesotidal estuary, vertically homogeneous and with semi-diurnal tidal cycle (Marquínez et al., 2003). It covers an area of 100.2 ha and a perimeter of 13.6 km, with an intertidal area of the

86% of its total surface. El Capitán river flows into El Capitán estuary, with an average flow of 0.2 m³/s, while the Turbio river flows into La Rabia or Zapedo estuary with an average flow of 0.6 m³/s (Fundación Leonardo Torres Quevedo convivelife.es/wp-content/uploads/2017/11/Annex_IIA2_Final1.pdf).

In average spring tide conditions (4 metres), the tidal prism of the estuary, that is, the tidal water input into the estuary, is approximately 36 m³/s. As can be seen, thus, the average flows of the two rivers are virtually insignificant in comparison with the tidal flow. On the other hand, anthropic interventions conducted in the last 100 years in the Oyambre estuary, and, in particular, the presence of several dams, have had an influence in the propagation of the tidal wave. The tidal prism has been significantly reduced.

Thus, in El Capitán estuary the tidal range is about 1.5 metres and in La Rabia estuary is 1 metre. This reduction in the tidal range has caused the expansion of the invading plant *Baccharis halimifolia*.

Works conducted in the Oyambre estuary have revealed that *B. halimifolia* grows in areas with a flooding period no longer than the 26% of the year, in salinities lower than 25 ‰ and water velocity and flow lower than 0.1 m/s and 0.85 m³/s respectively (Frau et al., 2014). The potential habitat model showed that this plant does not appear homogeneously throughout the estuary. Instead it prefers areas where the average values of the hydrodynamic variables are lower than the average values in the whole estuary. It is very probable that the anthropic changes that this estuary has undergone have caused the invasion of the exotic plant *B. halimifolia* covering approximately 35% of the Oyambre estuary in 2009. In some areas in the head of La Rabia estuary it covers up to the 80% of the surface. The two dams built in the XX century and removed in the years 2009-2010 (Fig. 1) seem to have been the cause of this invasion, as they prevented the normal water input during the high tide, which, in turn, reduced the salinity, increased

the sedimentation rate and, finally, filling up the estuary. In those same years, the plant was mechanically removed, but 4 years later of has recolonized wide areas of the estuary.

3. Materials and methods

3.1. Field

Thirty- two surface samples collected in the Oyambre estuary (Figs. 1 and 2), with a Boltovskoy scraper (Boltovskoy, 1965) in June 2014 during the low tide, have been analysed. The samples were dyed “in situ” with Rose Bengal tint in proportions of 1 litre of methanol per 1 gram of dye (Walton, 1952). Four of these samples have not yielded any microfauna (LARA-8, LARA-12, LARA-15 and LARA-B) and therefore the foraminifers of the remaining 28 samples have been studied.

Several physico-chemical parameters of the water have also been analysed at the time of sampling, such as temperature, conductivity and pH, at two opposite points: one in the head and the other in the mouth of each branch of the estuary. In order to conduct these analyses, the following equipment has been used: Orion 810 Meter (water dissolved oxygen and temperature), a Hanna HI 9033 Meter (conductivity), and a Hanna HI 9025 pH- Meter.

3.2. Laboratory

Rose Bengal allows to differentiate between live (tinted protoplasm) and dead (untinted shells) individuals (see Murray, 1991). As the agglutinated shells are difficult to dye due to the thickness of their shells or because of its protoplasm taking only up to the 10% of their volume (Altenbach, 1987), their preservation and brightness after the dyeing has also been carefully observed. Once washed, sieved and dried, the fraction bigger than 63 μm was analysed and up to 300 foraminifers were extracted, when possible, which is a

statistically representative number (Phleger, 1960). The samples with few individuals were concentrated by flotation using trichloroethylene.

In seven samples (LARA-9, LARA-10, LARA-11, LARA-14, LARA-18, LARA-20 and LARA-23) this number was not reached, despite all the sediment being analyzed. In these samples, the total amount of individuals has been studied.

3.3. *Taxonomy*

From a micropalaeontological point of view, a taxonomic analysis has been made according to the normative of Loeblich and Tappan (1988), updated in *WoRMS Editorial Board* (2018). The proportion among the different types of shells has been calculated: agglutinated, porcelanaceous and hyaline. The species have been classified according to their abundance as follows: main or dominant (> 10%), secondary (5-10%) and other (<5%). Several richness and diversity indexes have been obtained: nF (number of benthic foraminifers per gram of sediment), S (number of species per sample) and Fisher's α (the proportion between the number of individuals and species, according to Fisher et al., 1943). This last index can only be calculated if the samples yielded more than 100 individuals (Murray, 1991).

3.4. *Statistical analysis*

Cluster analysis has been conducted in order to know the live species assemblages and their distribution in the studied samples by means of the PAST program (Hammer et al., 2001; version 1.37, 2005). The samples LARA-9, LARA-10, LARA-11, LARA-14, LARA-18 and LARA-22 (Fig. 1) have not been taken into account due to the scarcity retrieved of individuals (<100). Therefore, just 22 samples have been included in the statistical analysis. Only species that represent >1% of the total in at least one of these 22 samples have been used. The UPGMA (Unweighted Pair-Group Method using arithmetic Averages) method, with the correlation index, has been used to analyse both

Q-type (samples) and R-type (species) clusters. In order to validate their statistical significance, several consistency, congruency and robustness tests have been conducted with the PAST program (e.g. using presence/absence data or eliminating some species or samples). Finally, to study the relationship between live species and the samples, a Detrended Correspondence Analysis (DCA) has been conducted, in which the two first axis represent the greater percentage of variance and could be interpreted as ecological variables that show the variation trend along the diagram.

4. Results

Up to 7177 foraminifers belonging to 41 species (Table 1) have been retrieved from the sediments of the Oyambre estuary. Of that number, 5550 were alive during sampling, while 1627 belong to the thanatocoenosis.

4.1. Physico-chemical parameters

The water in El Capitán branch of the Oyambre estuary showed at the moment of sampling the following range of values from the head to the mouth: temperature = 15.2-22.5°C; salinity = 2.6-10.8 ‰; dissolved oxygen = 0.11-10.17 mg/L; pH = 7.4-7.69. In the La Rabia branch the water measurements were as follows: temperature = 14-17.5°C; salinity = 0.45-20.7 ‰; dissolved oxygen = 0.16-12.33 mg/L; pH = 6.45-7.6.

4.2. Live foraminifers in the Oyambre estuary

The 5550 live benthic foraminifers belong to 24 species (Table 1). The main or dominant species are (Plate I): *Trochammina inflata* (Montagu) that accounts for the 27% of the total retrieved individuals, *Entzia macrescens* (Brady) that comprises the 22%, *Cibicides williamsoni* (Haynes) with a 15% and *Haynesina germanica* (Ehrenberg) with a total amount of 13%. The secondary species are *Balticammina pseudomacrescens* Brönniman, Lutzle and Whittaker and *Cibicides lobatulus*

(Walker and Jacob) that represent the 7% of the sample each. Finally, *Ammonia tepida* (Cushman) with a 4% and *Miliammina fusca* (Brady) with a 2% are also abundant.

4.3. Statistical analysis with samples and live species

The multivariable statistical analysis (cluster Q-type) comprises the samples into 4 groups (Fig. 3):

Group 1

It consists of three samples in which *C. lobatulus* is the most abundant species (Table 1, Fig. 3) and benthic foraminifers with hyaline shells are dominant (91-99.5%).

In the samples LARA-20 and LARA-23 the main species is *C. lobatulus* (76-77%) and the sediment that composes them is medium sand. They were taken at the mouth of the estuary (Fig. 1), where the highest diversity of this study is recorded ($S = 11-13$; $\alpha = 2.77-3.21$), in spite of the low richness of the samples ($nF = 2-4$).

The LARA-21 sample shows a dominant assemblage that consists of *C. lobatulus*, *C. williamsoni* and *H. germanica*. The sample is composed of silty sand and it was retrieved next to the channel of the mouth of El Capitán estuary. Its richness index is higher ($nF = 137$) and the diversity one is lower ($S = 9$; $\alpha = 1.91$).

Group 2

It includes 13 samples and it is characterized by an assemblage that consists of *T. inflata* and *E. macrescens*. In this group, agglutinated shells are dominant (55-100%) (Table 1).

It has been subdivided into three subgroups: 2A, 2B and 2C (Fig. 3).

Subgroup 2A. The samples it comprises (LARA-4, CAP-6, LARA-2 and LARA-17) consist of silty-sandy sediment and were retrieved in areas of the marsh vegetated by reeds (*Phragmites australis* (Cav.) Trin. ex Steud. and *Juncus maritimus* Lam) and some individuals of the exotic *Baccharis halimifolia* Linneo. The dominant benthic foraminifer species in this subgroup is *T. inflata* (37-94%). The richness of the samples

is low-medium ($nF = 17-388$) and the diversity low ($S = 2-9$; $\alpha = 0.3 - 1.91$) (Table 1).

The sample LARA-19, which was retrieved in the area of the marsh colonized by *Halimione portulacoides* (L. Aellen) and closest to the channel, also contains abundant individuals of *C. williamsoni* and *H. germanica*.

Subgroup 2B. The samples LARA-5 and CAP-1 consist mainly of silt and were retrieved in areas colonized by *B. halimifolia*. The dominant species is *E. macrescens*, in addition to *B. pseudomacrescens*. The richness and diversity indexes are as follows: $nF = 347-1267$; $S = 4-8$; $\alpha = 0.65-1.85$.

Subgroup 2C. It consists of silty-sandy samples (LARA-6, CAP-5, CAP-2, CAP-7, LARA-A and CAP-3) that were retrieved in areas of the marsh with mixed vegetation dominated by *J. maritimus* and *P. australis*, as well as areas where *B. halimifolia* is present. The sample CAP-3 was obtained in an area with annual *Salicornia* vegetation. The dominant assemblage in the subgroup 2C consists of *E. macrescens* and *T. inflata* in a similar proportion and the indexes show the following values: $nF = 28-8331$; $S = 3-9$; $\alpha = 0.53-1.76$.

Group 3

The samples LARA-7 and LARA-13 fill into this group (Fig. 3). They are made up of silty clayey sediment vegetated by small sized *Juncus*. They were obtained from the channels of the head of La Rabia estuary, where surface runoff occurs (Fig. 1).

This group is characterized by the abundance of *C. williamsoni* (65-94%) and the dominance of hyaline shells (67-94%). The richness index is the highest in the whole estuary ($nF = 489-15450$), though the diversity is very low ($S = 4-5$; $\alpha = 0.65-0.86$) (Table 1).

Group 4

It contains 4 samples (Fig. 3) and is characterized by the presence of *H. germanica* as dominant species, in addition to *A. tepida* and *C. williamsoni*.

The samples LARA-16 and LARA-1 were retrieved from the main channel and are made up of silty clay. Hyaline shells are dominant in these samples (93.5-96%).

However, in the samples LARA-3 and CAP-4, which were taken at the vegetated edges of the main channel, agglutinated shells are also abundant (24-56.5%) (Table 1).

The richness and diversity indexes show the following values: $nF = 7-674$; $S = 5-7$; $\alpha = 0.88-1.77$.

4.4. Dead foraminifers in the Oyambre estuary

Up to 1627 dead foraminifers have been retrieved from the Oyambre estuary, belonging to 36 species, of which 17 consisted exclusively of dead individuals (Table 1). The most abundant species in the thanatocoenosis are the same as in the biocoenosis (Plate I).

Thus, *T. inflata* (39% of the retrieved individuals), *C. lobatulus* (17%) and *E. macrescens* (13%) are the main or dominant species. *Haynesina germanica* is a secondary species (8%), while *A. tepida* (4%), *B. pseudomacrescens* (4%), *M. fusca* (3%) and *C. williamsoni* (2%) are other well represented species. All these species constitute 90% of the dead individuals.

5. Discussion

5.1. Foraminifers and environment: ecology

The most abundant foraminifer species from the Oyambre estuary have already been described as dominant in other estuaries from the Northern Atlantic (Murray, 1991, 2006; Alve and Murray, 2001; Diz and Francés, 2008). In the Spanish coast of the south of the Bay of Biscay, *A. tepida*, *C. lobatulus*, *C. williamsoni*, *E. macrescens*, *H. germanica*, *M. fusca* and *T. inflata* have been identified in the Gernika and Bilbao

estuaries in the Basque Country (Pascual, 1992; Pascual and Rodríguez-Lázaro, 2006), as well as in the estuaries of Cantabria: Santoña (Cearreta, 1988), San Vicente de la Barquera (Cearreta, 1989), Noja (Pascual et al., 2004, 2006) and Tina Mayor and Tina Menor (Rodríguez-Lázaro et al., 2013).

In those works, the distribution of the benthic foraminifer assemblages along the different ecological niches of the estuaries was revealed, from head to mouth. In the head, *E. macrescens* and *T. inflata* live in the vegetated mid and high marshes of the inner estuary, while *M. fusca* lives in the scarcely vegetated sandy low marshes.

Subtidal or intertidal euryhaline areas with silty sediments and mudflats are inhabited by *A. tepida* and *H. germanica*, as well as *C. williamsoni*, which can also be found in vegetated low marshes. Finally, *C. lobatulus* is a cosmopolitan marine species that is abundant in sands in the mouth of the estuaries (Table 2). However, *B.*

pseudomacrescens was first cited in the southern Bay of Biscay in the Oyambre estuary (Pascual and Martínez-García, 2014). It is an agglutinated species that lives with *E. macrescens* and was usually classified as this one until the work of Gehrels and Van De Plassche (1999), when it was used as a proxy of the tide level in marshes.

In marginal marine environments, the distribution on benthic foraminifers cannot be simply described in oxygen and nutrient availability parameters, as it happens in other oceanic areas (Van der Zwaan et al., 1999; Armynot du Châtelet et al., 2009), because other factors, such as hydrodynamism or the grain size of the sediment, could have a crucial role (Murray, 2001). These two factors could be invoked to explain the scarcity of foraminifers in samples LARA-9, LARA-10, LARA-11, LARA-14, LARA-18, LARA-20 and LARA-23.

The cluster R-type statistical analysis of the distribution of benthic foraminifer species in the Oyambre estuary shows three assemblages according to their ecological

environments (Fig. 4). The assemblage 1 consists of four species: *Triloculina oblonga* (Montagu), *A. tepida*, *H. germanica* and *C. williamsoni*, that are statically separated from the rest. These species are typical in the euryhaline environments of mudflats related with the main channel and the secondary tidal channels (Murray, 2006). The assemblage 2 contains seven species, such as the dominant *C. lobatulus*. This assemblage includes species that inhabit environments ranging from the outer estuary to the shallow continental shelf (Murray, 2006). Finally, the assemblage 3 is composed of five species, including *B. pseudomacrescens*, *M. fusca*, *E. macrescens* and *T. inflata*. These species live in different environments, from the low marsh to the high marsh – barren zone (Murray, 2006).

Not only the species delimit environments and provide data about the main ecosystems in the estuary. For example, the proportion of the different shells on benthic foraminifers varies in each area of the estuary (Murray, 1991). Thus, agglutinated foraminifers are abundant in the vegetated marsh, while the hyaline ones are found in subtidal areas and the porcelanaceous ones in the mouth of the estuary. On the other hand, the specific diversity index Fisher's α allows to distinguish between estuarine environments with low diversity due to the environmental stress ($\alpha < 1-3$) and the marine environments ($\alpha > 3$) (Murray, 1991).

All the ecological data yielded by benthic foraminifers could help us to explain the separation of the samples of the Oyambre estuary in four groups according to the cluster Q-type statistical analysis (Fig. 3). Group 1 contains the samples of the outer estuary with marine influence. Group 2 represents the low and mid marsh environments. Group 3 belongs to the secondary channels of the vegetated low marshes with fresh water input and, therefore, very low salinity. Finally, Group 4 comprises euryhaline environments of the inner and mid estuary both from the main channel and the mudflats (Table 2).

The differences among subgroups point to differences in environmental parameters such as: sediment type, distance to the main channel, height in relation to this channel or vegetation type.

With the aim of studying the relationship between benthic foraminifers and the distribution of the samples within the estuary, a correspondence analysis (DCA) have been conducted with the live assemblages (biocoenosis) as variables (Fig. 5). The factorial plane of axis 1 and 2 represent the 66.5% of the total variance. In the graphic representation of these two first axes the distribution of the 4 Groups of samples that relates to the results obtained with the cluster Q-type analysis is shown, and includes the species assemblages identified with the cluster R-type analysis (Fig. 4). Moreover, these groups of species and samples are separated along the axis 1 according to an increase in salinity from the left side of the diagram (lower values of axis 1) towards the right side (higher values of axis 1) (Fig. 5).

Thus, Group 1 (Fig. 5) forms the assemblage of the outer estuary, as it contains *C. lobatulus* as the dominant species, which is a marine species (Murray, 1991, 2006). However, the sample LARA-21, which is separated from the rest, also contains abundant euryhaline individuals from both mudflats and vegetated low marshes (26 and 20% respectively) (Table 3). Therefore, this sample marks the ecological limit between outer and mid estuary (Figs. 1 and 5).

Within the Group 2 (Figs. 3 and 5), which represents the marsh environments, the Subgroup 2A indicates vegetated mid-high marsh environments (Table 2), as *T. inflata*, which inhabits mid-high marshes (Scott et al., 2001) and feeds preferentially on organic matter from algae or vascular plants (Armynot du Châtelet et al., 2009), is dominant (Table 3). Besides, this species lives preferably on silty-sandy sediment (Nixon et al., 2009), a factor that seems to control its distribution along the Oyambre estuary, where

the Subgroup 2A comprises samples with the above mentioned sediment. The sample LARA-19 is in turn separated from the rest due to the abundant presence of the euryhaline species *C. williamsoni* (12%) and *H. germanica* (19%) in addition to *T. inflata* (37%) (Table 3), which points to the proximity of the channel in the marsh area. The Subgroup 2B (LARA-5 and CAP-1) points out to the highest environments of the vegetated marsh, as *E. macrescens* (50-56% respectively) is dominant with abundant individuals of *B. pseudomacrescens* (Table 3). This last species inhabits the highest zone of the continental marshes (Alve and Murray, 1999) (Table 2) and in Oyambre appears in areas colonized by *B. halimifolia*. *T. inflata* and *E. macrescens* in the Subgroup 2C (Fig. 3) are codominant and represent the assemblage of the vegetated high marsh that lives on sandy silts, far from the main channel. The samples of this subgroup are surrounded by *J. maritimus* (samples LARA-6 and CAP-5), *P. australis* (samples CAP-7 and LARA-A), vegetation patches of *B. halimifolia* (sample CAP-2) and remains of dead trees that belonged to an old flooded eucalyptus plantation and the annual *Salicornia* vegetation (sample CAP-3) (Table 3, Fig. 1).

Group 3 comprises the most euryhaline environments of the inner estuary. The dominant species *C. williamsoni* (Table 3) lives on silty channel beds with salinity ranging from 1 to 32 ‰ (Pascual, 1992; Pascual and Rodríguez-Lázaro, 2006; Rodríguez-Lázaro et al, 2013), as well as vegetated low marshes in areas with low drainage (Table 2, Figs. 3, 5). All these characteristics can be observed in Oyambre, where the salinity measured in the LARA-7 and LARA-13 sampling points showed values of 0.45 ‰.

Group 4 includes the euryhaline environments of the inner and mid estuary with *A. tepida* and *H. germanica*, species that inhabit the mudflats and the channels (Pascual, 1992; Pascual and Rodríguez-Lázaro, 2006; Armynot de Châtelet et al., 2018) (Table

2). The salinity is the parameter that controls their distribution and abundance (Horton and Murray 2007). In the samples LARA-16 and LARA-1, *A. tepida*, *H. germanica* and other hyaline shells (Table 3) are dominant, which points to a silty subtidal environment that relates to the main channel (Figs. 3 and 5). Nevertheless, the descent in the number of euryhaline individuals from the mudflats (40-60%) and the increase of the ones from vegetated mid-high marshes in the samples LARA-3 and CAP-4 could indicate a higher section of the channel in the marsh area.

5.2. *Balticammina pseudomacrescens* (benthic foraminifer) and its relationship with *Baccharis halimifolia* (plant)

Baccharis halimifolia Linneo is a shrub of the family of Asteraceae, also known as groundsel bush. It is a dioecious plant, that is, the male and female flowers appear in separate and distinct individuals, and they can reach up to 4 metres high. The vegetative activity period of *B. halimifolia* occurs mainly during spring and summer and from August or September onwards they start to lose their leaves, more noticeable in halophilic environments (Caño et al., 2013b). Although *B. halimifolia* reproduces sexually, it possesses a high capacity to resprout, which can allow the plant to regrowth from fragments or uprooted or chopped down individuals. *B. halimifolia* is native from the eastern coast of America, where it spreads from Canada to Mexico and the Caribbean (Campos et al., 2014). *B. halimifolia* was described in continental Europe in 1783 from a specimen cultivated in the Paris Botanical Garden (Caño et al., 2013a). In 1906, it was first cited as wild in the south of France and in 1941 in the Spanish coast of the south of the Bay of Biscay, in Lekeitio (Allorge, 1941). In 1953, its presence was cited in Cantabria for the first time (Guinea, 1953). Nowadays, *B. halimifolia* invades most of the estuaries of the Cantabrian coast, where it mostly develops in plants communities with middle salinity and flooding levels in estuaries, limit areas between

dune and marsh, postdune wet depressions and truly halophilic communities of estuaries (Campos et al., 2014). Besides, the lack of bushy competitors in estuaries favours the successful invasion of Sites of Community Importance (European Union) as subhalophilic reed beds of *J. maritimus* or subhalophilic reed beds of *P. australis*, among others. As a result, *B. halimifolia* is considered one of the 20 most dangerous exotic invading plants for other plants and animals in Spain (GEIB, 2006).

When studying the distribution of the benthic foraminifer species *B. pseudomacrescens*, it can be noted that it preferentially inhabits the areas colonized by *B. halimifolia* (Table 3). This fact had already been observed in other marshes such as the ones in Louisiana (Yeager et al., 2012). *B. pseudomacrescens* is an agglutinated foraminifer that was first described in the south of the Bay of Biscay in the Oyambre estuary (Pascual and Martínez-García, 2014). It was described by Brönnimann et al. (1989) as an endemic Baltic species, although it has later been recorded in marshes all around the world (Murray, 2006). It is a cosmopolitan species that lives restricted to rarely covered marshes (Murray and Alve, 1999), that is, the highest and closest to land marshes (Murray, 2006). It appears in areas within the marsh with low salinity levels (<13.8 ‰) and it can adapt to even lower levels, down to 3 ‰ (Riveiros et al., 2007). It has been cited living on algae filament (Edwards et al., 2004), strongly clinging to the vegetation by its umbilical side (Murray, 2006), as well as in wet and rotten dead leaves in the highest limit of the tidal range (Alve and Murray, 1999).

A large number of live *B. pseudomacrescens* individuals have been found in the areas covered by the exotic *B. halimifolia* plant, in contrast with the scarce or null presence of dead foraminifers. This fact can be clearly seen in the samples LARA-3 (L:82; D:8), CAP-2 (L:27; D:1) or CAP-1 (L:91; D:0) (Table 1). It is likely that the season during which the samples were retrieved is the cause of these results. Thus, June is the month

of the blossoming of *B. halimifolia* and the reproduction of many foraminifer species. Thus, in nearby estuaries it has been recorded a maximum in the juvenile foraminifers towards the end of spring and, in particular, for *Ammonia beccarii* and *H. germanica* in works conducted in the Santoña estuary (Cearreta, 1988) or for *Haynesina depressula* in the estuary of San Vicente de la Barquera (Cearreta, 1989).

In conclusion, the presence of *B. pseudomacrescens* in the same ecological niches as the exotic *B. halimifolia* plant would further confirm the hydrodynamic data provided by this plant. It should be noted that *B. halimifolia* fills in the niches of *Juncus* and *Phragmites*, that is, the highest marshes areas that are only covered during high tides with 80–90 coefficients (Cartografiado bionómico del Litoral de Cantabria http://dmacantabria.cantabria.es/informacion/Documentos/Cartografiado_bionomico_AguasTransicion_Costeras.pdf). Therefore, and despite the removal of the dams in the two branches of the estuary (Fig. 1), marine water still finds it difficult to flow into the estuary, as the presence of species that point to the limited reach of the tidal wave reveals.

5.3. Foraminifers and hydrodynamics

Since the first works conducted in the Atlantic about the differences between live and dead assemblages, the small percentage of biocoenosis that was usually obtained, sometimes lower than 2% (Rouvilleis, 1970), was revealed. On the contrary, the Oyambre estuary has a large biocoenosis, as the number of its live individuals shows (77%). These data widely surpass the number of live individuals recorded in other nearby estuaries, such as Tina Mayor (33% of the biocoenosis) or Tina Menor (53%) (Rodríguez-Lázaro et al., 2013).

A great amount of sediment that contains both live and dead individuals is accumulated in estuaries. Live and dead assemblages have been compared according to the criteria of

Murray (1991, 2001, 2006). Thus, live assemblages should be in equilibrium with their environment. Dead assemblages (thanatocoenosis), however, should represent the population during wide periods (months or years).

The dead assemblage may be modified by several post-mortem processes, such as dissolution and transport. In the Oyambre estuary, the successive dissolution stages of the shells of foraminifers described by Murray (1991, 2006) (the surface of the hyaline foraminifers becomes opaque and pitted, followed by the breaking of the last chamber) cannot be observed. Therefore, we consider that the most relevant post-mortem process is transport by currents.

This transport can be conducted by means of two mechanisms: suspension and bed load. Both of these mechanisms transport foraminifers from the continental shelf to the inner estuary and vice versa, taking advantage of the tidal cycle. Small sized foraminifers (<200 μm), such as *Bulimina*, *Cassidulina* or *Lagena*, as well as juvenile individuals from species with large shells as *Cibicides*, are affected by transport as suspended load. As bed load, the large foraminifers (shells >200 μm), such as *Cibicides* or *Quinqueloculina*, flow into the estuary pushed by the flood tidal currents. As a result, the assemblages that can be found in the estuaries consist of autochthonous and allochthonous or transported exotic individuals (Cearreta, 1988; Murray 1991, 2006) that accumulate in depositional or sedimentation areas.

In order to describe the taphonomic processes that have taken place in this estuary, the living and dead foraminifer assemblages have been compared using Sanders' similarity index (1960). This index is expressed as a percentage that if higher than 60% indicates good similarity (Altuna et al., 1993) and high similarity if it reaches 70% (Cearreta, 1988; Diz and Francés, 2009; Rodríguez-Lázaro et al., 2013).

In Oyambre, 10 out of the 22 samples used in the statistical analysis present very good similarity (>70%) and 5 of them good similarity (>60%), while 6 show lower values that reveal wide dissimilarities (samples LARA-1, LARA-13, LARA-17, LARA-21, CAP-3 and CAP-6) (Fig. 6). In the sample LARA-7, all the foraminifers belong to the biocoenosis, so that it has not been possible to calculate Sander's similarity index (Fig. 6). It is very likely for dead specimens to have been transported downstream by ebb currents (Fig. 7).

The samples LARA-13, LARA-17 and CAP-3 show dissimilarity due to the decrease in dead species in relation to the live ones. Thus, in LARA-13, there are 5 live species and 3 dead ones, while in LARA-17 the relation live/dead is 7/4 and in CAP-3 it is 6/3. The live species that are not represented in the thanatocoenosis are those with scarce individuals in these samples: *B. pseudomacrescens*, *H. germanica* (LARA-13, CAP-3), *A. tepida* (LARA-17, CAP-3), *T. oblonga* (LARA-17) (Table 1). In these samples, both the live and dead dominant assemblages are the same, but the percentage of each species in the biocoenosis and thanatocoenosis differs. The sample LARA-13 has the following dominant assemblage: *C. williamsoni* (L: 65%; D: 12%), *E. macrescens* (L: 12%; D: 16%) and *T. inflata* (L: 20%; D: 72%). Thus, hyaline shells (67%) are dominant in the live assemblages, while in the dead one agglutinated shells are more abundant (87.5%) (Table 1). This pattern repeats itself in the sample CAP-3: *C. williamsoni* (L: 15%; D: 1%), *E. macrescens* (L: 49%; D: 42%) and *T. inflata* (L: 26%; D: 56%), which represent the following percentage of live/dead individuals in relation to their type of shell: hyaline (L: 21.5%; D: 1%), agglutinated (L: 78%; D: 99%). In the sample LARA-17, the live/dead relation among the main species also varies: *E. macrescens* (L: 30%; D: 12%) and *T. inflata* (L: 63%; D: 83%). The above mentioned samples were taken in hardened sandy silts and silty clays colonized by high marsh

vegetation, *Juncus* and *Phragmites*, in protected areas of the estuary (Fig. 1) that are only flooded during the high tide of spring tides. In these areas, the sedimentary process of decantation has been registered. Thus, the largest dead specimens of *T. inflata* gather “in situ”. However, the smallest sized ones, such as *C. williamsoni* and to a lesser extent *J. macrescens*, are swept downstream by the weak ebb currents (Fig. 7).

In the sample CAP-6, the low diversity of the sample, with 2 live species and 1 dead, causes the dissimilarity. The dominant species is *T. inflata* (L: 94%; D: 100%) (Table 1) in both of them, as *E. macrescens*, which represent the 6% of the biocoenosis, does not appear in the dead assemblage. It is very likely that those individuals could have travelled down the estuary along the El Capitán channel pushed by the river flow and by the ebb tide out of the estuary (Fig. 7). The accumulation of dead individuals of *E. macrescens* downstream, in particular in the sample CAP-3 near a backwater area next to a dam (Fig. 1, Table. 1), validates this claim.

The sample LARA-1 contains 5 species of live foraminifers opposite to the 9 dead ones (Table 1). The most abundant species is *H. germanica* both in live and dead assemblages. Moreover, in the thanatocoenosis, two juvenile individuals of species that inhabit the continental shelf (*Cibicides refulgens* and *Cribratomoides jeffreysii*) have been found. This fact points to limited transport by suspension of individuals through the channel due to the tidal currents. *Miliammina fusca* and *T. inflata* dead individuals, which live on both sandy low marsh and vegetated high marsh environments (Table 2), also appear mixed together in this sample. These data confirm the movement of water along the channel in both directions (Fig. 7).

In the sample LARA-21, there are 9 live species, in contrast with the 15 dead ones (Table 1). Among the allochthonous species there are large *Massilina secans* and *Quinqueloculina seminula* individuals (>200 µm) that points to transport as bed load.

Transport by suspension is also working in this area, as the presence of adults of small sized species (<200 µm) proved, such as *Bolivina spathulata*, *Bulimina truncana*, *Cassidulina laevigata*, *Favulina hexagona* and *Lagena sulcata*.

There is a strong relationship between tidal range and the proportion of exotic (allochthonous) species transported as bed or suspension load in the estuary (Wang and Murray, 1983). Thus, in the mesotidal estuaries of Europe the percentage of exotic individuals is lower than 36% (Murray, 1991). In the Oyambre estuary, from the 41 species retrieved, 28 are exotic, considering *C. lobatulus*, *Quinqueloculina seminula* and *Rosalina globularis* as autochthonous species in the mouth, as they are able to live in the outer estuaries with salinity levels lower than 32‰ (Murray, 1991). Nevertheless, these species are exotic in the inner and mid estuary (Cearreta, 1988; 1999; Rodríguez-Lázaro et al., 2013). Transported species (Table 4) yield few individuals (171), which amounts to the 2.5% of the total individuals found in the Oyambre estuary. This percentage is noticeably lower than that from nearby estuaries. In the nearest estuary of San Vicente de la Barquera (Cearreta, 1989) there is an average of 10.5% of exotic shells and a maximum of 37.6%. Regarding the percentage of exotic in relation to the estuary zonation, in the Santoña estuary (Cearreta, 1988) there is a maximum of 19.5% near the mouth, an average of 7% in the outer estuary and a 2.5% in the inner estuary. These figures contrast with those obtained in Oyambre: 13.4% in the mouth, with a 18.5% maximum, an average of 0.9% in the mid estuary in La Rabia branch, and a 0.15% and 0.7% in El Capitán branch and La Rabia one respectively in the inner estuary (Table 4). These low percentages of exotic foraminifers are typical of microtidal estuaries (tidal range: 0-2 m), where the average of exotic individuals is lower than 9% (Wang and Murray, 1983).

In light of these data about the percentage of exotic benthic foraminifers retrieved from the Oyambre estuary, we conclude that, although it is considered as a mesotidal estuary (Marquínez et al., 2003), it only behaves as so in the area close to the mouth. However, in the mid an inner estuary, the assemblages relate to those found in microtidal estuaries, that is, which are relatively unaffected by the input of the tidal wave.

5.4. Foraminifers and height of tide

The distribution and abundance of the most abundant foraminifer species that appear in the Oyambre estuary are determined by the tide level (Haslett et al., 2001; Horton and Edwards, 2003, 2006; Pascual and Rodríguez-Lázaro, 2006; Rodríguez-Lázaro et al., 2013) (Table 2).

Thus, *A. tepida*, *C. williamsoni* and *H. germanica* inhabit mudflats and channels filled by the average high tide, even during neap tides (Table 1) (intertidal or subtidal areas - MHWNT (Mean High Water Neap Tide) to MHW (Mean High Waters)). *Haynesina germanica* is typical in mudflats and the beginning of the low area of the lowest marshes (Pascual and Rodríguez-Lázaro, 2006; Horton and Murray, 2007) and its distribution is limited in the upper limit by the MHWNT, which in the Bay of Biscay is +3.21 m (Pascual and Rodríguez-Lázaro, 2006) (Fig. 8). Mudflats are scarce in Oyambre (Table 3), although they are widespread in nearby estuaries in Cantabria: Santoña (Cearreta, 1988), San Vicente de la Barquera (Cearreta, 1989), Victoria and Joyel in Noja (Pascual et al., 2004, 2006) and Tina Mayor (Rodríguez-Lázaro et al., 2013).

Miliammina fusca lives in sandy low marshes with scarce vegetation (Nixon et al., 2009; Semensatto-Jr. et al., 2009) between MHWNT – MHW (Edwards et al., 2004; Kemp et al., 2017). In the Oyambre estuary, there is not a clearly limited area as the

above described, in contrast with other estuaries from the south of the Bay of Biscay such as Tina Menor (Rodríguez-Lázaro et al., 2013) where it is well developed. *Entzia macrescens* and *T. inflata* inhabit the vegetated mid and high marshes (Edwards et al., 2004), which is only covered by water during the high tide of the spring tides (Boomer, 1998; Horton and Murray, 2007; Fatela et al., 2009; Rodríguez-Lázaro et al., 2013; Kemp et al., 2017). They mark out the area between MHW (Mean High Waters) and MHWST (Mean High Water Spring Tide), that in this area of the Bay of Biscay comprises between +3.99 and +4.87 m (Pascual and Rodríguez-Lázaro, 2006; Rodríguez-Lázaro et al., 2013) (Fig. 8). Finally, *B. pseudomacrescens* lives from the highest areas of the vegetated high marsh, closest to land to the azoic zone, in areas that uncovered most of the time (Mean High Water Spring Tide (MHWST) to barren zone) (Fig. 8), so that it marks the upper limit of the influence of marine water in this estuary (Alve and Murray, 1999; Guilbault and Patterson, 2000; Gehrels and Newman, 2004; Horton and Edwards, 2006; Hawkes et al., 2010; Murray and Alve, 2011; Kemp et al., 2017) (Table 2). From the 22 analysed samples in the cluster Q-type analysis, 14 of them revealed as main assemblage typical species of the vegetated high marsh (*B. pseudomacrescens*, *E. macrescens* and *T. inflata*) (Table 3). All the mid and high estuary is colonized by the mentioned species that live over the MHW (Fig. 8), which points to the filling up of this estuary and the limited input of the tidal wave.

6. Conclusions

Up to 41 species, 24 of them live, have been identified for the first time in the Oyambre estuary in Cantabria (South of the Bay of Biscay). The biocoenosis represents 77% of the 7177 studied individuals. The most abundant species in the estuary, both in the biocoenosis and thanatocoenosis, are: *Ammonia tepida*, *Balticammina*

pseudomacrescens, *Cibicidoides lobatulus*, *Criboelphidium williamsoni*, *Entzia macrescens*, *Haynesina germanica*, *Miliammina fusca* and *Trochammina inflata*.

The statistical analysis (cluster and correspondence analysis) conducted with samples and live species have allowed us to distinguish between four groups of samples and three foraminifer assemblages along the Oyambre estuary. One assemblage defines the outer estuary with marine influence, where the dominant species is *C. lobatulus*. Mud flats in subtidal euryhaline environments, with limited extension in this estuary, show an assemblage that consists of *A. tepida* and *H. germanica*. Intra or supratidal silty areas with or without vegetation, where *C. williamsoni* dominates, are also scarce. However, the marsh area of the Oyambre estuary is particularly wide. This marsh consists mainly of silty sediment and there is no sandy low marsh, which in nearby Cantabrian estuaries is delimited by *M. fusca*. Therefore, the areas with tide levels between the MHWNT and the MHW are scarce. However, in the Oyambre estuary, there is a wide area above the MHW, where *T. inflata* and *E. macrescens* delimit the tide level between the MHW and MHWST.

The presence of *B. pseudomacrescens* in areas colonized by the exotic invading plant *B. halimifolia* confirms the filling up of the mid and inner estuary, as it marks the tide levels above the MHWST up to the barren zone. This foraminifer species has been found for the first time in the south of the Bay of Biscay in the Oyambre estuary.

A comparison between live and dead assemblages reveals, in general, a good similarity (Sander's index > 60%). The scarcity of samples that show dissimilarity points to decantation and, to a lesser extent, transport by suspension, as the main post-mortem processes. Foraminifers from the continental shelf are transported by suspension to the area of the mouth and, rarely, they travel upstream beyond the inner zone of the estuary, which indicates the limited reach of the tidal wave. The dissimilarity caused by the

accumulation “in situ” of species that live in the protected areas of the high marsh, rarely affected by tides (in MHWST), also shows the lack of hydrodynamism and, therefore, sedimentation by decantation.

The percentage of exotic or allochthonous species deposited in this estuary is very low: 13.4% in the mouth, 0.9% in the middle area of La Rabia branch and 0.15% and 0.7% in the inner area of El Capitán and La Rabia branches, respectively. This information indicates that the Oyambre estuary is only mesotidal in the mouth area. However, the mid and inner estuary show a greater resemblance with microtidal estuaries, which further confirms the limited effect of the tidal wave.

The works conducted in order to regenerate the Oyambre estuary during the years 2009 and 2010 that included the removal of two dams that prevented the input of water in the head of the estuary and the cut down of the exotic species *B. halimifolia*, do not seem to have successfully achieved their objective: recover the original hydrodynamic conditions of the marshes. The studied foraminifers, four years after the recovery works, pointed to the filling up of this estuary and the scarce or null reach of the tidal wave in the inner and mid estuary. Therefore, these results validate benthic foraminifers as reliable proxies of current tide levels and a useful work tool for tracking and monitoring the environmental recovery of the estuaries affected by anthropic activities.

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References

Alexander, S.P., Banner, F.T., 1984. The functional relationship between skeleton and cytoplasm in *Haynesina germanica* (Ehrenberg). *J. Foraminiferal Res.* 14 (3), 159-170.

<https://doi.org/10.2113/gsjfr.14.3.159>

Allorge, P., 1941. Essai de synthèse phytogéographique du Pays Basque. *B. Soc. Bot. Fr.* 88, 66. <https://doi.org/10.1080/00378941.1941.10834231>

Almogi-Labin, A., Perelis-Grossovicz, L., Raab, M., 1992. Living Ammonia from a hypersaline inland pool, Dead Sea area, Israel, *J. Foraminiferal Res.* 22, 257–266.

<https://doi.org/10.2113/gsjfr.22.3.257>

Altenbach, A.V., 1987. The measurement of organic carbon in foraminifera. *J. Foraminiferal Res.* 17, 106-110. <https://doi.org/10.2113/gsjfr.17.2.106>

Altuna, J., Cearreta, A., Edeso, J.M., Elorza, M., Isturiz, M.J., Mariezkurrena, K., Mujika, J.A., Ugarte, F., 1993. El yacimiento detrítico de Herriko Barra (Zarautz, País Vasco) y su relación con las transgresiones marinas holocenas, 2ª Reunión del Cuaternario Ibérico, AEQUA, vol.2, pp. 923-942.

Alve, E., Murray, J.W., 1999. Marginal marine environments of the Skagerrak and Kattegat: a baseline study of living (stained) benthic foraminiferal ecology.

Palaeogeogr. Palaeoclimatol. Palaeoecol. 146, 171–193. [https://doi.org/10.1016/S0031-0182\(98\)00131-X](https://doi.org/10.1016/S0031-0182(98)00131-X)

Alve, E., Murray, J.W., 2001. Temporal variability in vertical distributions of live (stained) intertidal foraminifera, southern England. *J. Foraminiferal Res.* 31, 12-24.

<https://doi.org/10.2113/0310012>

Armynot du Châtelet, E., Bout-Roumazielles, V., Riboulleau, A., Trentesaux, A., 2009. Sediment (grain size and clay mineralogy) and organic matter quality control on living benthic foraminifera. *Rev. Micropaléontol.* 52, 75–84.

<https://doi.org/10.1016/j.revmic.2008.10.002>

Armynot du Châtelet, E., Francescangeli, F., Bouchet, V.M.P, Frontalini, F., 2018.

Benthic foraminifera in transitional environments in the English Channel and the southern North Sea: A proxy for regional-scale environmental and paleo-environmental characterisations. *Mar. Environ. Res.* 137, 37-48.

<https://doi.org/10.1016/j.marenvres.2018.02.021>

Banner, F.T., Knigght-Bentjones, E.W., Wright, J.M., 1994. Protozoa, in: Hayward, P.J., Ryland, J.S.(Eds.), *The Marine Fauna of the British Isles and North-West Europe*. Vol. 1, Introduction and Protozoans to Arthropods. Oxford Science Publications, United Kingdom, pp. 36-50.

Boltovskoy, E., 1965. *Los Foraminíferos recientes*. Editorial Universitaria de Buenos Aires, 510 pp.

Boomer, I., 1998. The relationship between meiofauna (ostracoda, foraminifera) and tidal levels in modern intertidal environments of North Norfolk: a tool for palaeoenvironmental reconstruction. *Bull. Geol. Soc. Norfolk* 46, 17-29.

Brönnimann, P., Lutze, G. F., Whittaker, J. E., 1989. *Balticammina pseudomacrescens*, a new brackish water trochamminid from the western Baltic Sea, with remarks on the wall structure. *Meyniana* 41, 167-177.

Campos, J.A., Caño, L., Herrera, M., 2014. La invasión de *Baccharis halimifolia* en la costa cantábrica. *ambient@*, 109,78-91.

Caño, L., Campos, J.A., García-Magro, D., Herrera, M., 2013a. Replacement of estuarine communities by an exotic shrub: distribution and invasion history of

Baccharis halimifolia in Europe. *Biol. Invasions* 15, 1183–1188.

<https://doi.org/10.1007/s10530-012-0360-4>

Caño, L., García-Magro, D., Herrera, M., 2013b. Phenology of the dioecious shrub *Baccharis halimifolia* along an environmental gradient: consequences for the invasion of Atlantic subhalophilous communities. *Plant Biosystems* 147 (4), 1128–1138.

<https://doi.org/10.1080/11263504.2013.861537>

Cearreta, A., 1988. Distribution and ecology of benthic foraminifera in the Santoña estuary. *Rev. Esp. Paleontol.* 3, 23-38.

Cearreta, A., 1989. Foraminiferal assemblages in the ria of San Vicente de la Barquera (Cantabria, Spain). *Rev. Esp. Micropaleontol.* XXI (1), 67-80.

Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. *Mar. Micropaleontol.*, 17, 195-236.

[https://doi.org/10.1016/0377-8398\(91\)90014-W](https://doi.org/10.1016/0377-8398(91)90014-W)

Diz, P., Francés, G., 2008. Distribution of live benthic foraminifera in the ría de Vigo (NW Spain). *Mar. Micropaleontol.* 66, 165-191.

<https://doi.org/10.1016/j.marmicro.2007.09.001>

Diz, P., Francés, G., 2009. Postmortem processes affecting benthic foraminiferal assemblages in the ría de Vigo, Spain: implications for paleoenvironmental studies. *J. Foraminiferal Res.* 39 (3), 166-179.

<https://doi.org/10.2113/gsjfr.39.3.166>

Edwards, R. J., Wright, A. J., and van de Plassche, O., 2004, Surface distribution of salt-marsh foraminifera from Connecticut, USA: Modern analogues for high-resolution sea level studies. *Mar. Micropaleontol.*, 51, 1–21.

<https://doi.org/10.1016/j.marmicro.2003.08.002>

Fatela, F., Moreno, J., Moreno, F., Araújo, M.F., Valente, T., Antunes, C., Taborda, R., Andrade, C., Drago, T., 2009. Environmental constraints of foraminiferal assemblages

distribution across a brackish tidal marsh (Caminha, NW Portugal). *Mar. Micropaleontol.* 70, 70-88. <https://doi.org/10.1016/j.marmicro.2008.11.001>

Fisher, R. A., Corbett, A. S., Williams, C.B., 1943. The relationship between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42-58. <http://www.jstor.org/stable/1411>

Flor-Blanco, G., Flor, G., 2012. Clasificación geomorfológica y características de los estuarios cantábricos (NW de España) in: Gonzalez-Díaz, A. (Ed.) *Avances de la Geomorfología en España*, Publican Ediciones de la Universidad de Cantabria, Santander, 315-318.

Frau, D., Ondiviela, B., Galván, C., Juanes, J.A., 2014. The role of the hydrodynamic regime in the distribution of the invasive shrub *Baccharis halimifolia* (Compositae) in Oyambre Estuary (Cantabria, Spain). *Limnetica*, 33 (1), 1-12.

GEIB, 2006. TOP 20: Las 20 especies exóticas invasoras más dañinas presentes en España. GEIB, Serie Técnica 2.

Gehrels, W.R., Newman, S. W. G., 2004, Salt-marsh foraminifera in Ho Bugt, western Denmark, and their use as sea-level indicators: *Danish Journal of Geography* 104, 49–58. <https://doi.org/10.1080/00167223.2004.10649507>

Gehrels, W.R., Van de Plassche, O., 1999. The use of *Jadammina macrescens* (Brady) and *Balticammina pseudomacrescens* Brönnimann, Lutze and Whittaker (Protozoa: Foraminiferida) as sea-level indicators. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 149, 89-101. [https://doi.org/10.1016/S0031-0182\(98\)00194-1](https://doi.org/10.1016/S0031-0182(98)00194-1)

Gehrels, W.R., Roe, H.M., Charman, D.J., 2001. Foraminifera testate amoebae and diatoms as sea-level indicators in UK saltmarshes: a quantitative multiproxy approach. *J. Quaternary Sci.* 16, 201-220. <https://doi.org/10.1002/jqs.588>

- Guilbault, J.P., Patterson, R.T., 2000. Correlation between marsh foraminiferal distribution and elevation in coastal British Columbia, Canada. In: Hart, M.B., Kaminski, M.A., & Smart, C.W. (Eds.). Proceedings of the Fifth International Workshop on Agglutinated Foraminifera. Grzybowski Foundation Special Publication, 7, pp.117-125.
- Guinea, E., 1953. Geografía botánica de Santander, Diputación Provincial de Santander.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: PAleontological STatistics software package for education and data analysis., *Palaeontol. Electronica* 4, 1-9.
http://palaeo-electronica.org/2001_1/past/issue1_01.htm.
- Hansen, A., Knudsen, K.L., 1995. Recent foraminiferal distribution in Freemansundet and Early Holocene stratigraphy on Edgeoya, Svalbard. *Polar Research*, 14, 215-238.
<https://doi.org/10.3402/polar.v14i2.6664>
- Haslett, S.K., P. Davies, P., Strawbridge, F., 1997. Reconstructing Holocene sea-level change in the Severn Estuary and Somerset Levels: the foraminifera connection. *Archaeol. Severn Estuary* 8, 29-40.
- Haslett, S.K., Strawbridge, F., Martin, N.A., Davies, C.F.C., 2001. Vertical saltmarsh accretion and its relationship to sea-level in the Severn Estuary, U.K.: an investigation using foraminifera as tidal indicators. *Estuar. Coast. Shelf Sci.* 52, 143-153.
<https://doi.org/10.1006/ecss.2000.0740>
- Hawkes, A.D., Horton, B.P., Nelson, A.R., Hill, D.F. 2010. The application of intertidal foraminifera to reconstruct coastal subsidence during the giant Cascadia earthquake of AD 1700 in Oregon, USA. *Quaternar. Int.* 221, Issues 1–2, 116-140.
<https://doi.org/10.1016/j.quaint.2009.09.019>
- Hayward, B.W., Scott, G.H., Grenfell, H.R., Carter, R., Lipps, J.H., 2004. Techniques for estimation of tidal elevation and confinement (-salinity) histories of sheltered

harbours and estuaries using benthic foraminifera: examples from New Zealand. *The Holocene* 14, 218-232. <https://doi.org/10.1191/0959683604hl678rp>

Hippensteel, S.P., Martin, R.E., Nikitina, D., Pizzuto, J.E., 2000. The formation of Holocene marsh foraminiferal assemblages, middle Atlantic Coast, USA: implications for the Holocene sea-level change. *J. Foraminiferal Res.* 30 (4), 272–293.

<https://doi.org/10.2113/0300272>

Horton, B.P., Edwards, R.J., 2000. Quantitative paleoenvironmental reconstruction techniques in sea-level studies. *Archaeol. Severn Estuary* 11, 105-119.

Horton, B.P., Edwards, R.J., 2003. Seasonal distributions of foraminifera and their implications for sea-level studies, Cowpen Marsh, U.K. *Soc. Econ. Paleontol. Mineral. Special Publications of SEPM* 75, 21-30. <https://doi.org/10.2110/pec.03.75.0021>

Horton, B.P., Edwards, R.J., 2006. Quantifying Holocene sea-level change using intertidal foraminifera: lesson from the British Isles. *Cushman Found. Foraminiferal Res. Special Publication* 40, 97 pp. http://repository.upenn.edu/ees_papers

Horton, B.P., Murray, J.W., 2007. The roles of elevation and salinity as primary controls on living foraminiferal distributions: Cowpen Marsh, Tees Estuary, UK. *Mar. Micropaleontol.* 63, 169-186. <https://doi.org/10.1016/j.marmicro.2006.11.006>

Jorissen, F.J., 1987. The distribution of benthic foraminifera in the Adriatic Sea. *Mar. Micropaleontol.* 12, 21-48 [https://doi.org/10.1016/0377-8398\(87\)90012-0](https://doi.org/10.1016/0377-8398(87)90012-0)

Kemp, A.C., Horton, B.P., Nikitina, D., Vane, C.H., Potapova, M., Weber-Bruya, E.,

Culver, S.J., Repkina, T., Hill, D.F., 2017. The distribution and utility of sea-level indicators in Eurasian subArctic salt marshes (White Sea, Russia). *Boreas* 46, 562-584.

<https://doi.org/10.1111/bor.12233>

Loeblich, A.R., Tappan, H., 1988. *Foraminiferal genera and their classification*. Van Nostrand Reinhold, New York. https://books.google.pt/books?id=n_BqCQAAQBAJ

- López, E., 1979. Algal chloroplasts in the protoplasm of three species of benthic foraminifera: taxonomic affinity, viability, and persistence. *Mar. Biol.* 53, 201-211. DOI <https://doi.org/10.1007/BF00952427>
- Marquínez, J., Fernández, E, Fernández, S., 2003. Indicadores morfológicos del alcance de la onda mareal en estuarios: terrenos reclamados durante el pasado siglo en el estuario de Ribadesella (Costa Cantábrica). *Nat. Cantabrigae* 2, 1-10.
- Martins, M.V.A., Ruivo Dragao Gomes, V.C., 2004. Foraminíferos da margem continental NW Ibérica. Sistemática, Ecología e Distribuição. *Agenda Comum - Comunicação* lda. Aveiro.
- Mathieu, R., 1986. Sediments et foraminifères actuels de la Marge Continentale Atlantic du Maroc. These de Doctorat, Universite Pierre et Marie Curie, Paris.
- Murray, J.W., 1991. *Ecology and Palaeoecology of Benthic Foraminifera*. Longman Scientific and Technical, Harlow, England.
- Murray, J.W., 2001. The niche of benthic foraminifera, critical thresholds and proxies. *Mar. Micropaleontol.* 41, 1-7. [https://doi.org/10.1016/S0377-8398\(00\)00057-8](https://doi.org/10.1016/S0377-8398(00)00057-8)
- Murray, J.W., 2006. *Ecology and Applications of Benthic Foraminifera*, Cambridge University Press, Cambridge.
- Murray, J.W., Alve, E., 1999. Natural dissolution of modern shallow water benthic foraminifera: taphonomic effects on the palaeoecological record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 146, 195–206. [https://doi.org/10.1016/S0031-0182\(98\)00132-1](https://doi.org/10.1016/S0031-0182(98)00132-1)
- Murray, J.W., Alve, E., 2011. The distribution of agglutinated foraminifera in NW European seas: baseline data for the interpretation of fossil assemblages *Palaeontol. Electron.*, 14 (2), 1-41. https://palaeo-electronica.org/2011_2/248/index.html

Nixon, F.C.; Reinhardt, E.G., Rothaus, R., 2009. Foraminifera and tidal notches: Dating neotectonic events at Korphos, Greece. *Mar. Geol.* 257, 41–53.

<https://doi.org/10.1016/j.margeo.2008.10.011>

Pascual, A., 1992. Utilización de los foraminíferos bentónicos para un mejor conocimiento del medio ambiente en los estuarios vizcaínos (Gernika y Bilbao). *Rev. Esp. Micropal.* XXIV (1), 33-57.

Pascual, A., Martín-Rubio, M., Rodríguez-Lázaro, J., 2004. Repartición de los foraminíferos bentónicos recientes en la marisma Victoria (Noja, Cantabria). *Geogaceta* 36, 151-154.

Pascual, A., Elorza-Remón, M., Martín-Rubio, M., Rodríguez-Lázaro, J., 2006. Situación medioambiental de la marisma Joyel (Cantabria): datos aportados por los foraminíferos bentónicos. *Geogaceta* 40, 183-186.

Pascual, A., Martínez- García, B., 2014. Silting of the Oyambre estuary (Cantabria, Southern Bay of Biscay): data provided by the benthic foraminifers, in: Guy Bachelet, G., Gillet, H., Anschutz, P. (Eds.), *ISOBAY 14. XIV International Symposium on Oceanography of the Bay of Biscay*, Université de Bordeaux, pp.16

Pascual, A., Rodríguez-Lázaro, J., 2006. Marsh development and sea level changes in the Gernika Estuary (southern Bay of Biscay): foraminifers as tidal indicators. *Sci. Mar.* 70S1, 101-117. <https://doi.org/10.3989/scimar.2006.70s1101>

Phleger, F., 1960. Ecology and distribution of recent foraminifera. The Johns Hopkins Press. Baltimore. <https://doi.org/10.1017/S0025315400016349>

Ramírez del Pozo, J., Portero, J.M., Olivé, A., Martín Alafont, J.M., Aguilar S, M. J., Giannini, G., 1976. Mapa Geol. España 1:50.000, hoja nº 33 (Comillas). IGME Madrid.

Richter, G., 1964. Zur Ökologie der Foraminiferen: II. Lebensraum und Lebensweise von *Nonion depressulum*, *Elphidium excavatum* und *Elphidium selseyense*. Natur und Museum, 94, 421.

Riveiros, N.V., Babalola, A.O., Boudreau, R.E.A., Patterson, R.T., Roe, H.M., 2007. Modern distribution of saltmarsh foraminifera and thecamoebians in the Seymour-Belize Inlet Complex, British Columbia, Canada. Mar. Geol. 242, 39-63.

<https://doi.org/10.1016/j.margeo.2006.08.009>

Rodríguez-Lázaro, J., Pascual, A., Martínez García, B., 2013. Recent benthic foraminifers as indicators of the sedimentary dynamics of the Tina Mayor and Tina Menor estuaries (S Bay of Biscay, N Spain). J. Marine Syst. 109-110: S213-S232.

<https://doi.org/10.1016/j.margeo.2006.08.009>

Rouvillois, A., 1970. Biocoenose et taphocoenose des foraminifères sur le plateau continental Atlantique au large de l'île d'Yeu. Rev. Micropaléontol. 13, 188–204.

Sanders, H. L., 1960. Benthic studies in Buzzards Bay III. The structure of the soft bottom community. Limnol. Oceanogr. 5, 138-153.

<https://doi.org/10.4319/lo.1960.5.2.0138>

Schroeder-Adams, C., Cole, R., Medioli, R., Mudie, P., Scott, D., Dobbin, L., 1990. Recent arctic shelf foraminifera: seasonally ice covered vs. perennially ice covered areas. J. Foraminiferal Res. , 20, 8-36. <https://doi.org/10.2113/gsjfr.20.1.8>

Scott, D.K., Leckie, R.M., 1990. Foraminiferal zonation of Great Sippwissett Salt Marsh (Falmouth, Massachusetts). J. Foraminiferal Res. 20, 248–266.

<https://doi.org/10.2113/gsjfr.20.3.248>

Scott, D.B., Medioli, F.S., 1986. Foraminifera as sea-level indicators. In: O. Van de Plassche (Ed.), Sea-level research: a manual for the collection and evaluation of Data, Geobooks, Norwich, pp. 435-457. <https://doi.org/10.1007/978-94-009-4215-8>

- Scott, D. B., Medioli, F. S., Schafer, C. T., 2001. *Monitoring in Coastal Environments Using Foraminifera and Thecamoebian Indicators*. Cambridge University Press, London. <https://doi.org/10.1017/CBO9780511546020>
- Seiglie, G.A., 1975. Foraminifers of Guayanilla Bay and their use as environmental indicators. *Rev. Esp. Micropal.* 7, 453-487.
- Semensatto-Jr., D.L., Ferreira Funo, R.H., Dias-Brito, D., Coelho-Jr., C., 2009. Foraminiferal ecological zonation along a Brazilian mangrove transect: Diversity, morphotypes and the influence of subaerial exposure time. *Rev. Micropaléontol.* 52, 67–74. <https://doi.org/10.1016/j.revmic.2008.06.004>
- Van der Zwaan, G.J., Duijnste, I.A.P., den Dulk, M., Ernst, S.R., Jannink, N.T., Kouwenhoven, T.J., 1999. Benthic foraminifers: proxies or problems? A review of paleoecological concepts. *Earth Sci. Rev.* 46, 213–236. [https://doi.org/10.1016/S0012-8252\(99\)00011-2](https://doi.org/10.1016/S0012-8252(99)00011-2)
- Walton, W. R., 1952. Techniques for Recognition of Living Foraminifera: Cushman Found. Foram. Res. Contr. , 3, 56-60.
- Wang, P., Murray, J.W., 1983. The use of foraminifera as indicators of tidal effects in estuarine deposits. *Mar. Geol.* 51, 239-250. [https://doi.org/10.1016/0025-3227\(83\)90106-8](https://doi.org/10.1016/0025-3227(83)90106-8)
- Williamson, M.A., 1985. Recent foraminiferal diversity on the continental margin off Nova Scotia, Canada *J. Foraminiferal Res* 15, 43-51. <https://doi.org/10.2113/gsjfr.15.1.43>
- Williamson, M.A., Keen, C.E., Mudie, P.J., 1984. Foraminiferal distribution on the continental margin off Nova Scotia. *Mar. Micropal.* 9, 219-239. [https://doi.org/10.1016/0377-8398\(84\)90014-8](https://doi.org/10.1016/0377-8398(84)90014-8)

WoRMS Editorial Board (2018). World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed 2018-06-21. doi:10.14284/170

Yeager, K. M., Brunner, C. A., Kulp, M. A., Fischer, D., Feagin, R. A., Schindler, K. J., Prouhet, J., Bera, G., 2012. Significance of Active Growth Faulting On Marsh Accretion Processes in the Lower Pearl River, Louisiana. *Geomorphology*, 153, 127-143. <https://doi.org/10.1016/j.geomorph.2012.02.018>

FIGURES

Figure 1. Geographical location of the Oyambre estuary and sampling sites.

Figure 2. Distribution of samples according to tide level.

Figure 3. A- Multivariate analysis of the samples (cluster Q-type) based on the most abundant live species of benthic foraminifers identified from the Oyambre estuary, with the UPGMA method and the correlation index. B- Distribution of groups and subgroups in the study area.

Figure 4. Multivariate analysis of the most abundant live species (cluster R-type) identified in the studied samples from the Oyambre estuary, with the UPGMA method and the correlation index. In bold, dominant species (>10%).

Figure 5. Ordination analysis (direct gradient analysis) by Detrended Correspondence Analysis (DCA) of samples and species of benthic foraminifers. Q-type cluster groups of samples are separated. In italics and bold, dominant benthic foraminifer species. Along the axis 1, a salinity gradient is marked.

Figure 6. Sanders' similarity index comparing the live and dead assemblages in samples of Oyambre estuary.

Figure 7. Ebb current (A) and flood current (B) detected by benthic foraminifers in the Oyambre estuary.

Figure 8. Environments identified in the Oyambre estuary based on the ecological distribution of most abundant benthic foraminifer species related to tide levels. Specific composition of representative samples are shown using pie charts. MHWNT: mean high water neap tides; MHW: mean high water; MHWST: mean high water spring tides; m. a.s.l.: meters above sea level. A- La Rabia marsh; B- El Capitán marsh.

Plate I. Scanning Electron Microscope (SEM) microphotographs of most abundant benthic foraminifer species from Oyambre estuary. Scale bar = 100 μm . legend: l, live specimen; d, dead specimen; LARA-, CAP-, samples. A-B- *Trochammina inflata* (Montagu, 1808); A- Spiral side, l, CAP-6; B- Umbilical side, l, CAP-6. C-D- *Entzia macrescens* (Brady, 1870); C- Spiral side, l, LARA-5; D- Umbilical side, l, LARA-5. E- *Criboelphidium williamsoni* (Haynes, 1973), General view, l, LARA-7. F- *Haynesina germanica* (Ehrenberg, 1840), General view, l, LARA-1. G-H- *Balticammina pseudomacrescens* Brönniman, Lutzle and Whittaker, 1989; G- Spiral side, d, LARA-4; H- Umbilical side, d, LARA-4. I-J- *Cibicidoides lobatulus* (Walker and Jacob, 1798); I- Umbilical side, d, LARA-23; J- Spiral side, d, LARA-23. K-L- *Ammonia tepida* (Cushman, 1926); K- Spiral side, d, LARA-1; L- Umbilical side, l, LARA-1. M-N- *Miliammina fusca* (Brady, 1870); M- General view, l, LARA-3; N- General view, l, LARA-3.

BENTHIC FORAMINIFER OYAMBRE	LARA-1		LARA-2		LARA-3		LARA-4		LARA-5		LARA-6		LARA-7		LARA-9		LARA-10		LARA-11		LARA-13		LARA-14		LARA-A		LARA-16	
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
<i>Acervulina inhaerens</i> Schulze, 1854																												
<i>Ammonia beccarii</i> (Linné, 1758)																												
<i>Ammonia tepida</i> (Cushman, 1926)	17	5	1		7	1									2	1				2	1					1	67	25
<i>Asterigerinata mamilla</i> (Williamson, 1858)																												2
<i>Balticammina pseudomacrescens</i> Brönniman, Lutzle and Whittaker, 1989			15	6	82	8	54	19	13	14		1									3				17		1	
<i>Bolivina spathulata</i> (Williamson, 1858)																												
<i>Bulimina gibba</i> Fornasini, 1902																												
<i>Bulimina truncana</i> Gümbel, 1868																												
<i>Cassidulina laevigata</i> d'Orbigny, 1826																												
<i>Cibicides refulgens</i> de Montfort, 1808		1																										
<i>Cibicoides lobatulus</i> (Walker and Jacob, 1798)																											1	2
<i>Connemarella rudis</i> (Wright, 1900)																												
<i>Criboelphidium excavatum</i> (Terquem, 1839)	2	2			1																							
<i>Criboelphidium williamsoni</i> (Haynes, 1973)	12	4	4	1	11	1	8		10	1			292		2						184	4			39	1	26	2
<i>Crirostomoides jeffreysii</i> (Williamson, 1858)		1					5	1	5	5																		
<i>Cyclammina cancellata</i> Brady, 1879			1	1	1																							
<i>Elphidium crispum</i> (Linné, 1758)																												
<i>Elphidium oceanense</i> (d'Orbigny, in Fornasini, 1904)									1																			
<i>Entzia macrescens</i> (Brady, 1870)	10	3	46	14	21	10	42	8	68	41	89	66	8				6				33	5	5		119	2	3	1
<i>Eponides repandus</i> (Fichtel and Moll, 1798)																												
<i>Favulina hexagona</i> (Williamson, 1848)																												
<i>Haynesina germanica</i> (Ehrenberg, 1840)	213	41	25	2	105	6	1		1	1					33	2					1	1	5				127	48

BENTHIC FORAMINIFER OYAMBRE	LARA-17		LARA-18		LARA-19		LARA-20		LARA-21		LARA-22		LARA-23		Cap-1		Cap-2		Cap-3		Cap-4		Cap-5		Cap-6		Cap-7	
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
<i>Acervulina inhaerens</i> Schulze, 1854							3																					
<i>Ammonia beccarii</i> (Linné, 1758)											2																	
<i>Ammonia tepida</i> (Cushman, 1926)	6				14	3	4		18					2			4	1	2		70	17	29	1			4	1
<i>Asterigerinata mamilla</i> (Williamson, 1858)							2	1	4	3				1														
<i>Balticammina pseudomacrescens</i> Brönniman, Lutzle and Whittaker, 1989	7		27	7	10	5							3		91	27	1	8					5					15
<i>Bolivina spathulata</i> (Williamson, 1858)										1																		
<i>Bulimina gibba</i> Fornasini, 1902								1						1														
<i>Bulimina truncana</i> Gümbel, 1868										1																		
<i>Cassidulina laevigata</i> d'Orbigny, 1826										1																		
<i>Cibicides refulgens</i> de Montfort, 1808						3	3	13	2	5	6	2	1	3														
<i>Cibicoides lobatulus</i> (Walker and Jacob, 1798)					1	3	112	85	92	53	41	47	138	89									1					1
<i>Connemarella rudis</i> (Wright, 1900)														2														
<i>Criboelphidium excavatum</i> (Terquem, 1839)																												
<i>Criboelphidium williamsoni</i> (Haynes, 1973)					50	8			42	9			6				9		35	1	70		13	2			6	1
<i>Crirostomoides jeffreysii</i> (Williamson, 1858)																												
<i>Cyclammina cancellata</i> Brady, 1879																												
<i>Elphidium crispum</i> (Linné, 1758)							2	1	1	2		2		1														
<i>Elphidium oceanense</i> (d'Orbigny, in Fornasini, 1904)																												
<i>Entzia macrescens</i> (Brady, 1870)	71	8	16	3	29	3		1			1		4		173	1	90	11	113	34	49	2	129	2	14		123	1
<i>Eponides repandus</i> (Fichtel and Moll, 1798)												1		2														
<i>Favulina hexagona</i> (Williamson, 1848)										1																		
<i>Haynesina germanica</i> (Ehrenberg, 1840)	1	1			44	11	2		36	7	2		5				3		13		67	7	31	6			11	1

Table 1. Benthic foraminifer species determined in samples of the Oyambre estuary. Values are absolute frequencies of both live and dead individuals. Bold numbers depict most abundant species (>10%). In the lower part, richness and diversity indexes, as well as the test-types of foraminifers, are indicated.

Species	Distribution in estuaries of the Bay of Biscay	Tide range	Ecological preference
<i>Ammonia tepida</i> (Cushman, 1926)	Silty sediments and mudflats from intertidal or subtidal areas in waters with different salinity levels. It is also present in low marshes	Intertidal to subtidal areas - MHWNT (Mean High Water Neap Tide) to MHW	Typical of temperate waters (Murray, 2006), with salinity levels ranging from 15 to 56‰ (Almogi-Labin et al., 1992). It is present in waters between 0 and 50 metres deep, in transitional environments (Murray, 2006), on sandy silt (Seiglie, 1975; Murray, 2006). It shows an endofaunal lifestyle (Murray, 2006), it is an opportunistic species, common in polluted silty environments (Seiglie, 1975).
<i>Balticammina pseudomacrescens</i> Brönnimann, Lutze and Whittaker, 1989	Vegetated high marshes, closest to land area	MHWST (Mean High Water Spring Tide)	It is an epifaunal agglutinated species, which lives on marsh vegetation (Murray, 2006). It is very sensitive to pH variations (Gehrels and Newman, 2004). It inhabits the topmost highmarsh area and, therefore, it is used in palaeoenvironmental reconstruction as proxy for the higher tidal range in estuaries (Guilbault and Patterson, 2000; Gehrels and Newman, 2004; Horton and Edwards, 2006; Hawkes et al., 2010; Murray and Alve, 2011). As it lives in the highest area of continental marshes, it establishes the top limit of seawater influence in estuaries (Alve and Murray, 1999).
<i>Cibicidoides lobatulus</i> (Walker and Jacob, 1798)	Marine coastal and sandy mouths of estuaries	Intertidal to subtidal areas	It appears in waters with very variable temperature (Martins and Ruivo Dragão Gomes, 2004) and salinity levels (marine normal to estuarine, higher than 32‰) (Williamson et al., 1984). It lives in transitional to bathyal environments, though its abundance decreases towards the slope (Mathieu, 1986; Martins and Ruivo Dragão Gomes, 2004), in fine-grained sand to coarser substratum (Jorissen, 1987; Schröder-Adams et al., 1990; Banner et al., 1994; Hansen and Knudsen, 1995). It is an epifaunal species that lives within the first centimetre of the soil or above (Corliss, 1991; Murray, 2006), in well-oxygenated waters (Jorissen, 1987). It has a sessile and immobile lifestyle in high energy environments (Murray, 2006), where it withstands strong hydrodynamism (Williamson, 1985; Banner et al., 1994). It shows a bigger and coarser shell in cold waters than in warm waters, where it grows at a higher rate (Banner et al., 1994).
<i>Criboelphidium williamsoni</i> (Haynes, 1973)	Silty sediments and mudflats from intertidal or subtidal areas in waters with different salinity levels. It is also present in low marshes.	Intertidal to subtidal areas - MHWNT to MHW	It inhabits waters with variable temperature ranges (preferentially warm-temperate waters) and euryhaline salinity (Murray, 2006). It is typical of transitional environments, where it is a dominant species in marshes, on fine-grained sediment (Murray, 2006). It covers the almost horizontal surfaces of low marshes with low drainage (Haslett et al., 1997, 2001). It has an endofaunal lifestyle and it is common in substrates with strong variations in TOC content (Murray, 2006). They may contain chloroplasts of algal symbiont in low-oxygen content conditions (López, 1979).

<i>Entzia macrescens</i> (Brady, 1870)	Vegetated mid and high marshes of the inner estuary	MHW (Mean High Waters) - MHWST (Mean High Water Spring Tide)	It is an agglutinated species that lives on marsh vegetation (Murray, 2006). It is euryhaline and tolerates a wide range of temperatures (0 to 30°C). It lives on plant parts in clayey silt, in intertidal to high marsh environments (Murray, 1991), although it frequently appears in mid-high marshes (Scott et al., 2001). Its presence is favoured by the increase of the percentage of organic carbon, as it preferably feeds on organic matter from vascular plants (Armynot du Châtelet et al., 2009). It is epifaunal and infaunal down to 60 cm deep, herbivore or detritivore diet (Murray and Alve, 2011).
<i>Haynesina germanica</i> (Ehrenberg, 1840)	Silty sediments and mudflats from intertidal or subtidal areas in waters with different salinity levels	Intertidal to subtidal areas - MHWNT	It is an euryhaline species that inhabits subtidal mud flats in the head of the estuary, in areas with variable, though low, salinity (1-32‰) (Pascual and Rodríguez-Lázaro, 2006; Horton and Murray, 2007). It lives in a wide range of temperatures (-2 a 32°C) (Alexander and Banner, 1984). It is typical of estuaries (Murray, 2006), where it can be found on silt and sandy silt with a variable TOC content (Alve and Murray, 1999). It is a shallow endofaunal species (Richter, 1964) that can tolerate anoxic conditions (Banner et al., 1994) and may contain chloroplasts of algal symbiont in low-oxygen content conditions (López, 1979).
<i>Miliammina fusca</i> (Brady, 1870)	Silty sands with scarce vegetation: Low marshes	MHWNT - MHW	It is an euryhaline species (Murray, 1991) that lives in low marshes (Nixon et al, 2009; Semensatto-Jr. et al, 2009). It can also appear and be dominant even in vegetation lacking sediments (Armynot du Châtelet et al., 2009), such as fine-grained or silty sand. However, it is not present in highly-silty sediments (Alve and Murray 1999, Nixon et al, 2009; Rodríguez-Lázaro et al., 2013). It is an opportunistic species and very resilient to environmental stress (Semensatto-Jr. et al., 2009). It is epifaunal or infaunal down to 50 cm in marshes and lives in intertidal to shallow subtidal brackish waters (Murray and Alve, 2011).
<i>Trochammina inflata</i> (Montagu, 1808)	Vegetated mid and high marshes in the inner estuary	MHW - MHWST	It is an epifaunal agglutinated species that lives on marsh vegetation (Murray, 2006). It is euryhaline, tolerates a wide range of temperatures (0 to 30°C) and inhabits on plant parts-rich silt, from intertidal environments to high marshes (Murray, 1991), although they are more common in mid-high marshes (Scott et al., 2001), where they feed on algae or mixed algae-plants derived organic matter (Armynot du Châtelet et al., 2009). It is particularly abundant in sandy silt sediment (Nixon et al., 2009) that is favoured by an increase in the percentage of organic carbon (Armynot du Châtelet et al., 2009). It is epifaunal and infaunal down to 60 cm, with an herbivore or detritivore diet (Murray and Alve, 2011).

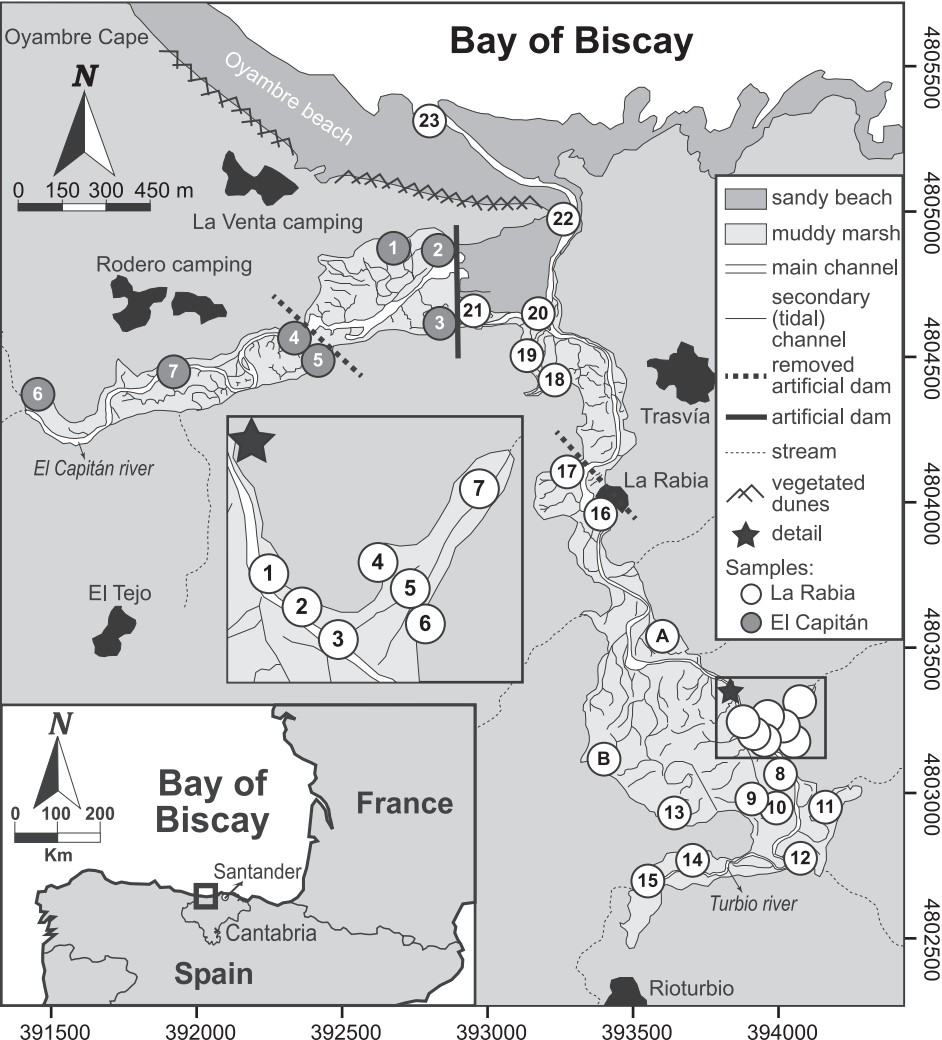
Table 2. Ecological preferences of the most characteristic benthic foraminifer species (>10%) in samples of Oyambre estuary. Based on different authors.

Oyambre estuary		Outer estuary			Inner-mid estuary																			
		Marine			Subtidal mudflat				Marsh															
		Mouth	Boundary		Main channel			Low intertidal marsh	Vegetated mid marshes			Secondary channel	Vegetated high marsh				High marsh-Barren zone							
Environment	Benthic foraminifer assemblage	LARA-20	LARA-23	LARA-21	LARA-3	LARA-16	LARA-1	Cap-4	LARA-7	LARA-13	LARA-4	Cap-6	LARA-2	LARA-17	LARA-19	LARA-6	Cap-5	Cap-2	Cap-7	LARA-A	Cap-3	LARA-5	Cap-1	
Marine shelf	<i>C. lobatulus</i>	77	76	44	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0
Subtidal mudflat	<i>A. tepida, H. germanica</i>	4	3	26	40	82	91	60	0	2	0.4	0	11	3	21	0	18	3	5	0	7	1	0	0
Mudflat and low intertidal marsh	<i>C. williamsoni</i>	0	3	20	4	11	5	25	94	65	3	0	1.5	0	19	0	4	3	2	14	15	7	0	0
Silty-sandy low marsh	<i>M. fusca</i>	0	0	0	7.2	0	0	1	0.3	0	8	0	1.5	0.4	3	1	0	1.5	1	3	0	13	0.3	0
Vegetated mid and high marshes	<i>T. inflata</i>	1	2	0	13	4	0	5	2.5	20	46	94	56	63	37	42	35	48	44	36	26	15	13.7	0
Vegetated high marshes	<i>E. macrescens</i>	0	2	0	7	1	4	18	2.5	12	18	6	21	29	11	57	42	34	42	41	49	50	56	0
Vegetated high marshes-Barren zone	<i>B. pseudomacrescens</i>	0	2	0	28.8	0	0	0	0	0	23	0	7	3	4	0	1	10	5	6	3	10	29.6	0
Total foraminifer percentage from vegetated high marshes		1	6	0	49	5	4	23	5	32	87	100	84	95	52	99	78	92	91	83	78	75	99.3	0
Sample groups according to multivariate analysis (cluster Q-type)		Gr- 1			Gr-4				Gr-3			Gr- 2A				Gr-2C				Gr- 2B				
Vegetated marshes	Dominant vegetation				B							B	P	B	P	H	J	J+P	B	J	J+P	S	B	B
	Accompanying vegetation								J			J				J	B			B	B	B		

Table 3. Environmental interpretation of Oyambre estuary based on characteristic benthic foraminifer assemblages. Values are percentages of the total foraminifer assemblages. Live (L), dead (D) specimens in the time of sampling. Sample locations in the estuary are indicated in the upper right. In the lower part ecological groups recognised in the multivariate analysis of samples (cluster Q-type), and vegetation type are indicated: B= *Baccharis halimifolia*; H= *Halimione portulacoides* , J= *Juncus maritimus*; P= *Phragmites australis*; S= *Salicornia*.

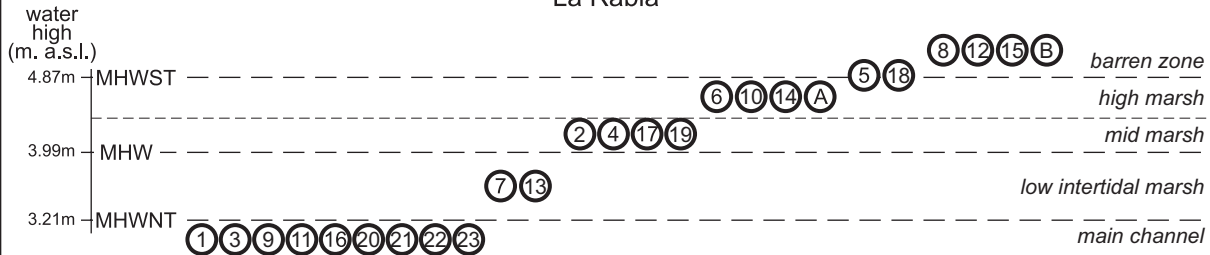
	Oyambre				El Capitán							La Rabia																		
Exotic foraminifers	LARA-23	LARA-22	LARA-20	LARA-21	Cap-1	Cap-2	Cap-3	Cap-4	Cap-5	Cap-6	Cap-7	LARA-19	LARA-18	LARA-17	LARA-16	LARA-A	LARA-1	LARA-2	LARA-3	LARA-4	LARA-5	LARA-6	LARA-7	LARA-9	LARA-10	LARA-11	LARA-13	LARA-14		
No. of exotic species	13	8	10	9	0	0	0	0	1	0	1	2	0	0	2	1	3	2	2	2	1	0	0	0	0	0	0	0	0	
No. of exotic individuals	48	24	33	23	0	0	0	0	1	0	1	7	0	0	5	1	6	3	2	7	10	0	0	0	0	0	0	0		
Total foraminifer percentage (%)	15	18.5	12.5	7.5	0	0	0	0	0.3	0	0.3	2	0	0	1.5	0.3	2	1	0.6	2	3	0	0	0	0	0	0	0		
Average of exotic (%)	13.4				0				0.15				0.9				0.7													
Estuarine zonation	Mouth				Mid estuary			Inner estuary				Mid estuary				Inner estuary														

Table 4. Exotic (allochthonous) foraminifers found in the Oyambre estuary.

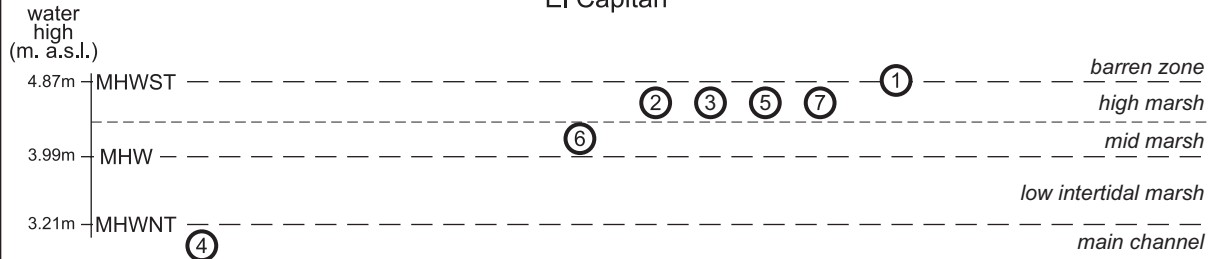


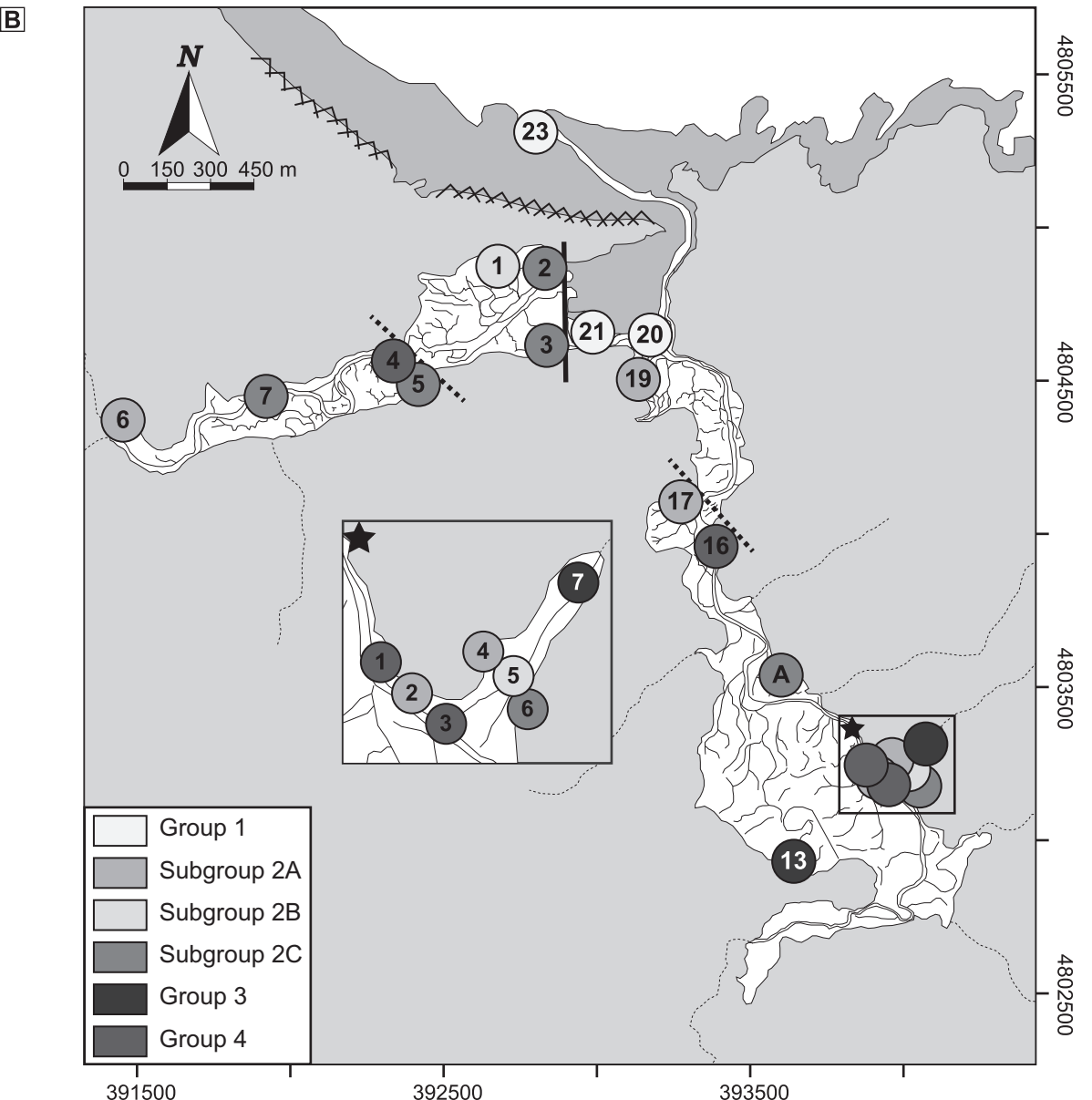
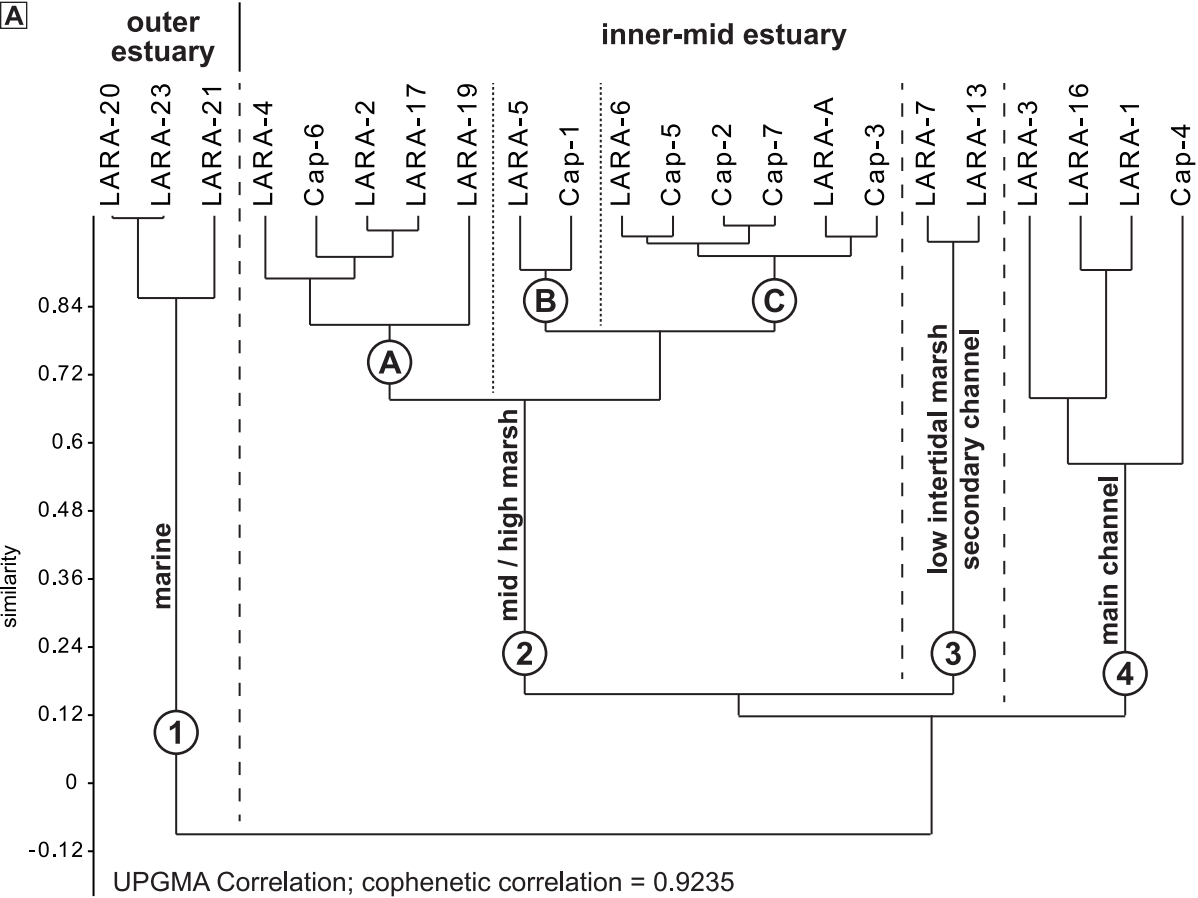
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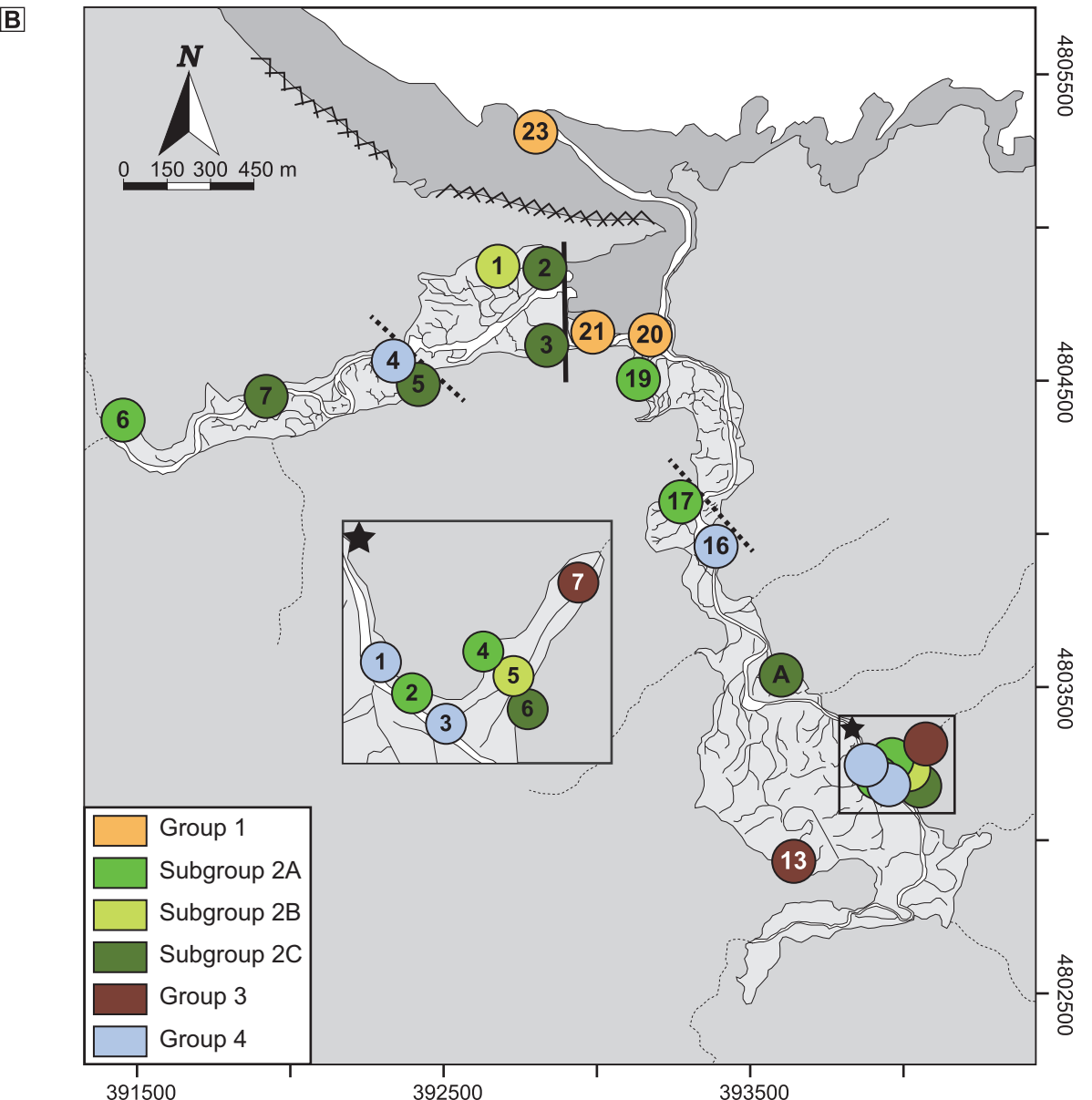
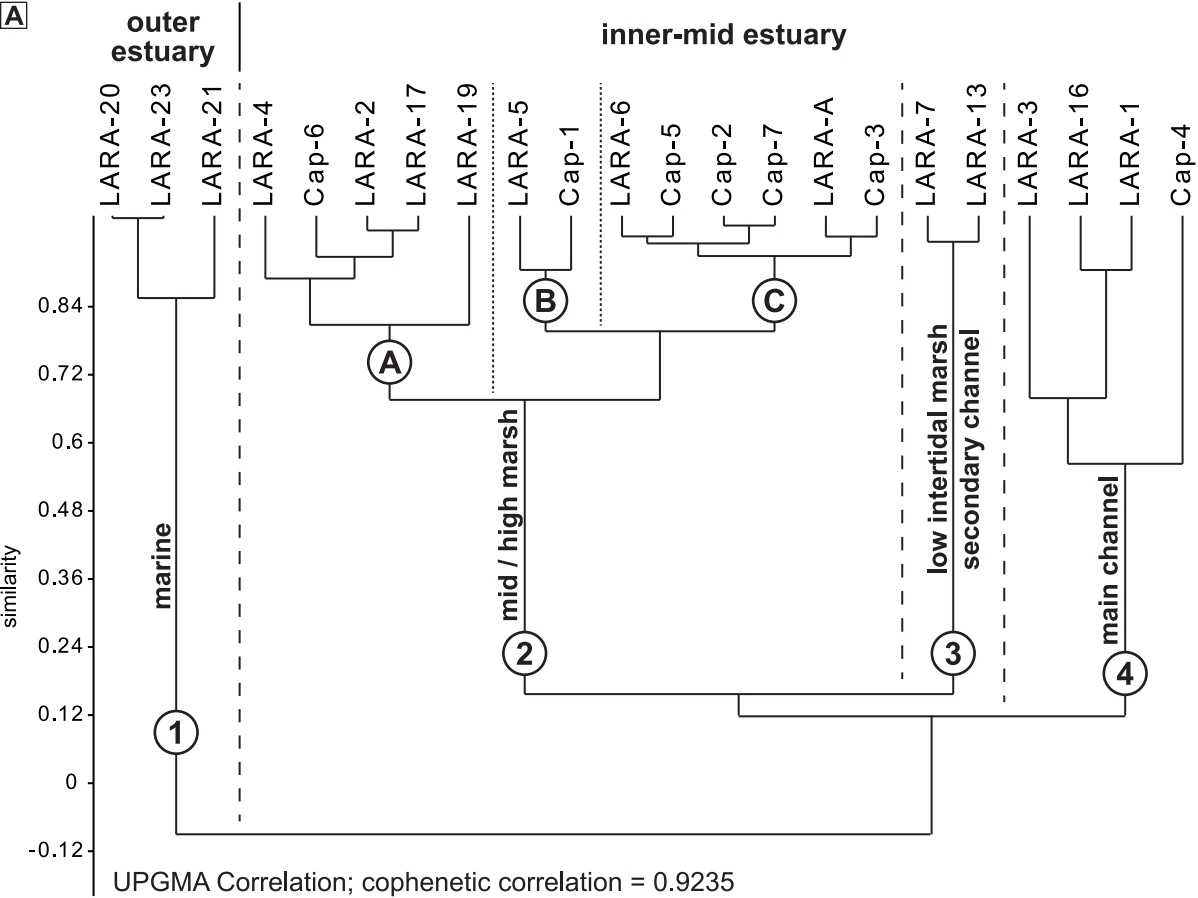
La Rabia

**B**

El Capitán





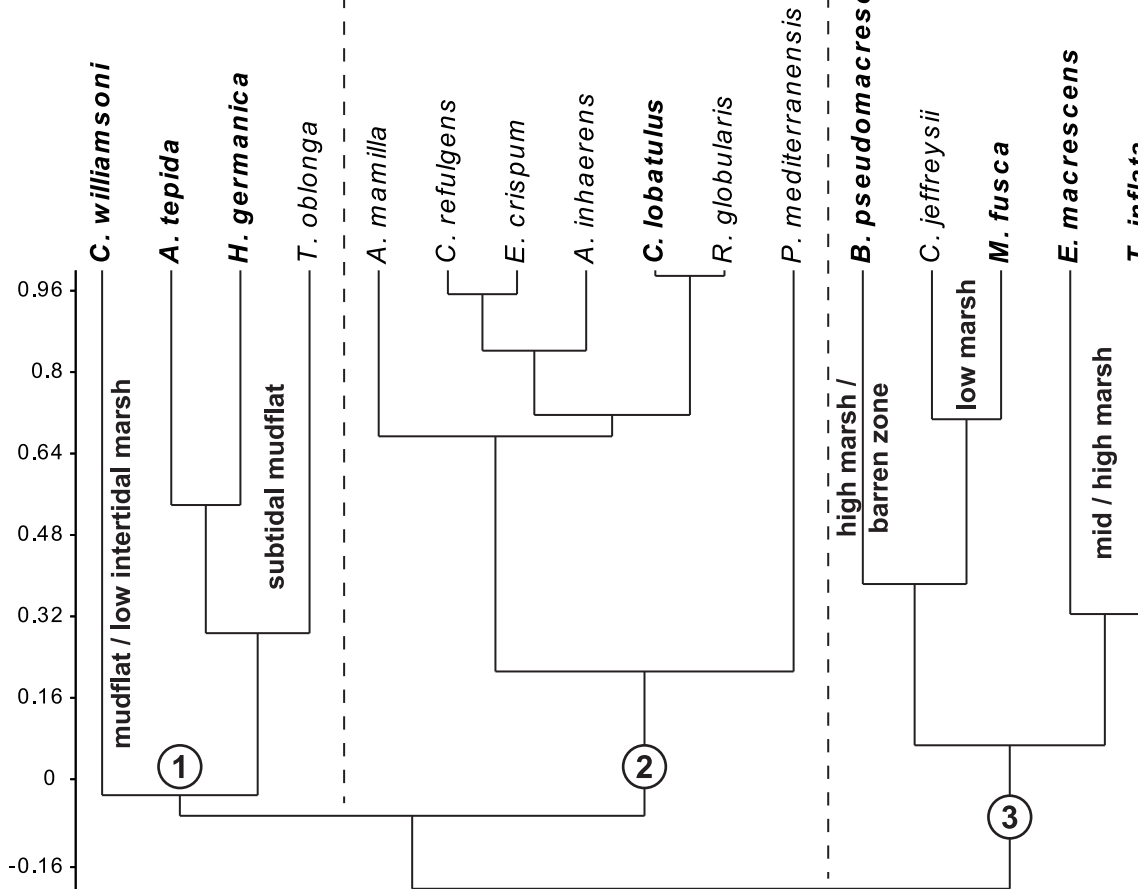


euirhaline

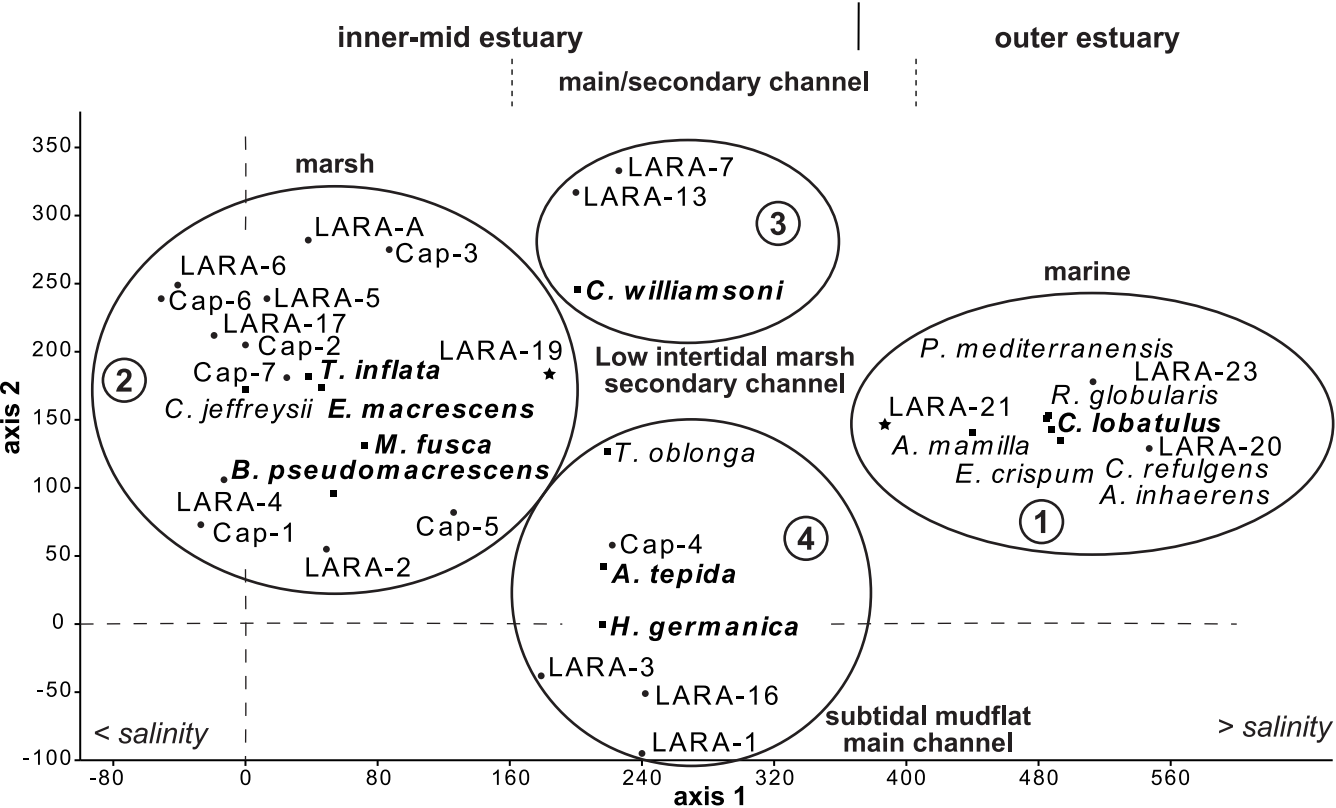
marine

marsh

similarity



UPGMA Correlation; cophenetic correlation = 0.9372



Axis 1: variance = 43.6%, eigenvalue = 0.7944; Axis 2: variance = 22.9%, eigenvalue = 0.3035

