



Indicative value of benthic foraminifera for biomonitoring: Assignment to ecological groups of sensitivity to total organic carbon of species from European intertidal areas and transitional waters

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ABSTRACT

This work contributes to the ongoing work aiming at confirming benthic foraminifera as a biological quality element. In this study, benthic foraminifera from intertidal and transitional waters from the English Channel/European Atlantic coast and the Mediterranean Sea were assigned to five ecological groups using the weighted-averaging optimum with respect to TOC of each species. It was however not possible to assign typical salt marsh species due to the presence of labile and refractory organic matter that hampers TOC characterization. Tests of this study species' lists with Foram-AMBI on two independent datasets showed a significant correlation between Foram-AMBI and TOC, confirming the strong relation between foraminifera and TOC. For one of the validation datasets, associated macrofaunal data were available and a significant correlation was found between the foraminiferal Foram-AMBI and the macrofaunal AMBI. The here proposed lists should be further tested with sensitivity-based indices in different European regional settings.

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1. Introduction

Benthic foraminifera are increasingly recognized as indicators of human-induced stress (e.g., Alve, 1995; Francescangeli et al., 2016, 2020; Polovodova Asteman et al., 2015), such as oil spills (e.g., Morvan et al., 2004), drill cutting (e.g., Mojtahid et al., 2006), heavy metals (e.g., Martins et al., 2013), urban sewage (e.g., Melis et al., 2019), and aquaculture (e.g., Debenay et al., 2015). Recent developments in benthic foraminiferal biotic indices (Alve et al., 2016; Bouchet et al., 2012; Barras et al., 2014; Dimiza et al., 2016; Jorissen et al., 2018) have provided further opportunities for the application of this meiobenthic group as a biological quality element for ecological quality status (EcoQS) assessment in legislations concerning transitional waters (hereafter TWs; see definition in McLusky and Elliott, 2007) and marine environments (see review in Sousa et al., 2020). Foraminiferal indices based either on species diversity (Alve et al., 2009; Bouchet et al., 2012, 2013) or on the sensitivity of species to organic pollution (Alve et al., 2016; Barras et al., 2014; Dimiza et al., 2016; Jorissen et al., 2018), have been designed and successfully applied to assess EcoQS of benthic habitats (Alve et al., 2019; Bouchet et al., 2012, 2013, 2018a, 2020; Damak et al., 2020; Denoyelle et al., 2010; Dijkstra et al., 2017; El Kateb et al., 2020; Francescangeli et al., 2016; Jesus et al., 2020; Mojtahid et al., 2006, 2008; Melis et al., 2019).

In 2011, the informal Foraminiferal Bio-Monitoring (FOBIMO) international working group (WG) was established with the aims (i) to standardize methods for the use of benthic foraminifera in environmental biomonitoring (Schönfeld et al., 2012) and (ii) to unify the effort of “foraminiferologists” to establish a common biotic index to assess the EcoQS (Alve et al., 2016; Jorissen et al., 2018). The first aim of the FOBIMO WG was to agree to focus on and design an index based on the ecological response of benthic foraminiferal species to total organic carbon (TOC). Specifically, this implied assessing the level of sensitivity/tolerance of foraminiferal taxa to TOC by assigning them to ecological groups (EGs). In the pioneer work of Alve et al. (2016), the authors proposed to assign benthic foraminifera to five EGs following the terminology and definitions used in the macrofauna-based AZTI Marine Biotic Index (AMBI) (Borja et al., 2000) *i.e.*, sensitive (EGI), indifferent (EGII), tolerant (EGIII), second-order opportunistic (EGIV) and first-order (most) opportunistic (EGV) (see further details in the Material and methods section). Recently, Jorissen et al. (2018) suggested using a more explicit terminology and definitions for benthic foraminifera; describing species belonging to EGIII as “third-order opportunists”.

In the species assignments used in macrofaunal AMBI, the peculiar natural features of intertidal, transitional and marine habitats or the various climate regime occurring in different geographical basins are not considered. This means that a species’ indicative value is the same in an estuary and in open marine waters or in the Mediterranean Sea and in the Baltic Sea. In fact, the use of a single species classification list means that the indicative value of a species is a static concept; *i.e.*, a species is expected to have a similar sensitivity or tolerance to organic matter (OM) wherever it occurs and regardless its adaptation ability. However, some species are known to be plastic enough to adapt to their environment variability and could change their autecology requirements along environmental gradients (see review in Zettler et al., 2013 and references therein). Hence, the FOBIMO WG decided to establish four sub-WGs reflecting four main types of environments *i.e.*, (i) North-East Atlantic and Arctic fjords, continental shelves, and slopes (Alve et al., 2016), (ii) open marine waters in the Mediterranean Sea (Jorissen et al., 2018), (iii) intertidal areas and TWs (the present contribution), and (iv) tropical environments. Each sub-WG had the aim to define a list of the response to TOC of as many species as possible. Earlier, the NE Atlantic and Arctic Oceans and the Mediterranean Sea open environments sub-WGs have already published their respective species (see above). These lists of species can be used in the different sensitivity-based indices designed for benthic foraminifera that use the relative

proportion of sensitive, tolerant and opportunistic species to assess EcoQS, either foraminifera-based AMBI (Foram-AMBI, Alve et al., 2016) or comparable methods (e.g., Barras et al., 2014; Dimiza et al., 2016). These studies show a strong response of marine species to TOC, which is explained by the fact that TOC in such marine systems mainly consists of labile organic matter. However, it is questionable if this method to assign species according to their response to TOC gradients is also applicable in intertidal areas and TWs, where TOC is reflecting labile and refractory organic matter (Pusceddu et al., 2003). Noticeably, salt marsh sediments commonly exhibit very high TOC values, due to the halophile vegetation, responsible for the presence of large quantities of poorly reactive organic matter (Armynot du Châtelet et al., 2009a; Leorri et al., 2018; Middelburg et al., 1997).

This paper presents the first results of the sub-WG on intertidal areas and TWs along the European Atlantic coasts from the Belgian-French border down to Portugal and in the Mediterranean Sea.

The construction of ecological species lists is hampered by the fact that benthic foraminiferal taxonomy may vary considerably among studies, which complicated a reliable assignment to EGs. Specifically, foraminiferal species are traditionally defined on morphological criteria and are therefore mostly morphospecies. Molecular studies have shown that some of these morphospecies include cryptic or pseudocryptic species (Darling et al., 2016; Hayward et al., 2004; Richirt et al., 2019).

Another complication is that intertidal areas and TWs are characterized by strong environmental gradients and high natural variability of physico-chemical parameters (e.g., salinity, temperature, grain-size, dissolved oxygen; Elliott and Quintino, 2007) coupled with natural organic matter enrichment (Pusceddu et al., 2003). Intertidal and TWs, therefore, often behave as naturally stressed environments (Dauvin, 2007; Elliott and Quintino, 2007), but also commonly experience high levels of anthropogenic stresses such as aquaculture (Bouchet and Sauriau, 2008), habitat destruction (e.g., agricultural uses, coastal reinforcements), urban sewage and industrial discharges (Armynot du Châtelet et al., 2004; Morvan et al., 2004). Species distribution in these environments is the result of the complex interplay between natural and human-induced stressors. Therefore, it is challenging to achieve a reliable assignment of benthic foraminiferal species from these environments to EGs according to species response by considering only TOC.

In this context, the present study aimed at (i) developing an objective protocol for the species’ assignment to EGs, (ii) investigating if it is possible to assign benthic foraminiferal species from intertidal areas and TWs from the considered geographical regions to the five EGs described in Alve et al. (2016) according to species responses to sediment TOC content, (iii) if applicable, validating the established lists by testing them using a sensitivity-based index on separate and independent datasets from the same geographic regions, and (iv) testing the hypothesis that species ecological requirements may vary between habitats/ecosystems and along latitudinal gradients by comparing species assignment lists from the present study. Because of the particular characteristics of foraminiferal habitats and communities, we decided to present the foraminiferal species assignments split in two lists: one for the English Channel/European Atlantic and one for the Mediterranean region. The recently developed Foram-AMBI (Alve et al., 2016), adapted from AMBI for benthic foraminifera, was used to test the reliability of these ecological species lists.

2. Material and methods

2.1. Ecological groups of sensitivity to TOC

Benthic macrofaunal species are traditionally assigned to five groups of sensitivity to OM (e.g., Borja et al., 2000; Glémarec and Hily, 1981; Hily, 1983; Simbora and Zenetos, 2002) based on the seminal work of Pearson and Rosenberg (1978). Species are meant to be indicative of the prevailing environmental conditions; *i.e.*, the level of organic carbon enrichment where they are found. Taken from Grall and Glémarec

(1997) and Borja et al. (2000), the following characteristics were used by Alve et al. (2016) and Jorissen et al. (2018) to assign benthic foraminiferal species to the five EGs considering their response to TOC. These characteristics are used in the present study:

- Group I (EGI). “Sensitive species” are sensitive to TOC enrichment. Their relative abundance is highest at the lowest TOC values and drops to zero as organic carbon concentration increases.
- Group II (EGII). “Indifferent species” are indifferent to initial stages of organic carbon enrichment. They never dominate the assemblage. They occur in low relative abundance over a broad range of organic carbon concentrations, but are absent at very high concentrations.
- Group III (EGIII). “Tolerant species” are tolerant to excess organic carbon enrichment. They may occur at low TOC; their highest frequencies are stimulated by organic carbon enrichment but they are absent at very high organic carbon concentrations. This group has been termed “third-order opportunistic species” by Jorissen et al. (2018).
- Group IV (EGIV). “second-order opportunistic species” show a clear positive response to organic carbon enrichment with maximum abundances between the maxima of EGIII and EGV.
- Group V (EGV). “first-order opportunistic species” exhibit a clear positive response to excess organic carbon enrichment with maximum abundances at a higher stress level induced by organic load than species belonging to EGIV. At even higher TOC concentrations, foraminifera are not able to survive.

Based on Hily’s model (Glémarec and Hily, 1981; Hily, 1984; Majeed, 1987), the theoretical succession of the relative abundance of each EG, was adapted to benthic foraminiferal species along a TOC gradient. According to Jorissen et al. (2018), the five categories are distributed as follows (Fig. 1).

2.2. Criteria to select datasets

Only previous studies in areas that strictly follow the definition of intertidal and TWs were selected. In the European Water Framework Directive (WFD, 2000/60/EC), TWs are defined as “bodies of surface water in the vicinity of river mouths which are partially saline in character as a result of their proximity to coastal waters but which are substantially influenced by freshwater flows” (European Communities, 2000, p. 6). In

the Mediterranean Sea, TWs also include mesohaline, poly-euhaline and hyperhaline lagoons (Reizopoulou et al., 2018). We decided to follow the definition of McLusky and Elliott (2007) who specified the different types of water bodies belonging to intertidal and TWs in the context of the implementation of the WFD and further marine legislations (see Table 1).

Three further criteria had to be met to retain the datasets used for the assignments:

- the study had to be based on living benthic foraminifera. Note that all datasets used in the present study are based on rose Bengal-stained fauna;
- the foraminiferal and TOC data had to be from the same station (less than 1 m from the sampling point); when the authors of the study only provide the OM content (studies 10, 12 and 18, Table 3), it was converted to TOC using the following formula: $LOI = \sim 2 \text{ TOC}$ (Barillé-Boyer et al., 2003; Frangipane et al., 2009);
- only samples containing >50 stained specimens were considered following Alve et al. (2016).

All studies from the English Channel/European Atlantic except one (see Appendix A) are based on the >63 μm fraction, whereas in the Mediterranean Sea studies are based on the fraction >63 or >125 μm (Appendix B). In total, 21 studies were selected from the English Channel/European Atlantic intertidal and TWs (Fig. 2, Appendix A) and 21 ones from the Mediterranean Sea (Fig. 2, Appendix B). The complete datasets are presented in Bouchet et al. (2021).

Due to lack of standardization, different methods were used in the different studies to measure TOC; from the classical loss-on-ignition (LOI) to the more sophisticated use of an elemental analyser (EA). While the latter directly quantifies TOC concentration, the LOI measures the OM content. It is still often used in large surveys because it allows for a quick and cheap measurement of sedimentary organic matter (Luczak et al., 1997). It is generally accepted that LOI may overestimate TOC content compared to EA (Barillé-Boyer et al., 2003). In the datasets from the English Channel/European Atlantic coast, the ranges of TOC obtained with LOI and EA are fairly similar. Apart from one study in the Ebro delta, all the studies in the Mediterranean Sea used an EA to measure TOC content. Therefore, TOC data from the different studies should be compared with caution.

Species names were homogenized among studies following the World Register of Marine Species (WoRMS, Hayward et al., 2020a). Only accepted scientific names from WoRMS are used in this study, and the

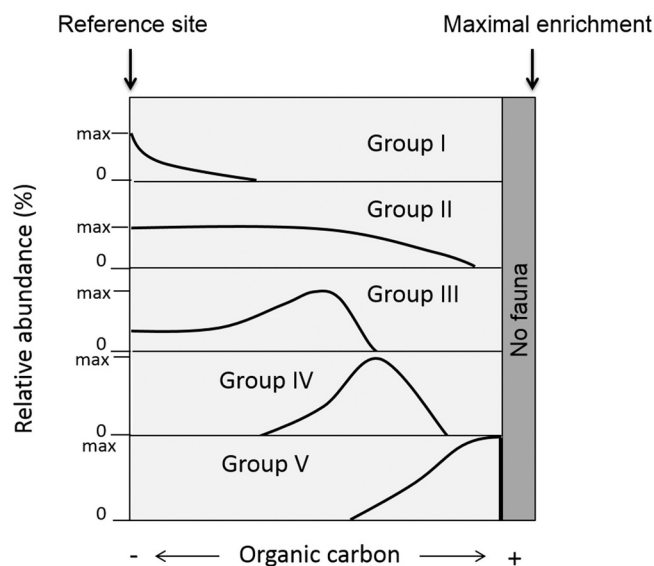


Fig. 1. Theoretical graph providing the succession of benthic foraminifera belonging to the five EGs according to their response to organic carbon enrichment. (From Jorissen et al. (2018))

Table 1

Water body types of intertidal areas and TWs according to McLusky and Elliott (2007); the “Artificial water body” type (European Communities, 2000, p. 6) was added to complete the original table.

Water body types	Natural features
Classical estuary	Tidally dominated at the seaward part; salinity notably reduced by freshwater river inputs; riverine dominance landward
Lentic non-tidal lagoon	Limited exchange with the coastal area through a restricted mouth; separated from sea by sand or shingle banks, bars, coral, etc., shallow area, tidal range <50 cm
Lentic micro-tidal lagoon	As above but with tidal range >50 cm
Ria	Drowned river valley, some freshwater inputs; limited exchanges with coastal waters
Delta	Low energy, characteristically shaped, sediment dominated, river mouth area; estuary outflow
Coastal freshwater/brackish water plume	Outflow of estuary or lagoon, notably diluted salinity and hence differing biota than surrounding coast
Semi-enclosed bay/lagoon	Low energy, notably limited exchange with the open sea waters
Artificial water body	Harbors and docks, constructed dredging pools and coastal water bodies connected to the sea, created by human activities.

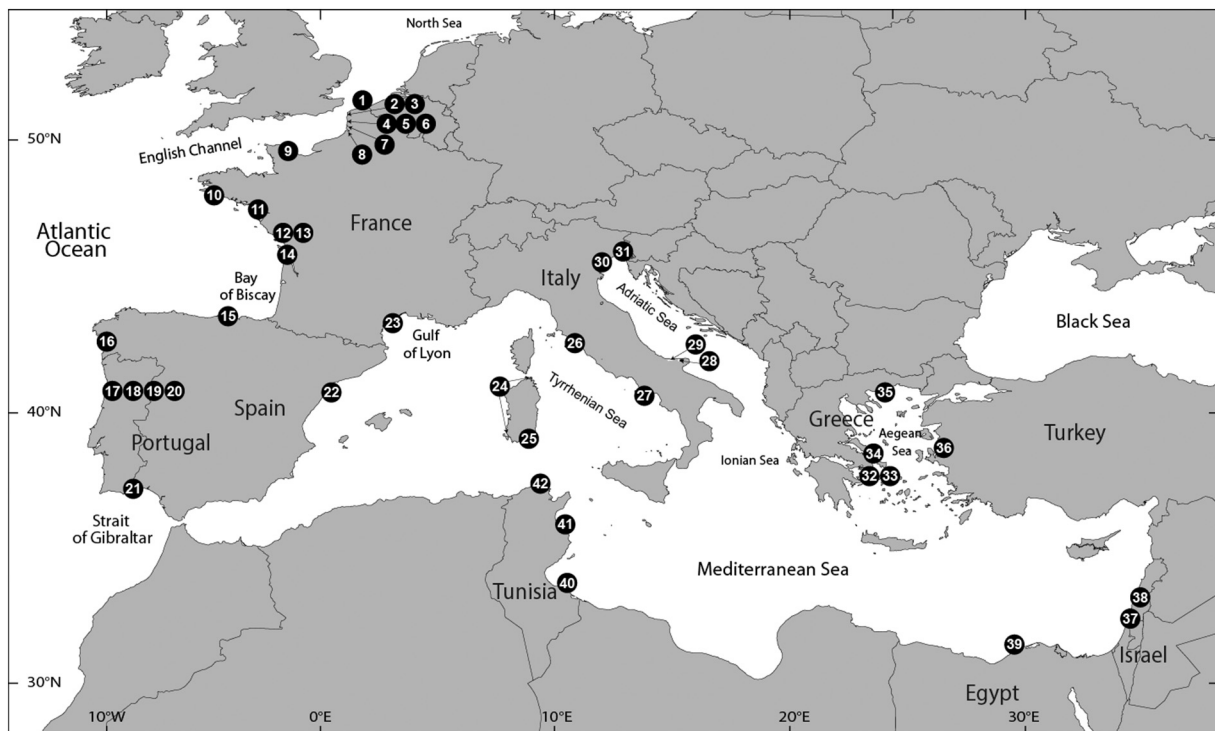


Fig. 2. Map showing the geographical distribution of the 42 studies used to assign the species from the English Channel/European Atlantic coast and the Mediterranean Sea intertidal and TWs. Numbers are the same in [Appendices A and B](#).

unique AphiaID identifier is reported for each species. The Aphia platform is an infrastructure aiming at capturing taxonomic and related data and information ([Vandepitte et al., 2015](#)). Each taxon added to the Aphia database receives a unique and persistent identifier, the AphiaID. Once assigned to, the name and its corresponding ID cannot be physically deleted from the database, ensuring that the information is not lost.

2.3. Species assignment according to relation with TOC content

Indicator species are meant to provide information about environmental conditions. The knowledge of the environmental requirements of a species can be used to detect changes in abiotic conditions or to assess the environmental health of the study area. The assignment of foraminiferal species to the five EGs involves determining which species are more abundant at low, medium and high TOC concentrations.

This can be achieved in different ways. The macrofaunal AMBI list is based on a literature review allowing an inventory of the individual species responses to organic matter gradients, completed in some cases by experts' opinion ([Borja et al., 2019](#)). If the latter sounds rather subjective, the former should be reasonably objective. The Foram-AMBI lists for open marine environments of the NE Atlantic and Arctic Oceans ([Alve et al., 2016](#)) and the Mediterranean Sea ([Jorissen et al., 2018](#)) are both based on an objective review of available datasets, sometimes (in case of inconclusive data) with a small contribution of best expert judgment ([Jorissen et al., 2018](#)). These publications included a few plots

aim was to seek for an objective method for species assignments in order to avoid using "best expert judgment". The weighted-averaging (WA) optimum and tolerance approach was used ([Birks et al., 1990](#); [Ter Braak, 1987](#)). The idea behind WA is that in a coastal lagoon with a certain TOC range, benthic foraminifera with their TOC optimum close to the coastal lagoon's TOC concentrations will most likely be the most abundant species. A simple and ecologically reasonable estimate of a benthic foraminiferal species' optimum is the average of all TOC values for intertidal areas and TWs in which the species occurs, weighted by the species relative abundance (WA regression). The estimated optimum allows to give an objective assessment of the species environmental requirements. To summarize, the WA optimum method is rapid, easy to implement, theoretically sound, robust ([Birks et al., 1990](#)) and leads to an objective assessment of species-specific indicative values.

2.4. Foram-AMBI

Foram-AMBI was used to test the species lists. It is adapted from the macrofauna-based AMBI ([Borja et al., 2000](#)), and was first introduced by [Alve et al. \(2016\)](#) for fjords, continental shelves and slopes in the North-East Atlantic and Arctic Oceans. Foram-AMBI uses the relative abundance of selected species to assess the EcoQS of marine systems and TWs.

Foram-AMBI was calculated using the AMBI formula ([Borja et al., 2000](#)):

$$\text{Foram-AMBI} = \{(0 \times \% \text{EGI}) + (1.5 \times \% \text{EGII}) + (3 \times \% \text{EGIII}) + (4.5 \times \% \text{EGIV}) + (6 \times \% \text{EGV})\} / 100$$

exemplifying species-specific relative abundance patterns plotted against TOC, to better explain the followed methodology.

In the present study's effort to produce lists of foraminiferal species for the European Atlantic and Mediterranean intertidal and TWs, the

For the validation and test phase of the species lists using Foram-AMBI, awaiting a specific calibration for foraminifera, EcoQS were determined following the criteria established for the macrofauna-based AMBI ([Table 2, Borja et al., 2000](#)). In view of the first available results,

Table 2

Criteria for determining EcoQS according to Foram-AMBI (following criteria of macrofauna AMBI, Borja et al., 2000) and correspondence with sediment TOC (Bakke et al., 2010; Viaroli et al., 2004).

EcoQS and associated color code	Bad	Poor	Moderate	Good	High
Foram-AMBI	>5.5	4.3–5.5	3.3–4.3	1.2–3.3	<1.2
Total organic carbon (%)	>4.1	3.4–4.1	2.5–3.4	2.0–2.5	<2.0

the class limits must probably be redefined for foraminifera.

2.5. Testing the ecological assignment lists

In order to test our species assignment to EGs according to their response to TOC, Foram-AMBI was applied on two independent datasets from the English Channel/European Atlantic coast area and the Mediterranean Sea, which were not included in the master tables for calculation of the species assignment (to avoid circular arguments). Great attention was paid to find studies where a clear organic carbon gradient enrichment was observed.

In the English Channel/European Atlantic coast area, Foram-AMBI was applied on a study of the effects of oyster farming on living benthic foraminifera in SW France (Bouchet, 2007). Oyster farming leads to organic matter enrichment in the surrounding environment (Bouchet and Sauriau, 2008). The sampling stations were located in four different unvegetated intertidal mudflats harboring oyster parks actively used by shellfish operators: Rivedoux (R), Yves (Y), Charente (CH) and Daires (D) (Fig. 3; more details on the sampling sites in Bouchet and Sauriau, 2008). At all sampled stations, benthic foraminifera and macrofauna were sampled at the same time, allowing for a sound comparison between Foram-AMBI and AMBI, which is based on benthic macro-invertebrates (AMBI results were published in Bouchet and Sauriau,

2008).

In the Mediterranean Sea, Foram-AMBI was tested on data from the harbor of Cagliari in the South of Sardinia in Italy (Schintu et al., 2016) where a clear OM enrichment gradient was observed. This harbor includes the oil terminal of one of the largest oil refineries in the Mediterranean Sea. Sampling was carried out in four unvegetated zones of the harbor: (i) stations H1–H7: the historical port (HP), (ii) stations L1–L3: the Santa Gilla lagoon, (iii) stations G1–G10: the gulf facing the industrial areas, and (iv) stations B1–B3: control stations (Fig. 4).

2.6. Statistical analysis

The next two steps were followed to assign benthic foraminiferal species to the five EGs:

1. The WA optimum and tolerance were computed for each species to determine its preference with respect to TOC (%) using the optimos.prime R package (Sathicq et al., 2020).
2. Species assignment to EGs was done as follows: if a species had an optimum in the TOC range 0–2%, the species was assigned to EG1; in the range 2–2.5%, the species was assigned to EG2; in the range 2.5–3.4%, 3.4–4.1%, and above 4.1% to EGII, EGIII, EGIV and EGV. This is based on TOC-derived EcoQS (see Table 2; Bakke et al., 2010; Viaroli et al., 2004). One species' list per region was produced.

Typical example for each EG is shown for each region to visualize pattern of species response along the TOC gradient. A locally weighted scatterplot smooth line (LOESS) was fitted to each scatter plot. Marginal plots were added to each scatter plot to show the frequency of distribution of occurrences along the TOC gradient. The median of the distribution of the occurrences was also computed.

Two master tables (available in Bouchet et al., 2021) were used in the above-described procedure. These master tables included TOC percentages and species relative abundances data of the 21 studies from the

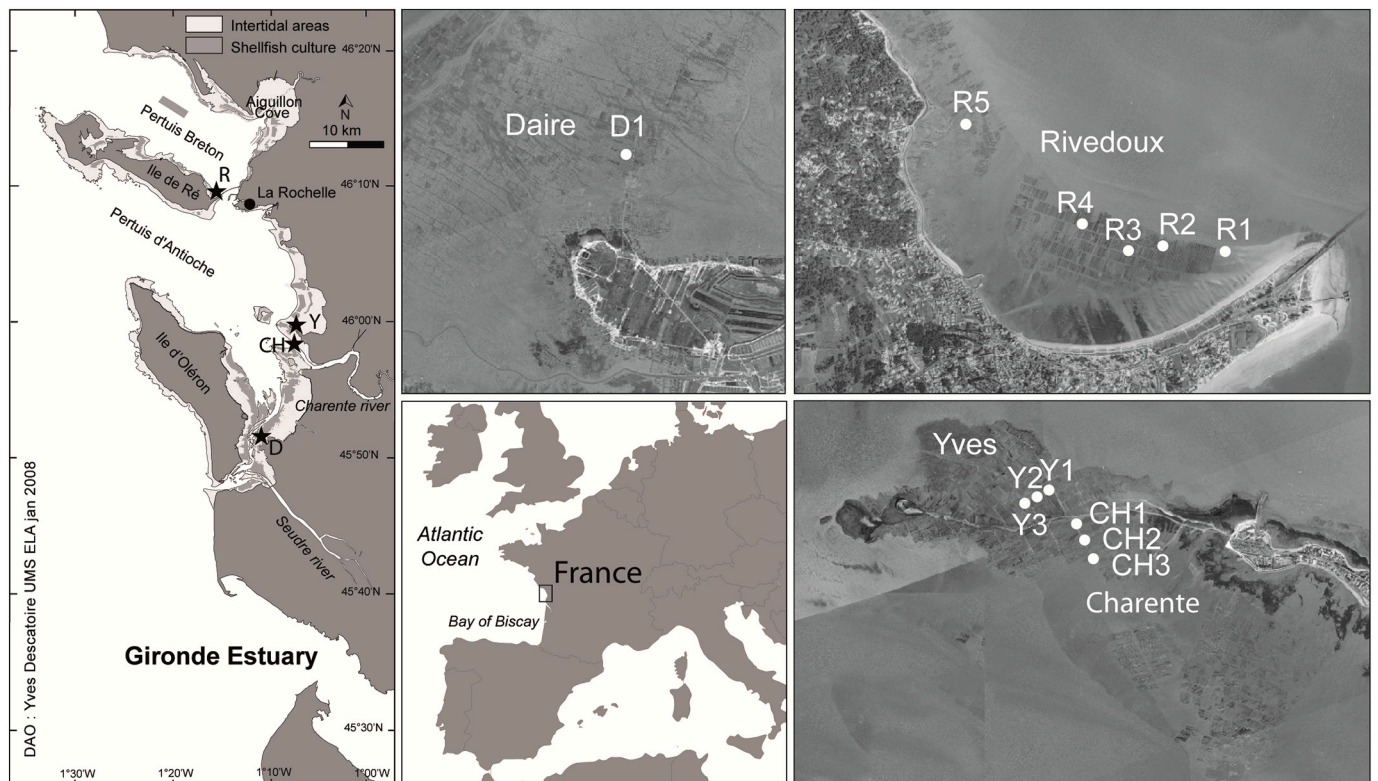


Fig. 3. Map of the sampling stations in the Pertuis Charentais (CH: Charente, D: Daires, R: Rivedoux and Y: Yves), SW France (from Bouchet and Sauriau, 2008).

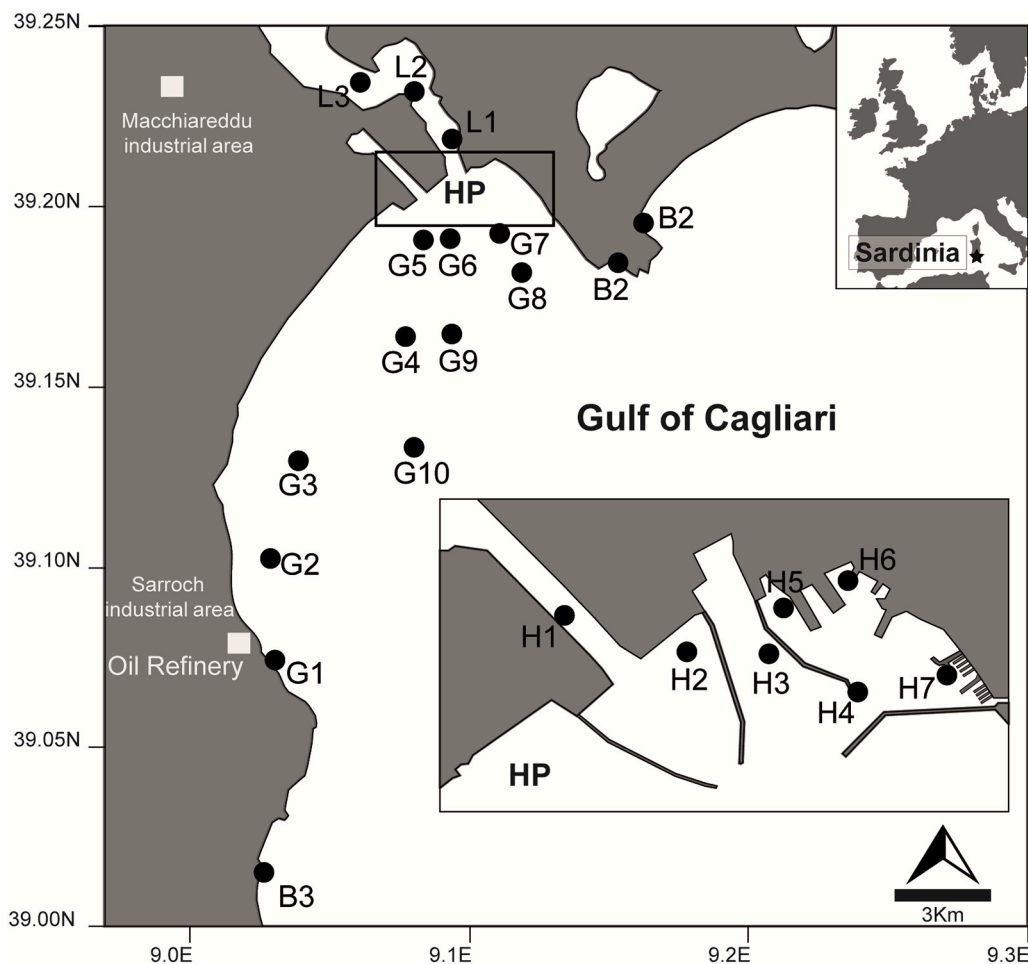


Fig. 4. Map of the sampling stations in the harbor of Cagliari in Sardinia (Italy). HP = historical port. (Adapted from Schintu et al. (2016)).

English Channel/European Atlantic coast (587 samples) and the 21 studies from the Mediterranean Sea (301 samples).

As the distribution of OM, AMBI and Foram-AMBI was normally distributed (Kolmogorov-Smirnov test, $p > 0.01$), parametric statistics were used for the Cagliari and Pertuis parameters. The relation between Foram-AMBI, AMBI and organic matter (TOC values being not available for the Pertuis Charentais and Cagliari datasets) was quantified by mean of a Pearson's correlation coefficient R^2 .

All these calculations were made using the statistical language R version 3.6.3 (R Core Team, 2020).

3. Results

3.1. Species assignments to EGs according to total organic carbon

3.1.1. The English Channel/European Atlantic coast

In the English Channel/European Atlantic intertidal and TWs datasets, TOC ranged between 0 and 16% (Appendix A). Fig. 5 presents a typical example of species-response curves for each of the five EGs. Most of the five figured species had a characteristic unimodal distribution pattern. However, the relative abundance distribution of *Criboelphidium excavatum* and *C. williamsoni* was bimodal, with peaks at ~ 0 –1% and ~ 7 –12%, and at ~ 2 –4% and ~ 7 –9%, respectively. In total, 77 species from this geographic region were assigned: 22 in EGI, 13 in EGII, 23 in EGIII, 6 in EGIV and 13 in EGV (Appendix C). Despite their high optimum values, typical salt marsh species (*Balticammina pseudomacrescens*, *Entzia macrescens* and *Trochammina inflata*), which are dominant in environments characterized by very high natural TOC values, were not

assigned. This is further explained in the discussion.

3.1.2. The Mediterranean Sea

In the Mediterranean Sea intertidal and TWs datasets, TOC ranged between 0.07 and 17.8% (Appendix B). Fig. 6 presents typical examples of species-response curves for the five EGs. The relative abundance of most of the five figured species had unimodal distribution patterns. However, the relative abundance distribution of *Criboelphidium gunteri* was bimodal, with peaks at ~ 2 –3% and ~ 9 –11%. In total, 79 species from this geographic region were assigned: 42 in EGI, 7 in EGII, 17 in EGIII, 4 in EGIV and 9 in EGV (Appendix D). Despite their high optimum values, typical salt marsh species (*Trochammina inflata*, *Entzia macrescens* and *Haplophragmoides wilberti*), which are dominant in environments characterized by very high natural TOC values, were not assigned. This point is further addressed in the discussion.

3.1.3. Comparison of species assignments between the existing lists of benthic foraminifera

In total, the two lists established in this study for the English Channel and the European Atlantic and the Mediterranean Sea intertidal and TWs have 35 species in common (Table 3). Among these 35 species, ten species were assigned to the same EG in both regions, ten with a difference in their assignment of only one category, whereas fifteen taxa showed an offset of two categories or more. Very surprisingly, the Elphidiidae *Criboelphidium excavatum*, *C. gunteri* and *C. williamsoni*, *Bolivina* spp. and *Quinqueloculina* spp. exhibited an offset of three to four categories.

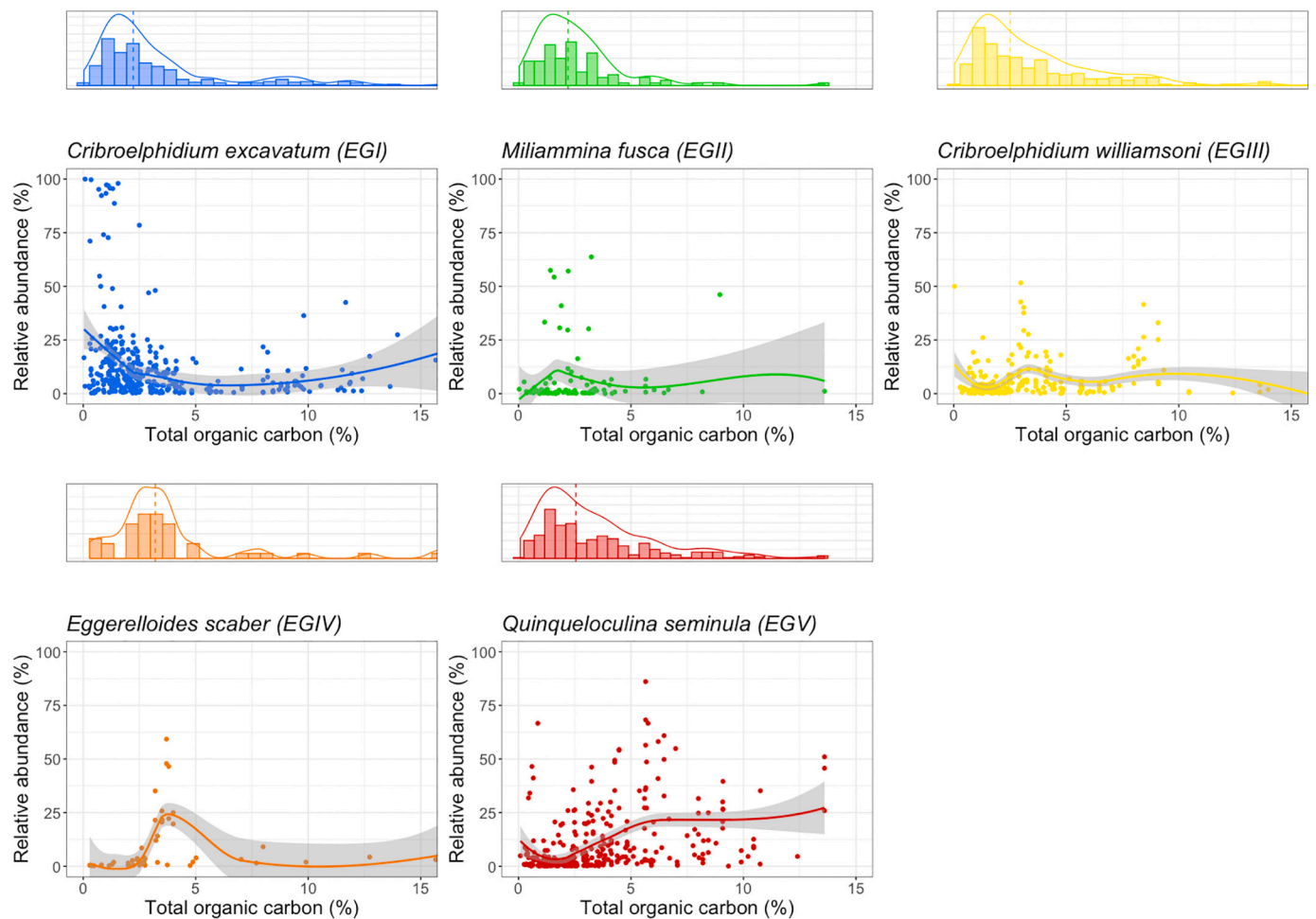


Fig. 5. Scatter plot fitted with a locally weighted scatterplot smooth line to visualize species response patterns along the total organic carbon (%) gradient. Typical examples are given for each of the five Foram-AMBI EGs from the English Channel/European Atlantic intertidal and TWs (one example per EG, shaded area is the 95% confidence interval): *Criboelphidium excavatum* (EG I), *Miliammina fusca* (EG II), *Criboelphidium williamsoni* (EG III), *Eggerelloides scaber* (EG IV) and *Quinqueloculina seminula* (EG V). Marginal plots showed the frequency distribution of occurrences along the TOC gradient; and dashed line marked the median.

3.2. Test of the validity of the species' lists

3.2.1. The English Channel/European Atlantic coast

In the Pertuis Charentais dataset, there was a significant positive correlation between Foram-AMBI and OM, and between AMBI and OM ($R^2 = 0.67$ $p = 0.001$ and $R^2 = 0.66$ $p = 0.001$; Fig. 7A and B; respectively). All foraminiferal species occurring at the sampling sites were assigned in EGs. Foram-AMBI ranged from 1.9 to 3.3 (Fig. 7A) and AMBI from 1.2 to 4 (Fig. 7B). They were significantly correlated ($R^2 = 0.56$, $p < 0.01$; Fig. 7C). Based on Foram-AMBI, EcoQS varied between good and moderate (Fig. 7). Both indices agreed that the best EcoQS was at the reference sampling station R1. Assessments of EcoQS derived from Foram-AMBI and AMBI partially match but were in some cases contradictory. There was 50% of full agreement between the two indices derived-EcoQS (Fig. 7A and B).

3.2.2. The Mediterranean Sea

In the harbor of Cagliari, there was a significant positive correlation between Foram-AMBI and organic matter ($R^2 = 0.42$, $p = 0.001$; Fig. 7D). The relative abundance of species unassigned to EGs varied from 0.4 to 16.9%. Stations with the lowest organic matter (OM) values exhibited High EcoQS (Fig. 7D). With increasing OM content, Foram-AMBI-derived EcoQS changed to good i.e., slightly disturbed. There was a cluster of six samples with low TOC and low Foram-AMBI while all other samples had higher TOC and higher Foram-AMBI values.

4. Discussion

4.1. Natural variability of intertidal and TWs and reference conditions

The promising results of the present study do not, however, warrant an easy implementation of Foram-AMBI and comparable methods in intertidal areas and TWs. Biotic indices based on the indicator species concept, like AMBI, are not fully reliable to assess EcoQS in these water body types (i.e., Borja et al., 2003; Blanchet et al., 2008; Bouchet and Sauriau, 2008; Salas et al., 2004). In fact, the natural features of these ecosystems hamper the disentangling of natural- and human-induced changes. In particular, silt, clay and OM sedimentary contents are naturally high in intertidal areas and TWs, promoting tolerant and opportunistic species, while sensitive species naturally decline (Elliott and Quintino, 2007; Munari and Mistri, 2008). In intertidal areas and TWs, benthic communities could therefore be naturally similar to those found in anthropogenically-disturbed habitats (Blanchet et al., 2008; Munari and Mistri, 2008). Consequently, pristine, naturally disturbed intertidal areas and TWs could easily be misclassified in moderate to bad EcoQS (the so-called “estuarine quality paradox”; Dauvin, 2007; Dauvin and Ruellet, 2009; Elliott and Quintino, 2007), severely complicating the decision-making (Blanchet et al., 2008; Muniz et al., 2005; Quintino et al., 2006; Salas et al., 2004). The natural features of intertidal areas and TWs may also affect the outcome of sensitivity-based foraminiferal indices like Foram-AMBI and comparable methods. The definition of

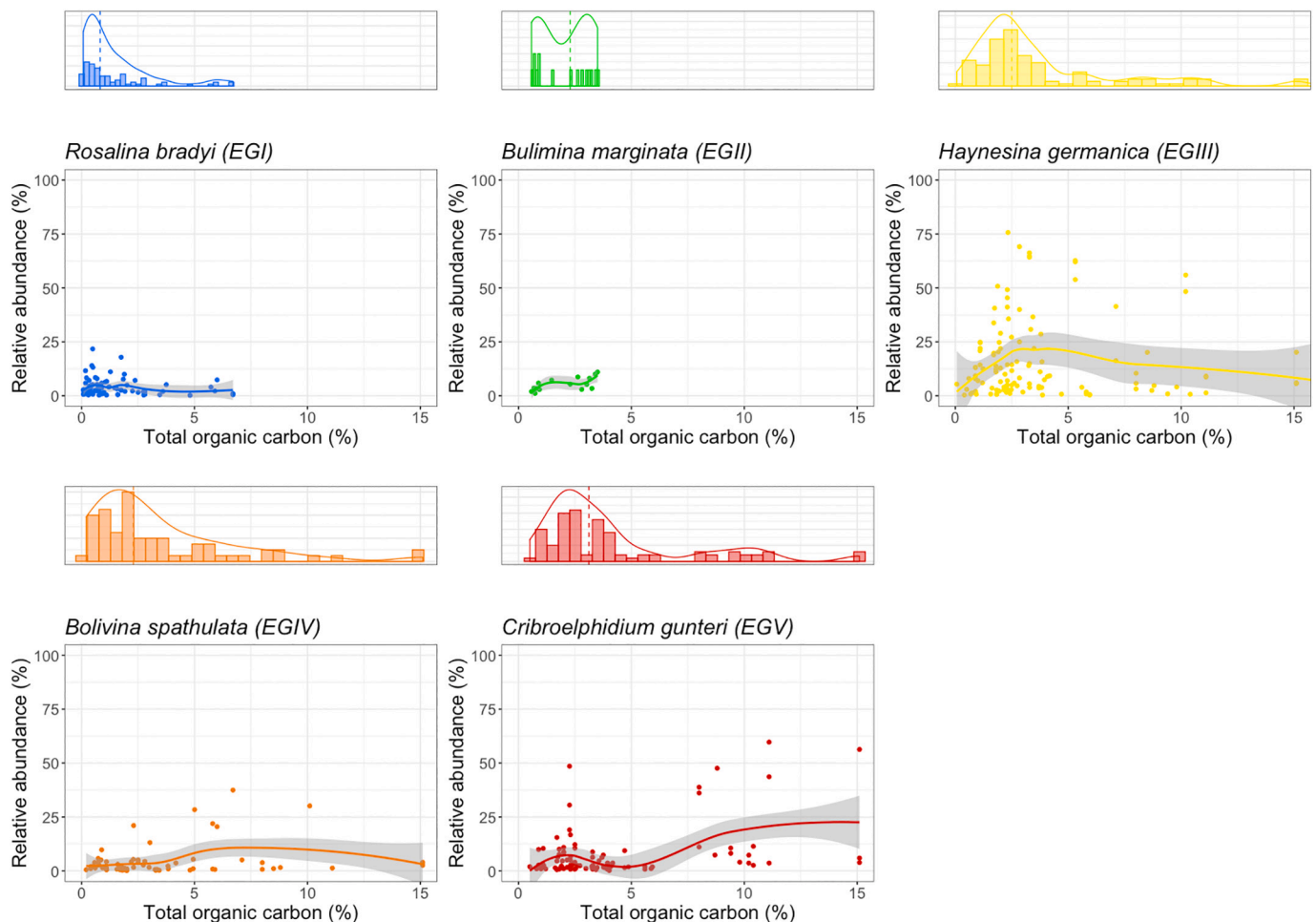


Fig. 6. Scatter plot fitted with locally weighted scatterplot smooth line to visualize species response patterns along the total organic carbon (%) gradient. Examples are given for each of the five Foram-AMBI EGs from the Mediterranean Sea intertidal and TWs (one example per EG, shaded area is the 95% confidence interval): *Rosalina bradyi* (EG I), *Bulimina marginata* (EG II), *Haynesina germanica* (EG III), *Bolivina spathulata* (EG IV) and *Cribroelphidium gunteri* (EG V). Marginal plots showed the frequency distribution of occurrences along the TOC gradient; the dashed line marks the median.

water-body type-specific or local reference conditions is absolutely necessary to overcome such limitations. In fact, in order to assess the health of TWs and marine systems, it is mandatory to define reference conditions or to set targets according to marine legislations. For instance, a more robust assessment of EcoQS for TWs was obtained with benthic foraminifera using site-specific local reference conditions in the Oslofjord (Norway) (Dolven et al., 2013), in the Boulogne-sur-Mer harbor (France) (Francescangeli et al., 2016) and in the Santos estuary (Brazil) (Jesus et al., 2020). Furthermore, geochemical analyses of dated sediment cores can be used in combination with benthic foraminifera to determine ecological reference conditions in TWs (Klootwijk et al., 2021; Hess et al., 2020).

4.2. Assignment of benthic foraminifera from intertidal and TWs to EGs according to TOC response patterns

It is generally accepted that EcoQS obtained with AMBI (and Foram-AMBI) are valid only if species unassigned to EGs account for less than 20% (Borja and Muxika, 2005). In the two validation tests of the Foram-AMBI, there were virtually no unassigned species in the Pertuis Charpentais dataset, and only 16.9% in the Harbor of Cagliari, warranting the validity of the EcoQS assessment. This suggests that enough species from intertidal and TWs have been assigned to test the lists over a large spatial scale in Europe.

For decades, increased supply of OM to coastal waters has been

considered to have a negative effect on ecosystems (Pearson and Rosenberg, 1978). As a consequence, TOC has become a typical indicator of environmental stress. Salt marshes are, per definition, vegetated by halophilic plants which are terrestrial in origin (Middelburg et al., 1997). Therefore, marsh habitats are expected to be characterized by high TOC (Armynot du Châtelet et al., 2018) whether or not they are impacted by human activities and discharge of organic carbon. Consequently, in salt marshes, TOC may be not a suitable indicator of human-induced stress. In the present study, TOC was the only ecological factor considered for species assignment to EGs. Commonly, in salt marshes, sediment contains a mix of refractory and labile OM (Armynot du Châtelet et al., 2009a; Leorri et al., 2018; Middelburg et al., 1997). Noticeably, the labile (food) directly stimulates growth and reproduction, while the refractory (terrestrial origin) TOC is not directly bioavailable (Pusceddu et al., 2009). Furthermore, environmental conditions encountered at low tide (e.g., aerial exposure, low salinity, thermal stress) (Alve and Murray, 1999; Francescangeli et al., 2017) as well as seasonal changes (e.g., desiccation or increased salinity during the dry season) further constrain foraminiferal species (Cearreta et al., 2002; De Rijk and Troelstra, 1997). Species distribution patterns in salt marshes are therefore mainly the outcome of a complex interplay between a number of natural stressors (see review in Murray, 2006).

In case we would have rigorously applied the method to use the WA optimum to classify species to EG's, the dominant species in salt marshes *Entzia macrescens*, *Trochammina inflata*, *Haplophragmoides wilberti* and

Table 3

Comparison of species assignments between the English Channel and European Atlantic intertidal and TWs (ECEA) and the Mediterranean Sea intertidal and TWs (MedS).

	ECEA	MedS
<i>Ammobaculites balkwilli</i>	II	III
<i>Ammonia parkinsoniana</i>	II	I
<i>Ammonia tepida</i>	III	III
<i>Asterigerinata mamilla</i>	I	I
<i>Aubignyna perlucida</i>	V	V
<i>Bolivina dilatata</i>	III	II
<i>Bolivina ordinaria</i>	II	V
<i>Bolivina pseudoplicata</i>	II	V
<i>Bolivina striatula</i>	V	I
<i>Bolivina variabilis</i>	III	I
<i>Bolivina spathulata</i>	III	IV
<i>Bulimina elongata</i>	IV	III
<i>Bulimina marginata</i>	IV	II
<i>Buliminella elegantissima</i>	III	III
<i>Cibicidoides lobatulus</i>	I	I
<i>Cribrorophidium excavatum</i>	I	III
<i>Cribrorophidium gunteri</i>	III	V
<i>Cribrorophidium poeyanum</i>	I	III
<i>Cribrorophidium williamsoni</i>	III	I
<i>Elphidium advenum</i>	III	I
<i>Haynesina depressula</i>	I	I
<i>Haynesina germanica</i>	III	III
<i>Hopkinsina atlantica</i>	V	IV
<i>Hopkinsina pacifica</i>	V	V
<i>Miliammina fusca</i>	II	III
<i>Miliolinella subrotunda</i>	II	I
<i>Nonionoides turgidus</i>	III	III
<i>Planorbulina mediterraneensis</i>	I	I
<i>Quinqueloculina carinatastriata</i>	V	I
<i>Quinqueloculina jugosa</i>	V	III
<i>Quinqueloculina lata</i>	V	II
<i>Quinqueloculina seminula</i>	V	I
<i>Quinqueloculina stelligera</i>	V	I
<i>Rosalina bradyi</i>	II	I
<i>Stainforthia fusiformis</i>	IV	V

Balticammina pseudomacrescens would all have been assigned to EGIV/EGV, because of the consistently very high TOC values found in these environments. It implicitly means that we would interpret them as (strongly) opportunistic, and, additionally, that a high relative frequency of these taxa would indicate a polluted environment. The studied species distribution patterns are largely restricted to salt marshes where they naturally occur in high abundances (Alve and Murray, 1999; Debenay et al., 2000; Cearreta et al., 2002; Fatela et al., 2009; Scott et al., 1996). The assignment of these typical salt marsh species to EGs IV and V would, in view of their systematically very high frequency in natural, apparently unpolluted, salt marshes, appear to be incorrect. For this reason, we did not assign typical salt marsh species to EGs.

4.3. Test of the species' assignments

In both validation datasets, Foram-AMBI yielded a positive significant correlation with organic matter content indicating that this sensitivity index calculated with the present study lists reflects the change in EcoQS along an OM gradient. In the Pertuis Charentais, the un-impacted station R1 had the lowest value, indicating a higher proportion of sensitive species. It was therefore possible to discriminate between this reference station and the impacted ones. Note that all stations are situated at the same level in the tidal zone and in similar habitats, so that differences in EcoQS are not due to the natural features of each of the sampling stations. In the harbor of Cagliari, Foram-AMBI adequately distinguished between high and good EcoQS.

In the Pertuis Charentais, a significant positive correlation between Foram-AMBI and AMBI values (based on macrofauna) confirmed previous correlations found between foraminiferal and macrofaunal communities and indices (Alve et al., 2019; Bouchet et al., 2018b). However,

only a 50% agreement in terms of EcoQS between Foram-AMBI and AMBI was reported. In this study, EcoQS boundaries established for AMBI (Borja et al., 2000) were used to infer EcoQS based on Foram-AMBI. Discrepancies in EcoQS assessment may suggest that specific Foram-AMBI-adapted criteria should be developed. For instance, intercalibration between the two indices may help improving the use of Foram-AMBI. This was successfully done in Norway when adapting the Norwegian Quality Index based on macrofauna (NQI_m) to the foraminiferal one (NQI_f) (Alve et al., 2019).

The results of the tests showed that the classification, obtained with the calculation of the WA optimum values for each species, probably adequately reflects differences in species tolerance to organic load-related stress. The outcome was a reliable assessment of EcoQS in the Pertuis Charentais and in the Harbor of Cagliari. The WA optimum method allowed for an objective assessment of the ecological requirement of each species along the TOC gradient. As for now in European intertidal and TWs, more tests on other independent data sets are, nevertheless, needed to further confirm the findings of this work, and most likely to improve the present study lists of species.

4.4. Potential problems due to benthic foraminiferal taxonomy

Different taxonomical schools co-exist in the foraminiferal community. Unfortunately, this sometimes leads to major inconsistencies with regards to species identification. Scientists working on other biological groups like macro-algae, phytoplankton or benthic macro-invertebrates organize workshops on a regular basis to compare and homogenize their taxonomy. After 20 years of workshops, scientists working on planktonic foraminifera have now agreed and published a global taxonomy of Cretaceous and Paleogene species and genera. In this way, they manage to minimize the remaining taxonomical inconsistency. This issue has also been raised by previous studies assigning benthic foraminifera to EGs (Alve et al., 2016; Jorissen et al., 2018). It appears relevant to keep organizing benthic foraminifera taxonomical workshops to intercalibrate the different taxonomical schools.

Since taxonomy is still mostly based on morphological criteria, taxonomical names used for the same foraminiferal species are rather inconsistent between researchers. For marine species, the WoRMS database provides an authoritative and comprehensive list of marine species including also information on synonymy. It is continuously revised, ensuring that it is kept up-to-date. Benthic foraminifera are included in the database (Hayward et al., 2020a), but foraminiferal studies rarely refer to it, unlike researchers working on benthic macro-invertebrates, for instance, for whom WoRMS is the database of reference for species names. It was therefore a true challenge to “homogenize” species names between studies to build up an accurate and reliable master table for this present work. To clearly and easily compare different foraminiferal studies, similar species concepts and consistent use of names are necessary. At the moment, WoRMS seems to be a relevant option to archive accepted scientific names (and associated synonyms) of benthic foraminiferal species. However, to ensure a high quality and to obtain the acceptance of the WoRMS database by a larger part of the community, the section concerning foraminiferal species needs the input of much more researchers working on foraminifera (Hayward et al., 2020b). Additionally, molecular analyses and a detailed morphological analysis based on SEM images of sequenced specimens have to be combined to confirm or refute the taxonomical identifications. The contribution of molecular studies has yet to be implemented in WoRMS.

4.5. Phylogeographic studies of (pseudo)cryptic species

In all studies considered for the species assignments, the taxonomy of benthic foraminifera was based on morphological criteria. However, cases such as cryptic species (different biological species with identical morphologies), morphological convergence (unrelated species showing

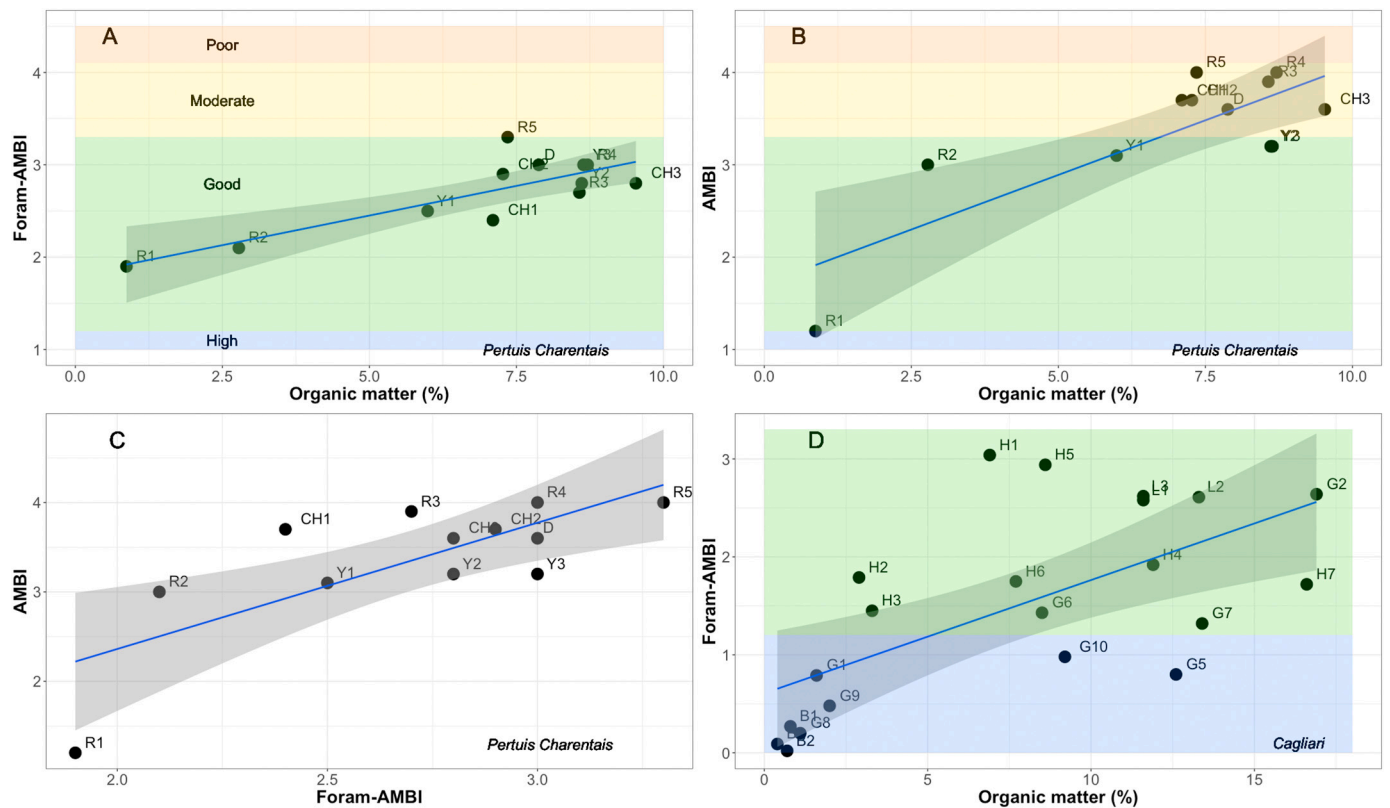


Fig. 7. Relationship between indices and OM in the Pertuis Charentais (A, B and C) and in the harbor of Cagliari (D). Linear regression models are in blue, grey shaded areas being the 95% confidence interval. In panel A, B and D, EcoQS are reported (for class boundaries see Table 1). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the same morphological characteristics) or ecophenotypic variations (same species looking different under different ecological conditions) are common, and make it virtually impossible to determine species by using morphology alone (Darling and Wade, 2008; Haynes, 1992; Pawlowski and Holzmann, 2008). The wide occurrence of cryptic species, which is starting to be visible through the increasing number of molecular studies, is a challenge for environmental biomonitoring (Feckler et al., 2014). In benthic foraminifera, the presence of cryptic species is now well documented in Elphidiidae (Darling et al., 2016; Pillet et al., 2013; Schweizer et al., 2011) and *Ammonia* (Bird et al., 2020; Hayward et al., 2004; Richirt et al., 2019). The present evidence suggests that different cryptic lineages in these taxa may have different ecological requirements, based on the observation of physiological (Jaufrais et al., 2018) or spatial distribution pattern differences (Bird et al., 2020; Richirt et al., 2019). Potentially, in the intertidal areas and TWs of the English Channel and the European Atlantic Ocean, one or several phylotypes of *C. excavatum* may be sensitive (e.g., highest abundances at low TOC) while others may be more opportunistic (e.g., highest abundances at high TOC). In such cases, it is important to combine morphological analyses and molecular identification (also called DNA barcoding or genetic characterization) (Hayward et al., 2004; Schweizer et al., 2005, 2009). Recently, a study on the genus *Ammonia* combined morphological and molecular taxonomies to determine morphological criteria for identifying the different phylotypes (Richirt et al., 2019). It is now possible to implement these morphological criteria in routine surveys to differentiate between the different pseudo-cryptic *Ammonia* species T1, T2 and T6. However, these morphological criteria for *Ammonia tepida* have only been available since 2019. In the studies used here, researchers pooled most *Ammonia* specimens under the name *A. tepida*.

Until data on the ecological requirements for each of the *Ammonia tepida* phylotypes are available, we decided to follow the taxonomy used

in the different studies even though we are fully aware that this is still an ongoing problem to be solved. This issue is however not specific to the work of our FOBIMO sub-WG on intertidal and TWs, as the other sub-WGs also had to cope with the same situation (Alve et al., 2016; Jorissen et al., 2018). Such improvements obtained by combining morphological and molecular analyses are important, considering that environmental biomonitoring uses the indicative value of species. However, their taxonomical identification needs to be cost effective, rapid and accurate.

Phylogeographic studies may help to better distinguish and identify possible cryptic species, and to describe the distribution pattern of the different phylotypes. Such studies, including large environmental surveys, allowing to understand the ecological requirements of each cryptic lineages, would complement morphological taxonomy. It will further help to assign species to the relevant EG. Therefore, ecological studies on cryptic species present a major topic for further scientific research projects.

4.6. Geographical variability of benthic foraminiferal EG assignments

The results of this study show that there can be an offset of up to four categories in species assignments to EGs depending on habitat type (different water-body types in TWs) or latitudinal gradient (from Northern Europe to the Mediterranean Sea). Noticeably, Elphidiidae, *Bolivina* spp. and *Quinqueloculina* spp., which are often the most abundant species, exhibited such large variations. Similar variations along latitudinal gradients and habitats types have been reported for macro-invertebrate species. For instance, the bivalve *Cerastoderma glaucum*, the polychaeta *Ampharete baltica* and *Hediste diversicolor* showed varying tolerance to OM content under different salinity regimes (Zettler et al., 2013).

In benthic foraminifera, these differences between areas and

environments may be explained by taxonomic discrepancies between the different regions (the same name given to different species or different names given to the same species) or plastic adaptation of the same species to different areas. For example, *Criboelphidium gunteri* and *C. oceanense/C. oceanensis*, which share similar morphological features, are often mixed (Barbieri and Vaiani, 2018; Murray, 1979). It is therefore rather difficult to conclude if the assignment of *C. gunteri* in different EGs in the two studied regions (EGIII in the English Channel and Eastern Atlantic and EGV in the Mediterranean Sea) is due to local adaptation *i. e.*, plasticity or simply the result of taxonomical misidentification. The same may also apply to *Bolivina variabilis* (EGIII in the English Channel and Eastern Atlantic and EGI in the Mediterranean Sea), since the taxonomy is complex in bolivinids, leading to some confusions between morphological species. Furthermore, some of these morphospecies are known to shelter different cryptic or pseudocryptic species that are not separated when using the morphological concept, but could have different ecological requirements. For example, *C. excavatum* is assigned to EGI in the English Channel and Eastern Atlantic while it is assigned to EGIII in the Mediterranean Sea. The taxonomic situation of this morphospecies is rather confused because of its high intraspecific morphological variability, leading to the description of ecophenotypes, subspecies and species (Feyling-Hanssen, 1972). However, molecular studies showed that some of *C. excavatum* ecophenotypes can be raised to species (Darling et al., 2016). Similarly, *Quinqueloculina seminula* (Kaushik et al., 2019) contains cryptic species which might exhibit different ecological features explaining the assignment to EGV in the English Channel and Eastern Atlantic while it is assigned to the EGI in the Mediterranean Sea. This is however highly speculative; it may also be hypothesized that wrong taxonomical identification or plasticity in *C. excavatum* and *Q. seminula* may explain such differences.

Explaining the geographical variability of benthic foraminiferal EG assignments observed in this study remains quite uncertain. Describing and understanding the response of benthic foraminiferal species to TOC and to other natural and human-induced stressors in different habitats and along latitudinal gradients requires further work. This is in line with the increasing use of generalized linear mixed models (GLMMs) in biostatistics since non-normal data that involve random effects (*e.g.*, multimodal data based on different observers and/or environments) need to be carefully and appropriately handled (Bolker et al., 2009).

5. Conclusion

The present study shows that the classification probably adequately reflects differences in species tolerance to organic load-related stress. The tests of the species' lists on the two validation datasets can be considered a promising start which is worthy to pursue using other datasets. The assignment of typical salt marsh species was however not possible, since their classification in the opportunist EGs was not reflecting their natural ecological requirements. Furthermore, this study does not ensure that Foram-AMBI and comparable methods will perform well in all European waters. There is hence an urgent need to apply and

test sensitivity-based foraminiferal indices in different ecosystems and against different pollution sources. Otherwise, the community of foraminiferologists also suffers from severe taxonomical heterogeneity. A great effort must be devoted in the near future to encourage intercalibration exercises.

CRediT authorship contribution statement

Vincent M.P. Bouchet: Conceptualization, Supervision, Investigation, Data curation, Formal analysis, Visualization, Writing – original draft. **Fabrizio Frontalini:** Investigation, Writing – original draft. **Fabio Francescangeli:** Investigation, Visualization, Writing – original draft. **Pierre-Guy Sauriau:** Formal analysis, Visualization, Writing – review & editing. **Emmanuelle Geslin:** Supervision, Writing – review & editing. **Maria Virginia Alves Martins:** Investigation, Writing – review & editing. **Ahuva Almogi-Labin:** Writing – review & editing. **Simona Avnaim-Katav:** Investigation, Writing – review & editing. **Letizia Di Bella:** Writing – review & editing. **Alejandro Cearreta:** Investigation, Writing – review & editing. **Rodolfo Coccioni:** Writing – review & editing. **Ashleigh Costelloe:** Writing – review & editing. **Margarita D. Dimiza:** Writing – review & editing. **Luciana Ferraro:** Investigation, Writing – review & editing. **Kristin Haynert:** Writing – review & editing. **Michael Martínez-Colón:** Writing – review & editing. **Romana Melis:** Investigation, Writing – review & editing. **Magali Schweizer:** Writing – review & editing. **Maria V. Triantaphyllou:** Investigation, Writing – review & editing. **Akira Tsujimoto:** Writing – review & editing. **Brent Wilson:** Writing – review & editing. **Eric Arminot du Châtelet:** Supervision, Investigation, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Datasets from the English Channel/European Atlantic coast used for species assignments

Dataset	Region	Country	Local study area	Water body type	Reference	Number of samples	Foram size fraction	TOC method	% TOC range
1	English Channel	France	Grand-Fort Philippe	Classical estuary	(Francescangeli, 2017)	12	>63 µm	CHN Elemental analyser	0.4–2.7
2	English Channel	France	Liane estuary	Classical estuary	Arminot du Châtelet et al. (2011)	53	>63 µm	CHN Elemental analyser	0.3–5.9
3	English Channel	France	Boulogne sur Mer Harbour	Artificial water body	(Francescangeli, 2017)	12	>63 µm	CHN Elemental analyser	0.03–3.9
4	English Channel	France	Canche estuary	Classical estuary	Francescangeli et al. (2017)	103	>63 µm	CHN Elemental analyser	0.03–13.6

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Dataset	Region	Country	Local study area	Water body type	Reference	Number of samples	Foram size fraction	TOC method	% TOC range
5	English Channel	France	Canche estuary	Classical estuary	Armynot du Châtelet et al. (2018)	63	>63 µm	CHN Elemental analyser	0.03–13.6
6	English Channel	France	Canche estuary	Classical estuary	(Francescangeli, 2017)	12	>63 µm	CHN Elemental analyser	1.2–3.8
7	English Channel	France	Authie estuary	Classical estuary	(Francescangeli, 2017)	12	>63 µm	CHN Elemental analyser	0.7–1.8
8	English Channel	France	Somme estuary	Classical estuary	(Francescangeli, 2017)	16	>63 µm	CHN Elemental analyser	0.3–2.2
9	English Channel	France	Bay of Veys	Coastal freshwater/brackish water plume	Bouchet (unpublished)	6	>63 µm	LOI	0.8–1.55
10	Atlantic	France	Crouesty harbor	Artificial water body	Armynot du Châtelet (2003)	14	>63 µm	LOI	0.1–16
11	Atlantic	France	Loire estuary	Classical estuary	Mojtahid et al. (2016)	32	>150 µm	LECO-CS200® analyser	0.1–2.6
12	Atlantic	France	Aiguillon bay	Coastal freshwater/brackish water plume	Armynot du Châtelet et al. (2009b)	41	>63 µm	LOI	6.1–13.6
13	Atlantic	France	Aiguillon Bay/Ré Island	Coastal freshwater/brackish water plume	Bouchet et al. (2009)	3	>63 µm	LOI	9.1–9.9
14	Atlantic	France	Ronce Perquis	Coastal freshwater/brackish water plume	Bouchet et al. (2007)	5	>63 µm	LOI	3.6–5.9
15	Atlantic	Spain	Plentzia estuary	Classical estuary	Cearreta et al. (2002)	5	>63 µm	Walkey method	3.6–9.3
16	Atlantic	Spain	Ria de Vigo	Ria	Diz et al. (2006)	28	>63 µm	LECO-CS200® analyser	2–4
17	Atlantic	Portugal	Ria de Aveiro	Ria	Martins et al. (2015)	53	>63 µm	LOI	0.1–7.4
18	Atlantic	Portugal	Ria de Aveiro	Ria	Martins et al. (2013)	29	>63 µm	LOI	1–10.7
19	Atlantic	Portugal	Ria de Aveiro	Ria	Martins et al. (2010)	15	>63 µm	LOI	0.6–10.7
20	Atlantic	Portugal	Ria de Aveiro	Ria	Martins et al. (2016)	31	>63 µm	LOI	1.4–3.8
21	Atlantic	Portugal	Guadiana estuary	Classical estuary	Camacho et al. (2014)	42	>63 µm	CHN Elemental analyser	0.2–8.9

Location of the different areas is shown in Fig. 2. TOC: total organic carbon, LOI: loss of ignition.

Appendix B. Datasets from the Mediterranean Sea coast used for species assignments

Dataset	Region	Country	Local study area	Water body type	Reference	Number of samples	Foram size fraction	TOC method	% TOC range
22	Mediterranean Sea	Spain	Ebro delta	Delta	Benito et al. (2016)	36	>63 µm	LOI	0.89–17.8
23	Mediterranean Sea	France	Bagès-Sigean lagoon	Lentic non-tidal lagoon	Foster et al. (2012)	11	>125 µm	CHN Elemental analyser	0.5–3
24	Mediterranean Sea	Italy	Sardinia island	Semi-enclosed bay/Lagoon	Schintu et al. (2015)	18	>63 µm	LOI	0.5–10.1
25	Mediterranean Sea	Italy	Santa Gilla	Lentic tidal lagoon	Frontalini et al. (2009)	17	>63 µm	CHN Elemental analyser	1.7–2.5
26	Mediterranean Sea	Italy	Orbetello	Lentic non tidal lagoon	Frontalini et al. (2010)	7	>63 µm	CHN Elemental analyser	2.84–7.11
27	Mediterranean Sea	Italy	Naples harbor	Artificial water body	Ferraro et al. (2006)	54	>125 µm	CHN Elemental analyser	0.12–5.73
28	Mediterranean Sea	Italy	Varano lake	Lentic non tidal lagoon	Frontalini et al. (2013)	24	>125 µm	CHN Elemental analyser	1.1–4.2
29	Mediterranean Sea	Italy	Lesina lagoon	Lentic tidal lagoon	Frontalini et al. (2010)	11	>63 µm	CHN Elemental analyser	4.7–10.4
30	Mediterranean Sea	Italy	Venice lagoon	Lentic tidal lagoon	Coccioni et al. (2009)	12	>63 µm	CHN Elemental analyser	8–15.1
31	Mediterranean Sea	Italy	Marano and Grado lagoon	Lentic tidal lagoon	Melis (unpublished data)	11	>63 µm	CHN Elemental analyser	0.1–4.5
32	Mediterranean Sea	Greece	Saronikos gulf	Semi-enclosed bay/lagoon	Portela (2017)	11	>125 µm	CHN Elemental analyser	0.4–3.2
33	Mediterranean Sea	Greece	Saronikos gulf	Semi-enclosed bay/lagoon	Dimiza et al. (2016)	10	>125 µm	CHN Elemental analyser	0.6–3.1
34	Mediterranean Sea	Greece	Evoikos gulf	Semi-enclosed bay/lagoon	Gorejja (2013)	8	>125 µm	CHN Elemental analyser	0.3–0.9
35	Mediterranean Sea	Greece	Kavala bay	Semi-enclosed bay/lagoon	Delliou (2013)	6	>125 µm	CHN Elemental analyser	0.1–0.8
36	Mediterranean Sea	Turkey	Gulf of Izmir	Semi-enclosed bay/lagoon	Bergin et al. (2006)	9	>250 µm	Hach method	2.4–6.7
37	Mediterranean Sea	Israel	Timsah pond	Lentic non-tidal lagoon	Flako-Zaritsky et al. (2011)	2	>63 µm	CHN Elemental analyser	10.6–12.6
38	Mediterranean Sea	Israel	Betzet, Naaman, Poleg, Lachish estuaries	Classical estuary	Avnaim-Katav et al. (2016)	7	>63 µm	CHN Elemental analyser	0.1–2.5
39	Mediterranean Sea	Egypt	Abu-Qir bay	Semi-enclosed bay/lagoon	Elshanawany et al. (2011)	18	>63 µm	LECO-CS200® analyser	0.1–6.7

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Dataset	Region	Country	Local study area	Water body type	Reference	Number of samples	Foram size fraction	TOC method	% TOC range
40	Mediterranean Sea	Tunisia	Djerba lagoon	Lentic non-tidal lagoon	El Kateb et al. (2018)	9	>63 µm	CHN Elemental analyser	0.07–0.9
41	Mediterranean Sea	Tunisia	Monastir bay	Semi-enclosed bay/lagoon	Damak et al. (2019)	10	>125 µm	Walker and Black method	0.5–5.25
42	Mediterranean Sea	Tunisia	Bizerte lagoon	Lentic non-tidal lagoon	Alves Martins et al. (2015)	10	>63 µm	CHN Elemental analyser	3.2–5.9

Location of the different areas is shown in Fig. 2. TOC: total organic carbon, LOI: loss of ignition.

Appendix C. Assigned species from the English Channel/European Atlantic intertidal and TWs per ecological group (EG)

Accepted scientific name	Accepted AphiaID	Optimum	Tolerance –	Tolerance +	EG
<i>Cribolephidium poeyanum</i>	113244	0.6	0.2	1.9	I
<i>Subanomalina pauperata</i>	847845	0.9	0.5	1.9	I
<i>Asterigerinata mamilla</i>	112933	1.1	0.6	2.0	I
<i>Neocorbina nitida</i>	N.D.	1.3	0.7	2.3	I
<i>Haynesina depressula</i>	113293	1.3	0.8	2.2	I
<i>Lepidodeuterammina eddystonensis</i>	817119	1.4	0.8	2.5	I
<i>Elphidium pereirum</i>	N.D.	1.5	1.3	1.7	I
<i>Cribolephidium excavatum</i>	254680	1.6	0.6	4.0	I
<i>Gavelinopsis praegiri</i>	113159	1.6	0.9	2.7	I
<i>Elphidium margaritaceum</i>	113279	1.6	0.8	3.1	I
<i>Planorbulina mediterraneensis</i>	113634	1.6	1.1	2.4	I
<i>Polysaccammina hyperhalina</i>	867465	1.6	0.6	4.5	I
<i>Lepidodeuterammina ochracea</i>	114306	1.7	1.1	2.5	I
<i>Cibicidoides lobatulus</i>	988323	1.7	0.7	3.8	I
<i>Bolivina robusta</i>	466349	1.7	1.0	2.8	I
<i>Arenoparrella mexicana</i>	417609	1.7	0.8	3.5	I
<i>Paratrochammina (Lepidoparatrochammina) haynesi</i>	736766	1.8	1.2	2.5	I
<i>Elphidium cuvillieri</i>	113263	1.8	0.8	3.8	I
<i>Reophax nana</i>	114011	1.8	1.3	2.5	I
<i>Elphidium pulvereum</i>	528472	1.8	1.0	3.3	I
<i>Discorbis vilardeboanus</i>	113154	1.8	1.0	3.4	I
<i>Leptohalysis scottii</i>	578704	1.9	1.5	2.4	I
<i>Spirillina vivipara</i>	113737	2.0	1.1	3.7	II
<i>Rosalina bradyi</i>	113167	2.0	1.3	3.0	II
<i>Cribolephidium magellanicum</i>	113242	2.0	1.4	2.9	II
<i>Ammobaculites balkwilli</i>	163639	2.0	1.4	3.1	II
<i>Ammotium morenoi</i>	736481	2.1	1.2	3.7	II
<i>Cibicidoides ungerianus</i>	112889	2.1	1.3	3.4	II
<i>Haplophragmoides manilaensis</i>	417577	2.1	1.6	2.7	II
<i>Miliolinella subrotunda</i>	112564	2.1	0.8	5.4	II
<i>Bolivina pseudoplicata</i>	112982	2.2	1.1	4.5	II
<i>Miliammina fusca</i>	114064	2.3	1.2	4.3	II
<i>Bolivina ordinaria</i>	112978	2.3	0.7	7.2	II
<i>Ammoscalaria pseudospiralis</i>	113918	2.4	1.5	3.7	II
<i>Ammonia parkinsoniana</i>	418095	2.4	2.1	2.7	II
<i>Bolivina dilatata</i>	112973	2.5	1.7	3.6	III
<i>Haynesina germanica</i>	113294	2.5	1.0	6.1	III
<i>Bolivina variabilis</i>	112998	2.5	1.0	6.4	III
<i>Buliminella elegantissima</i>	113747	2.5	1.3	4.9	III
<i>Ammotium cassis</i>	114029	2.6	2.2	3.1	III
<i>Eilohedra vitrea</i>	466420	2.7	2.3	3.1	III
<i>Miliammina obliqua</i>	465995	2.7	1.6	4.6	III
<i>Cribolephidium williamsoni</i>	1026169	2.7	0.9	8.2	III
<i>Bolivinelina translucens</i>	526512	2.7	2.3	3.2	III
<i>Ammonia tepida</i>	112857	2.8	1.1	7.1	III
<i>Tiphotrecha comprimata</i>	114331	2.8	1.3	5.9	III
<i>Nonionella stella</i>	113604	2.8	2.0	4.0	III
<i>Bolivina spathulata</i>	112988	2.9	2.4	3.5	III
<i>Fursenkoina complanata</i>	466392	2.9	2.5	3.5	III
<i>Bolivinelina pseudopunctata</i>	112999	3.0	2.3	3.9	III
<i>Bulimina gibba</i>	113040	3.1	2.5	3.7	III
<i>Nonionoides turgidus</i>	466471	3.2	2.5	4.0	III
<i>Siphotrechammina lobata</i>	522046	3.2	1.1	9.0	III
<i>Cribolephidium gunteri</i>	1026170	3.2	1.2	8.7	III
<i>Textularia earlandi</i>	114273	3.2	1.3	7.9	III
<i>Bulimina elegans</i>	901990	3.2	1.2	8.6	III
<i>Elphidium advenum</i>	113254	3.3	2.9	3.6	III
<i>Cribolephidium gerthi</i>	1026171	3.3	1.7	6.5	III
<i>Stainforthia fusiformis</i>	113070	3.4	1.8	6.5	IV
<i>Balticammina pseudomacrescens</i>	556254	3.4	2.8	4.2	NA
<i>Bulimina marginata</i>	113042	3.5	3.2	3.8	IV

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Accepted scientific name	Accepted AphiaID	Optimum	Tolerance –	Tolerance +	EG
<i>Cornuspira involvens</i>	112488	3.6	1.5	8.5	IV
<i>Cribrostomoides jeffreysii</i>	114035	3.6	3.6	3.6	IV
<i>Eggerelloides scaber</i>	113938	3.7	2.6	5.2	IV
<i>Bulimina elongata</i>	933974	3.9	2.5	5.9	IV
<i>Hopkinsina atlantica</i>	582285	4.1	2.0	8.7	V
<i>Trochammina inflata</i>	114348	4.1	1.9	9.1	NA
<i>Quinqueloculina seminula</i>	112674	4.3	1.9	9.7	V
<i>Rotaliammina concava</i>	850049	4.3	2.3	8.0	V
<i>Entzia macrescens</i>	742429	4.7	2.4	9.0	NA
<i>Aubignyna hambensis</i>	146404	5.1	3.6	7.1	V
<i>Quinqueloculina carinatastriata</i>	466057	5.2	4.2	6.3	V
<i>Elphidium articulatum</i>	113257	5.3	2.9	9.6	V
<i>Quinqueloculina lata</i>	112644	5.4	2.3	12.7	V
<i>Bolivina striatula</i>	112989	6.2	3.4	11.6	V
<i>Quinqueloculina stelligera</i>	920885	7.1	3.2	15.8	V
<i>Hopkinsina pacifica</i>	113728	7.4	4.8	11.6	V
<i>Fusulina lucida</i>	909789	7.6	4.2	13.7	V
<i>Quinqueloculina jugosa</i>	112641	7.6	4.8	12.1	V
<i>Aubignyna perlucida</i>	466408	11.2	10.0	12.5	V

For each species, accepted scientific name and AphiaID (source: WoRMS), optimum and tolerance range to TOC are also reported. *Balticammina pseudomacrescens*, *Trochammina inflata* and *Entzia macrescens* are not assigned (NA).

Appendix D. Assigned species from the Mediterranean Sea intertidal and TWs per ecological group (EG)

Accepted scientific name	Accepted AphiaID	Optimum	Tolerance –	Tolerance +	EG
<i>Criboelphidium incertum</i>	113240	0.1	0.1	0.2	I
<i>Sigmavirgulina tortuosa</i>	113392	0.2	0.1	0.5	I
<i>Cibicides refulgens</i>	112877	0.2	0.1	0.7	I
<i>Sigmoilina costata</i>	112693	0.2	0.1	0.5	I
<i>Astrononion stelligerum</i>	113552	0.2	0.1	0.7	I
<i>Asterigerinata mamilla</i>	112933	0.4	0.2	1.1	I
<i>Haynesina depressula</i>	113293	0.5	0.2	1.2	I
<i>Elphidium complanatum</i>	113261	0.5	0.2	1.2	I
<i>Rosalina macropora</i>	113173	0.7	0.2	3.1	I
<i>Cibicidoides lobatulus</i>	988323	0.7	0.3	1.9	I
<i>Rosalina bradyi</i>	113167	0.8	0.3	2.1	I
<i>Triloculina trigonula</i>	112772	0.8	0.2	2.4	I
<i>Textularia agglutinans</i>	114264	0.8	0.5	1.3	I
<i>Elphidium crispum</i>	113262	0.8	0.3	2.4	I
<i>Cassidulina carinata</i>	183041	0.9	0.7	1.0	I
<i>Rosalina globularis</i>	113171	0.9	0.2	4.2	I
<i>Planorbulina mediterraneensis</i>	113634	0.9	0.3	2.7	I
<i>Elphidium advenum</i>	113254	0.9	0.2	4.0	I
<i>Peneroplis pertusus</i>	112815	0.9	0.3	2.8	I
<i>Quinqueloculina laevigata</i>	112642	1.0	0.2	4.2	I
<i>Ammonia beccarii</i>	112849	1.1	0.3	3.4	I
<i>Porosononion granosum</i>	954808	1.1	0.5	2.2	I
<i>Massilina secans</i>	163641	1.1	0.3	4.7	I
<i>Quinqueloculina stelligera</i>	920885	1.1	0.3	4.5	I
<i>Nonionoides grateloupi</i>	418051	1.2	0.7	2.1	I
<i>Ammonia parkinsoniana</i>	418095	1.2	0.2	6.1	I
<i>Quinqueloculina berthelotiana</i>	112816	1.2	0.7	2.2	I
<i>Bolivina variabilis</i>	112998	1.3	0.4	4.1	I
<i>Peneroplis planatus</i>	112817	1.4	0.6	3.3	I
<i>Adelosina mediterraneensis</i>	112536	1.4	0.5	4.2	I
<i>Miliolinella subrotunda</i>	112564	1.5	0.5	4.4	I
<i>Discorinopsis aguayoi</i>	417645	1.5	0.4	6.1	I
<i>Quinqueloculina carinatastriata</i>	466057	1.6	0.8	3.0	I
<i>Quinqueloculina bicostata</i>	417701	1.6	0.8	3.1	I
<i>Criboelphidium williamsoni</i>	1026169	1.6	0.9	2.7	I
<i>Siphonaperta aspera</i>	593433	1.6	2.9	0.8	I
<i>Spirillina vivipara</i>	113737	1.6	0.3	8.8	I
<i>Bolivina striatula</i>	112989	1.7	0.4	7.9	I
<i>Quinqueloculina seminula</i>	112674	1.8	0.7	4.7	I
<i>Cycloforina contorta</i>	112516	1.8	0.8	3.9	I
<i>Adelosina longirostra</i>	112535	1.8	1.0	3.5	I
<i>Adelosina milletti</i>	522161	1.9	1.1	3.3	I
<i>Adelosina cliarensis</i>	112529	2.0	0.9	4.1	II
<i>Bulimina marginata</i>	113042	2.1	1.2	3.8	II
<i>Quinqueloculina lata</i>	112644	2.2	0.6	8.5	II
<i>Valvulinera bradyana</i>	112960	2.2	1.2	3.9	II
<i>Bolivina dilatata</i>	112973	2.2	0.9	5.7	II
<i>Rectuvigerina phlegeri</i>	113755	2.3	1.3	4.0	II

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Accepted scientific name	Accepted AphiaID	Optimum	Tolerance –	Tolerance +	EG
<i>Ammobaculites exiguus</i>	417589	2.3	2.0	2.7	II
<i>Quinqueloculina jugosa</i>	112641	2.4	1.1	5.0	III
<i>Vertebralina striata</i>	112785	2.4	1.0	5.5	III
<i>Ammonia tepida</i>	112857	2.4	0.9	6.1	III
<i>Ammobaculites balkwilli</i>	163639	2.4	1.4	4.2	III
<i>Ammoscalaria rumiana</i>	113919	2.4	2.0	3.0	III
<i>Bulimina elongata</i>	933974	2.5	1.3	4.9	III
<i>Cribrorhaphidium excavatum</i>	254680	2.5	2.0	3.3	III
<i>Triloculina marioni</i>	112763	2.6	1.3	5.0	III
<i>Cribrorhaphidium selseyense</i>	754247	2.6	1.7	4.1	III
<i>Buliminella elegantissima</i>	113747	2.7	0.4	16.2	III
<i>Haynesina germanica</i>	113294	3.0	1.5	5.8	III
<i>Nonionoides turgidus</i>	466471	3.0	2.3	4.0	III
<i>Cribrorhaphidium poeyanum</i>	113244	3.2	2.5	4.1	III
<i>Textularia bocki</i>	114267	3.2	2.7	3.7	III
<i>Miliammina fusca</i>	114064	3.2	2.4	4.3	III
<i>Discorbinella bertheloti</i>	113143	3.3	2.5	4.3	III
<i>Adelosina pulchella</i>	112538	3.3	1.8	6.1	III
<i>Ammonia batava</i> subsp. <i>compacta</i>	1381806	3.4	2.6	4.5	IV
<i>Bolivina spathulata</i>	112988	3.6	1.5	8.5	IV
<i>Porosonion subgranosus</i>	556479	3.8	2.7	5.2	IV
<i>Hopkinsina atlantica</i>	582285	3.9	3.1	4.8	IV
<i>Bolivina ordinaria</i>	112978	4.2	3.4	5.1	V
<i>Bolivina pseudoplicata</i>	112982	4.3	3.3	5.5	V
<i>Cribrorhaphidium gunteri</i>	1026170	4.7	2.1	10.7	V
<i>Rosalina irregularis</i>	113172	4.8	4.1	5.6	V
<i>Aubignyna perlucida</i>	466408	5.2	1.8	15.3	V
<i>Quinqueloculina oblonga</i>	912989	5.2	3.5	7.8	V
<i>Quinqueloculina costata</i>	523480	5.9	3.2	11.0	V
<i>Trochammina inflata</i>	114348	8.2	3.9	17.3	NA
<i>Entzia macrescens</i>	742429	8.4	3.9	17.9	NA
<i>Hopkinsina pacifica</i>	113728	10.2	7.7	13.7	V
<i>Stainforthia fusiformis</i>	113070	10.4	8.5	12.8	V
<i>Haplophragmoides wilberti</i>	113955	11.1	8.4	14.8	NA

For each species, accepted scientific name and AphiaID (source: WoRMS), optimum and tolerance range to TOC are also reported. *Trochammina inflata*, *Entzia macrescens* and *Haplophragmoides wilberti* are not assigned (NA).

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