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Article *in* Revue de Micropaléontologie · June 2018

DOI: 10.1016/j.revmic.2018.04.001

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Revue de micropaléontologie
Revue de micropaléontologie xxx (2017) xxx–xxx

60th Anniversary special volume

Definition of benthic foraminiferal bioprovinces in transitional environments of the Eastern English Channel and the Southern North Sea

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Abstract

The available benthic foraminiferal data in transitional environments along the English Channel and the Southern North Sea were computed to identify foraminiferal-based bioprovinces. A total of 901 samples characterized by 246 dead species and 656 samples represented by 99 living species were arranged in 3 large bioprovinces, namely England, France and the East English Channel. Dominant species such as those belonging to *Haynesina* and *Cribroelphidium* genera were widely distributed geographically. By contrast, high degrees of foraminiferal endemism were found in Belgian waters and the Canche and Liane estuaries. The results of our study reveal that dead foraminifera are better indicators of biogeographical provinces than living ones, which are related to environmental units.

Keywords: Benthic foraminifera; English Channel; North Sea; Bioprovince; Transitional environment

1. Introduction

Foraminifera represent one of the three Phyla within the Infrakingdom Rhizaria, a protistan supergroup (Adl et al., 2012). Foraminifera are single celled marine organisms adapted to all marine environments from coastal to deep-sea (Scott et al., 2001). They are enclosed in soft or hard shells (test), the latter having the capacity of being preserved in sediments. Traditionally, foraminifera have been applied by micropaleontologists as stratigraphical index fossils and for paleoenvironmental reconstructions. More recently, their application has been extended to paleoclimatological, ecological and environmental inferences. The value of foraminifera as ecological and environmental proxies relies on their widespread distribution, high abundance, species richness and diversity, specific ecological requirements and short life and reproductive cycles (Frontalini and Coccioni, 2011; Murray, 2006). In transitional areas (i.e., estuaries, marshes, tidal flats, lagoons and coastal lakes), variations in benthic foraminiferal assemblages reflect changes in the environmental conditions (Armynot du Châtelet et al., 2016; Frontalini and Coccioni, 2011). Foraminifera are inferred to be among the most abundant and diversified shelled taxa in our oceans (Sen Gupta, 1999a). These features make them highly suitable for distributional and biogeographic studies (Buzas and Culver, 1989; Gooday and Jorissen, 2012; Murray and Alve, 2016). Foraminiferal biogeography has been applied to identify assemblages typical of particular habitats in different geographic regions (Murray, 1991; Pawlowski and Holzmann, 2008). Some census reports of foraminiferal species richness have been documented for selected areas such as the Gulf of Mexico (Sen Gupta and Smith, 2010), the Aegean Sea (Frontalini et al., 2015), the Korean Peninsula area (Kim et al., 2016), the Aegean Sea coastal waters (Dimiza et al., 2016). However, very few biogeographic species-based studies, either morphological or molecular, have been performed (Hayward et al., 2007; Murray, 2013; Murray and Alve, 2016; Pawlowski et al., 2013). Despite this lack of studies, it is important to have information on the ranges of species to establish the extent of species richness and diversity on a regional scale (Gooday et al., 2004; Levin et al., 2001). Using robust statistical analyses to determine the biogeographical distribution of foraminiferal species, even at a regional level,

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https://doi.org/10.1016/j.revmic.2018.04.001
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is vital for understanding, managing and protecting biodiversity in the context of future climatic change and human-induced environmental perturbations.

The region comprising the eastern English Channel (East of 1.6°W) and the southern North Sea (South 56°N along UK and West Netherlands coasts) has been the focus of recent benthic foraminiferal investigations. The marginal areas of this region experience a meso-macro tidal regime that induces a strong natural stress on the benthic coastal population. The very first studies of benthic foraminifera were reported by Cushman (1947) along Belgian waters, Murray (1968) in the Avon estuary (South England). Since then, more than 20 studies in this area have been performed (Armynot du Châtelet et al., 2018; Murray, 2006). Except for Rosset-Moulinier (1986) and Cushman (1947), who investigated infra-circalittoral (20 to 40 m water depth) benthic foraminiferal assemblages along the English Channel, the studies have been carried out fairly comprehensively in transitional areas.

In the light of it, the aims of the present paper are to:

- provide new information on the species richness of benthic foraminifera in transitional environments over the broad area of the Eastern English Channel and the Southern North Sea;
- to define the biogeographical patterns and bioprovinces based on either living or dead foraminiferal species and interpret their significance.

2. Material and methods

2.1. Area of study and data

The dataset was retrieved from the heterogeneous area between the eastern English Channel and the southern North Sea. The dataset, based on 17 publications (Fig. 1), included all the available studies in transitional areas (i.e., estuary, bay, harbor) where either living (stained) or dead benthic foraminiferal data were supplied (Table 1). Among all the available studies, only those containing complete information (precise localization, occurrence table) were retained. It is assumed that if a species was found as living, it could be also observed as dead. Studies considering only living fauna could also be incorporated in the total fauna database. Taxa were registered according to the specific geographical area and environmental units of occurrence. Based on floral vertical distribution and water depth, the tidal frame environmental units are: subtidal, tidal flat, tidal channel, low, middle and high salt marsh. Globally, 16 geographical areas were investigated. Data are separated in two datasets, one for living and the other for dead foraminifera. Tables are transformed in binary data with species' presence/absence in a given sample. This procedure helps increase the number of accepted samples without retrieving counting tables each time (Hohenegger, 2005).

2.2. Statistical treatment

For the first step, the species richness distribution was evaluated through the analysis of commonalities where the differences among multiple datasets (groups of samples) were depicted by intersecting them. Although the typical way to observe data from different groups is the Euler diagram (generally for 3–4 groups), here, as the number of groups was higher, the *Upset* solution was adopted (Conway et al., 2017; Gehlenborg, 2016; Lex et al., 2014). The analysis of commonalities was carried out twice using different ways to group samples:

- geographical area, which commonly corresponds to a single study;
- transitional environmental units, namely subtidal, tidal channel, tidal flat, low, middle and high marsh.

The resulting graphs show the species occurring in a single group (a single geographical area or a single transitional environment unit) or a combination of areas and units. For each case, the number of species and number of samples in the intersection are provided. The interpretation of the species richness is supported by an analysis of a rarefaction curve. This curve is constructed by a random selection from 1 to 901 samples. The selection is performed hundred times. For each combination, the data are represented by a box-and-whisker plot.

For the second step, since this co-occurring matrix also showed multiple and complex interactions, it was organized with clustering techniques prior to constructing a network of interaction between area and units. In order to carry out this organization, the two databases (dead and living fauna) were modified. Depending on the environmental units and geographical areas, the samples were arranged in 48 groups for the dead fauna and 27 groups for the living one. In each group, species occurrence was synthesized as a mean occurrence per group. The resulting tables were then described using a classical tree-based representation of data by hierarchical clustering methods. The Euclidian distance and its implementation of Ward amalgamation method (Murtagh and Legendre, 2014) were used. The layout design was based on the Fruchterman-Reingold layout algorithm that places the vertices on the plane using the force-directed layout algorithm (Fruchterman and Reingold, 1991). The objective was to identify groups with a geographical consistency.

For the third step, the analysis of co-occurrence of species in the area based on the same databases of step 2 was carried out. Representing systems of interacting elements as networks invoke complex phenomena that arose from the analysis of the geographical distribution of the species and the samples. In order to identify sets of related nodes, known as communities (Radicchi et al., 2004) (Kalinka and Tomancak, 2011). This approach was enhanced by clustering the links between nodes, rather than clustering the nodes themselves (Evans and Lambiotte, 2009/in/Kalinka and Tomancak, 2011 #2728). It was possible for nodes to belong to multiple communities, and this, in turn, revealed the overlapping and nested structure of the network while simultaneously identifying key nodes occurring across several communities (Kalinka and Tomancak, 2011). In order to create a layout for the nodes in the geographical framework, only the strongest interactions between

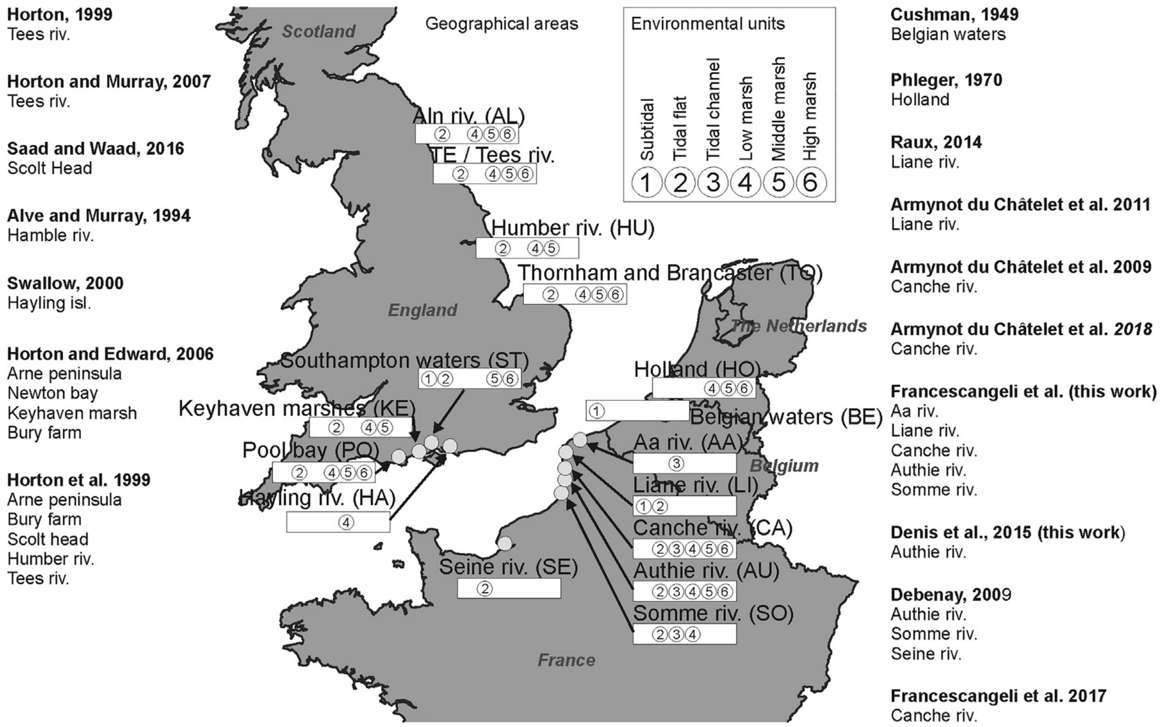

Fig. 1. Map of the study area with localization of the geographical areas and environmental units (relative acronyms used in other figures are provided).

Table 1
Selected studies with authors, year of publication, geographical area, living and/or dead fauna. Sieve fraction and sampling procedure were also reported when available. Data are published within the following references (Alve and Murray, 1994; Armynot du Châtelet et al., 2009; Armynot du Châtelet et al., 2017b; Armynot du Châtelet et al., 2011; Cushman, 1947; Debenay, 1999; Denis et al., 2016; Francescangeli, 2017; Francescangeli et al., 2017; Horton, 1999; Horton and Edward, 2006; Horton et al., 1999b; Horton and Murray, 2007; Phleger, 1970; Raux, 2014; Saad and Wade, 2016; Swallow, 2000).

Study	Year	Area	Living	Dead	Sieve	Sampling procedure
Cushman	1949	Belgian waters	No	Yes	Not indicated	Not indicated
Phleger	1970	Holland	Yes	No	Not indicated	Not indicated
Alve and Murray	1994	Hamble riv.	Yes	Yes	63	Ring for intertidal and small grab underwater
Horton	1999	Tees riv.	No	Yes	63	1 cm thick
Horton and Edward	1999	Arne peninsula, Bury farm, Scolt Head, Humber riv., Tees riv.	No	Yes	63	1 cm thick
Swallow	2000	Hayling riv.	Yes	No	63	1 cm thick
Horton and Edward	2006	Arne peninsula, Newton bay, Keyhaven marsh, Bury farm	No	Yes	63	1 cm thick
Horton and Murray	2007	Tees riv.	Yes	No	63	1 cm thick
Armynot du Châtelet et al.	2009	Canche riv.	Yes	No	63	1 cm thick
Debenay	2009	Authie, Seine, Somme riv.	Yes	Yes	50	Ring for intertidal and small grab underwater
Armynot du Châtelet et al.	2011	Liane riv.	Yes	Yes	50	1 cm thick within VanVeen grab
Raux	2014	Liane riv.	Yes	No	63	1 cm thick
Saad and Waad	2016	ScoltHead	Yes	No	53	1 cm thick
Francescangeli et al.	2017	Canche riv.	Yes	No	63	1 cm thick
Armynot et al.	2017b	Canche riv.	Yes	Yes	63	1 cm thick
Denis et al.	This work	Authie riv.	Yes	No	63	2 cm thick
Francescangeli et al.	This work	Canche, Authie, Liane, Aa, Somme estuaries	Yes	No	63	1 cm thick

species and geographical area/environmental unit groups were selected by a mean occurrence sill within the group of 0.75 (i.e., the given species occurs in 75% of samples in the group). Then a Jaccard similarity matrix was computed comparing the total occurrence of species with area/estuaries and plotted as a map.

The statistical treatments were carried out using the R software (R Core Team, 2016) with the following packages: for commonalities analysis UpSetR (Gehlenborg, 2016); for clustering network: igraph (Csardi and Nepusz, 2006), factoextra (Kassambara and Mundt, 2017), ggsci (Xiao, 2017); for co-occurence network: qgraph (Epskamp et al., 2012), linkcomm (Kalinka and Tomancak, 2011); for mapping the data: maps (Becker and Wilks, 2017), mapdata (Becker and Wilks, 2016) plotrix (Lemon, 2006) and for the calculation of the Jaccard similarity matrix: ade4 (Dray and Dufour, 2007).

3. Results

The dataset consisted of 901 samples and 246 foraminiferal species. Samples were mainly distributed in the Canche and Tees estuaries. Only a few samples were from Aa, Keyhaven, Seine and Somme (Table 2). Samples were principally located in low marsh and tidal flat units (Table 2). All species were benthic except the planktonic *Turborotalita quinqueloba* observed by Horton (1999) and Horton and Edward (Horton and Edward, 2006) in British estuaries. Benthic species were primarily represented by hyaline test (71%), while a minor percentage was represented by porcelaneous test (16%) and agglutinated test (13%). A total of 656 samples contained living fauna.

A total of 246 dead species were reported in the areas under consideration with 59 species were only encountered in Belgian waters (Cushman, 1947), 31 in the Canche estuary (Armynot du Châtelet et al., 2018b), 13 in the Liane estuary (Armynot du Châtelet et al., 2011), 10 in Tees (Horton, 1999; Horton and Murray, 2007) and 3 in Holland transitional areas (Phleger, 1970) and 2 in the Aln estuary (Horton and Edward, 2006) (Fig. 2A). The remaining species co-occurred in 2 to 16 geographical areas. These species were observed in 1 to 6 environmental units (Fig. 2B). Ninety-nine species were observed as living. They were recognized in a single geographical area and were also found in 2 to 4 estuaries (Fig. 3A) and 4 environmental units (Fig. 3B). The largest numbers of species in a single area were in the Canche (14) and Tees (13) estuaries. Some living species were also endemic to the Authie (5), Liane (4), Holland (3), Seine (3) and Southampton areas (2). Eighteen species occurred only in tidal channels, 4 only in tidal flats, and 2 in middle or low marshes. Most of the species were distributed with limited dimension groups rather than being ubiquitous within the entire geographical area or environmental units. The rarefaction curves confirm these findings by showing a slow increase of the species richness with an increase of the observed samples (Fig. 4).

The tree calculated using dead fauna revealed a strong dichotomy between the two sides of the English Channel (Fig. 5). Samples from Belgian, Holland and Southampton waters (subtidal and tidal flat) were also separated from these two groups. Within each of these biogeographical provinces, a good level of consistency was observed among the geographical areas. On the other hand, for the living fauna (Fig. 6), groups were mostly organized in environmental units with:

- tidal flats, low marshes, and tidal channels;
- salt marshes from low to high marshes;
- subtidal and tidal flats.

Only samples from low marshes appeared to be poorly sorted and were grouped with the third environmental unit.

The strongest similarities between communities of dead species were found within the French coast estuaries (Fig. 7A). For the living communities, the similarity is essentially equivalent among all the sites (Fig. 8A).

The dead and living communities were composed of 34 and 13 clusters, respectively (Supplementary data 1 and 2). There were significant differences in the distribution of the dead communities between the UK and the European continent (Figs. 7B). For example, the green community was distributed along the British coast, whereas the brown/yellow one along the Dutch continental coast had its own community with significant presence of *Ammonia beccarii*, *Elphidium translucens* and *Nonion tiburyensis*. Liane estuary harboured two communities, one in the subtidal unit and one in the tidal flat unit. The most frequently observed species were *Cribroelphidium williamsoni* occurring in 14 communities, *Haynesina germanica* in 13, *C. excavatum* in 12, *Cribroelphidium magellanicum* in 10, *Entzia macrescens* and *Buliminella elegantissima* in 9, *Trochammina inflata* in 8, *Cribroelphidium gerthi* and *Cibicidoides lobatulus* in 7. For the living communities, a separation between the two sides of the English Channel was clear as well (Supplementary material 3). Very similarly to dead fauna, the living communities

Table 2
Number of samples according to geographical area and environmental unit. The number of observed living and dead foraminiferal taxa are also reported.

	N sample	N living species	N dead species
Aa	12	41	41
Aln	20	0	29
Authie	88	55	84
Belgian waters	47	0	118
Canche	178	61	115
Hayling	72	12	12
Holland	60	7	7
Humber	20	0	19
Keyhaven	13	0	6
Liane	90	45	70
Pool	18	0	19
Seine	17	17	49
Somme	18	45	74
Southampton	39	9	19
Tees	162	26	56
Thornham Brancaster	47	0	24
High marsh	110	34	45
Middle marsh	133	33	67
Low marsh	266	70	147
Tidal flat	283	78	135
Tidal channel	20	48	54
Subtidal	89	29	157

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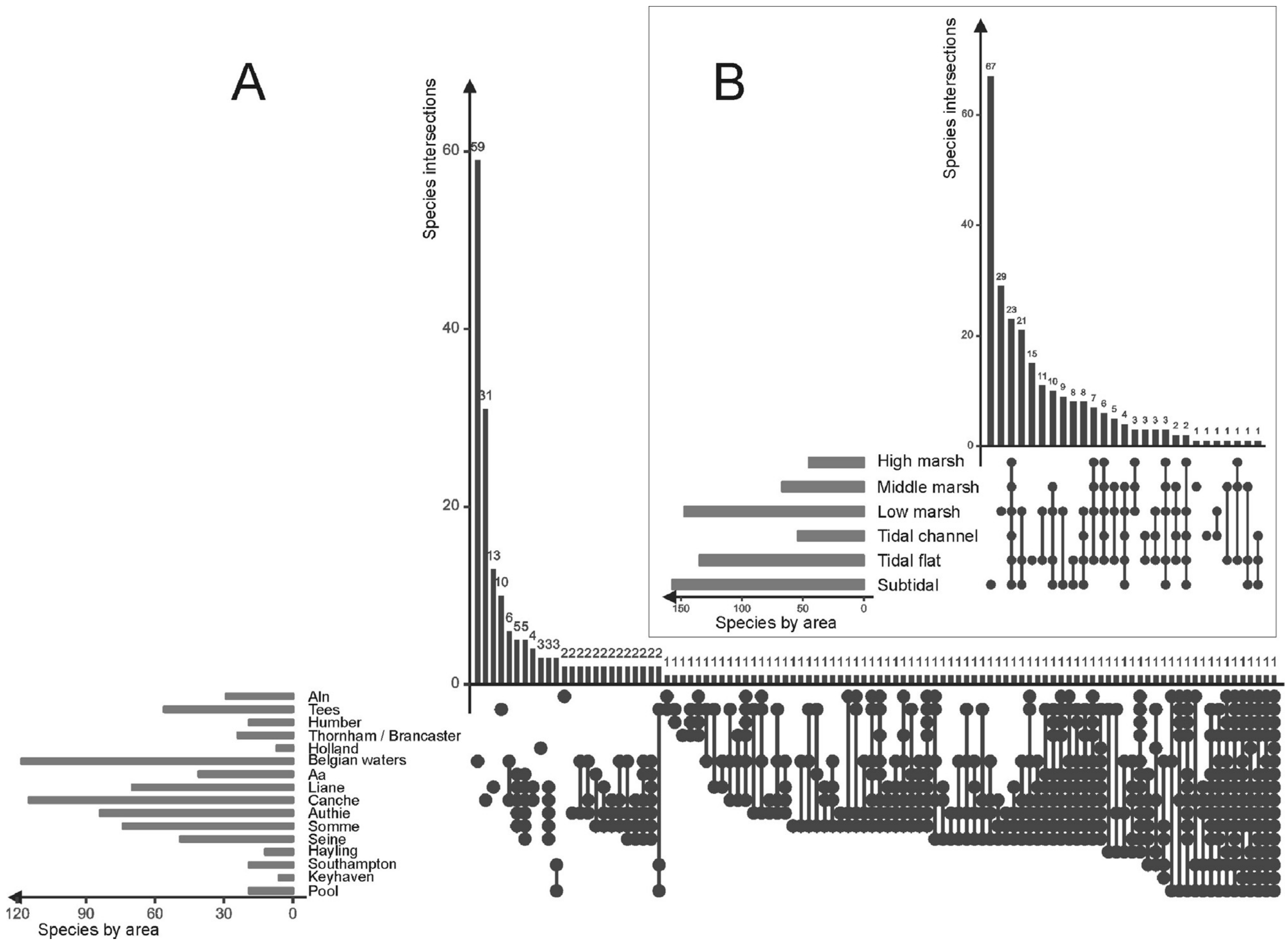

Fig. 2. Matrix layout for all intersections between the occurrence of species and the 16 areas (A) and the 6 environmental units (B) sorted by position. Dark circles in the matrix indicate dead species that are part of the intersection. Lack of combination is not presented.

were observed with geographical non-homogeneous distribution (Fig. 8B). The most common species in living communities were *H. germanica* occurring in 6 communities, and *C. excavatum* and *C. williamsoni* in 5. Three communities were present in the Aa (tidal flat), Somme (tidal channel), Holland (salt marsh) and Tees (low and middle marshes) geographical units (Supplementary material 4).

4. Discussion

4.1. Benthic foraminiferal communities

In the different foraminiferal communities along transitional areas of the studied region, the most frequently observed species corresponded to the most common taxa occurring in meso-macro tidal areas. For instance, *Entzia macrescens*, *Trochammina inflata, Haynesina germanica*, *Cribroelphium excavatum* or *C. williamsoni* are typical marginal marine taxa recognized worldwide (e.g., Murray, 2006, 2007; Murray, 2013; Scott and Medioli, 1978; Scott et al., 2001). It is well known that foraminifera living in transitional environments, particularly in marsh areas, are vertically constrained by the tidal frame (Gehrels, 1994; Horton et al., 1999a; Horton and Murray, 2007; Scott et al., 2001). Although transitional assemblages are marked by identical or similar groups of species in discontinuous geographic locations, biogeography might influence the zonation of benthic foraminifera (Sen Gupta, 1999b). We noticed that about 25% of the total species richness was reported specifically in Belgian waters. However, this could be ascribed by the fact that samples from that geographical area were entirely taken in subtidal environments. Since the Belgian water samples were collected in 1949, another possibility is that some sort of climate evolution occurred in the last few decades. Accordingly, over the last 100 years, Hawkins et al. (Hawkins et al., 2003) detected environmental changes in marine ecosystems of the English Channel. The authors documented a period of warming of the sea from the 1920s to the 1950s, with increases in the abundance of species of fish, plankton and intertidal organisms that were commonly found in warmer waters. Taking into account the period of the study, we can also hypothesize that many foraminiferal taxa were included on this occasion but never recognized afterwards. The Liane river, which also has a subtidal frame, was considered as a distinct community with 13 endemic species observed, perhaps because of the disturbance of the assemblages caused by its highly polluted harbor (Armynot du Châtelet et al., 2011; Armynot du Châtelet et al., 2017a; Francescangeli et al., 2016). Among the 16 geographical areas, Liane estuary is the only one that is heavily impacted by

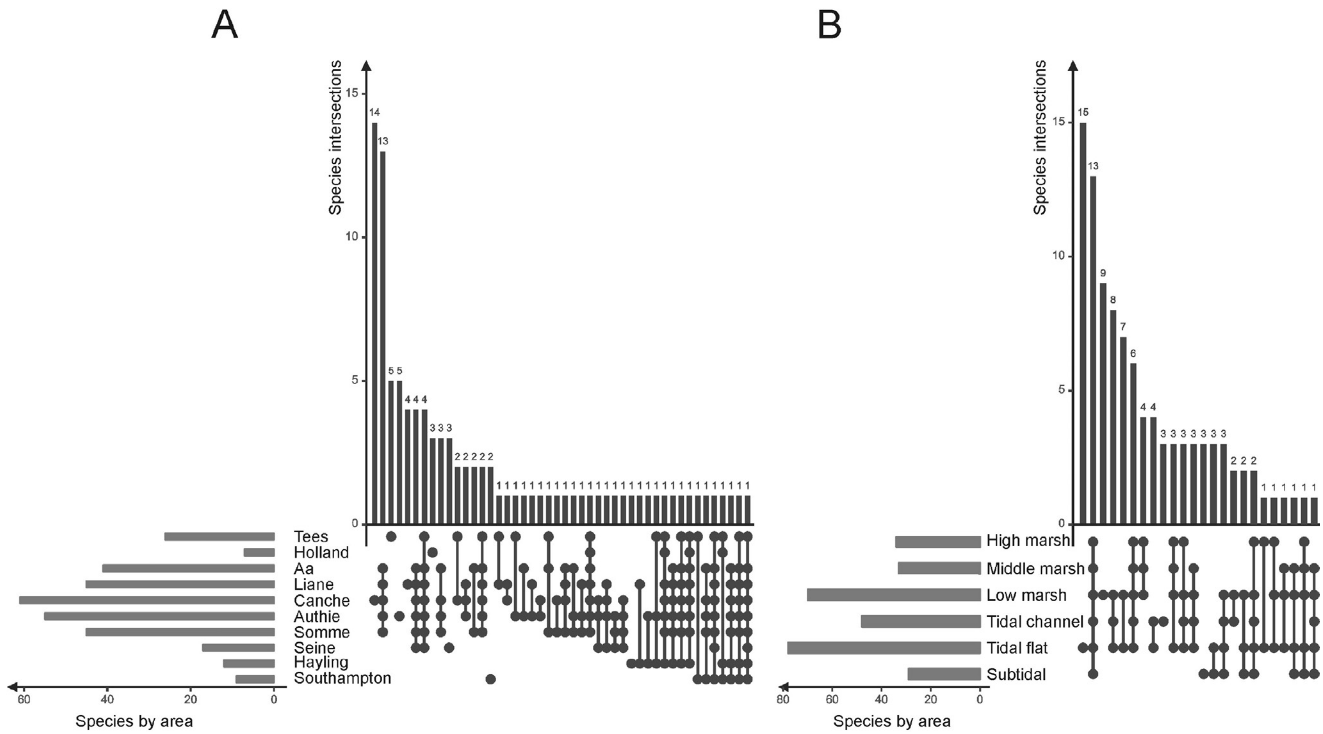

Fig. 3. Matrix layout for all intersections between the occurrence of living species and the 10 areas (A) (No living species in Belgian waters' study) and the 6 geographical units (B) sorted by position. Dark circles in the matrix indicate living species that are part of the intersection. Lack of combination is not presented.

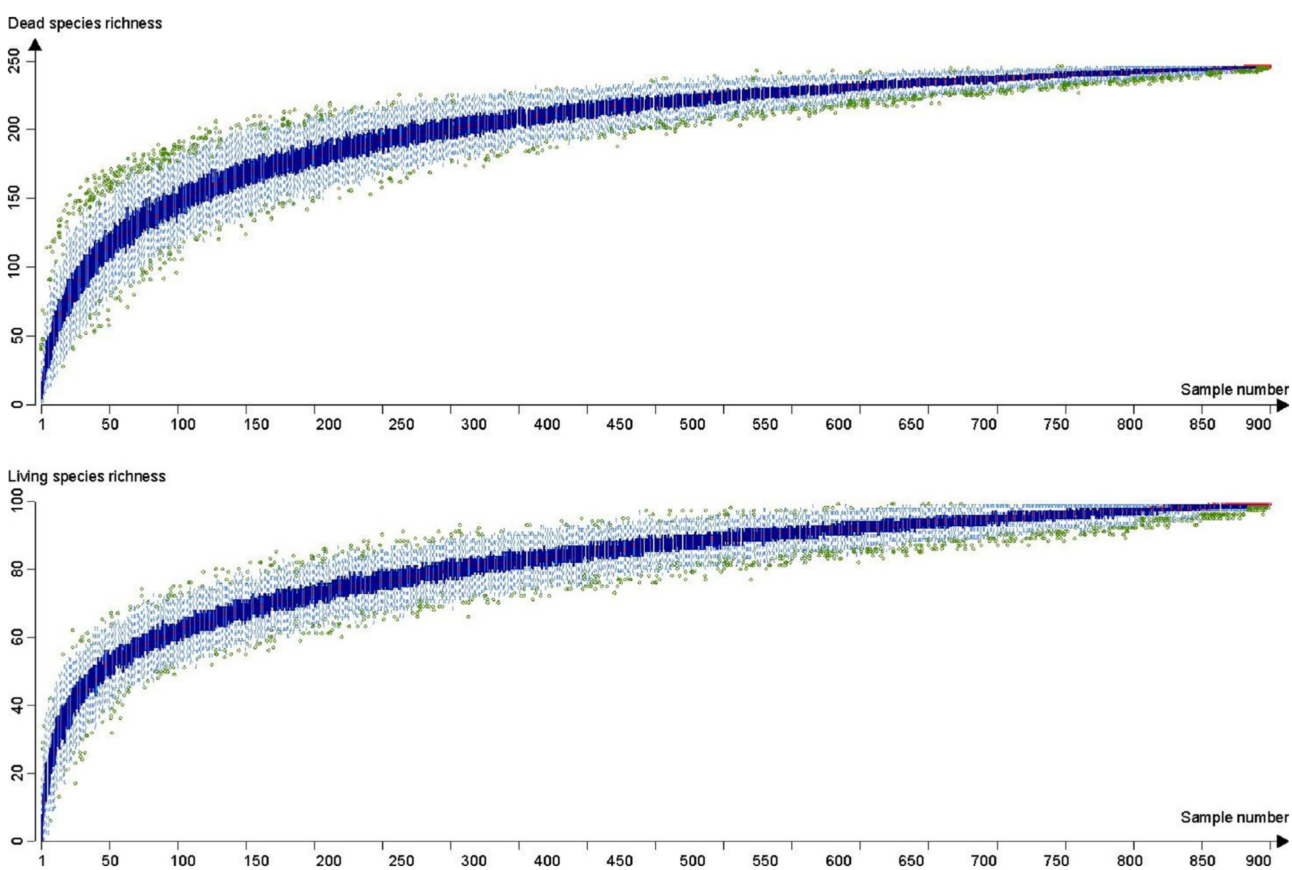

Fig. 4. Rarefaction curves for the dead (above) and the living (below) fauna. For each sample number, the dispersion of the data are depicted by box-whisker plot. The dark blue curve is the interval between the lower (Q1) and upper (Q3) quartile; the light blue are the whiskers and green points are the outliers.

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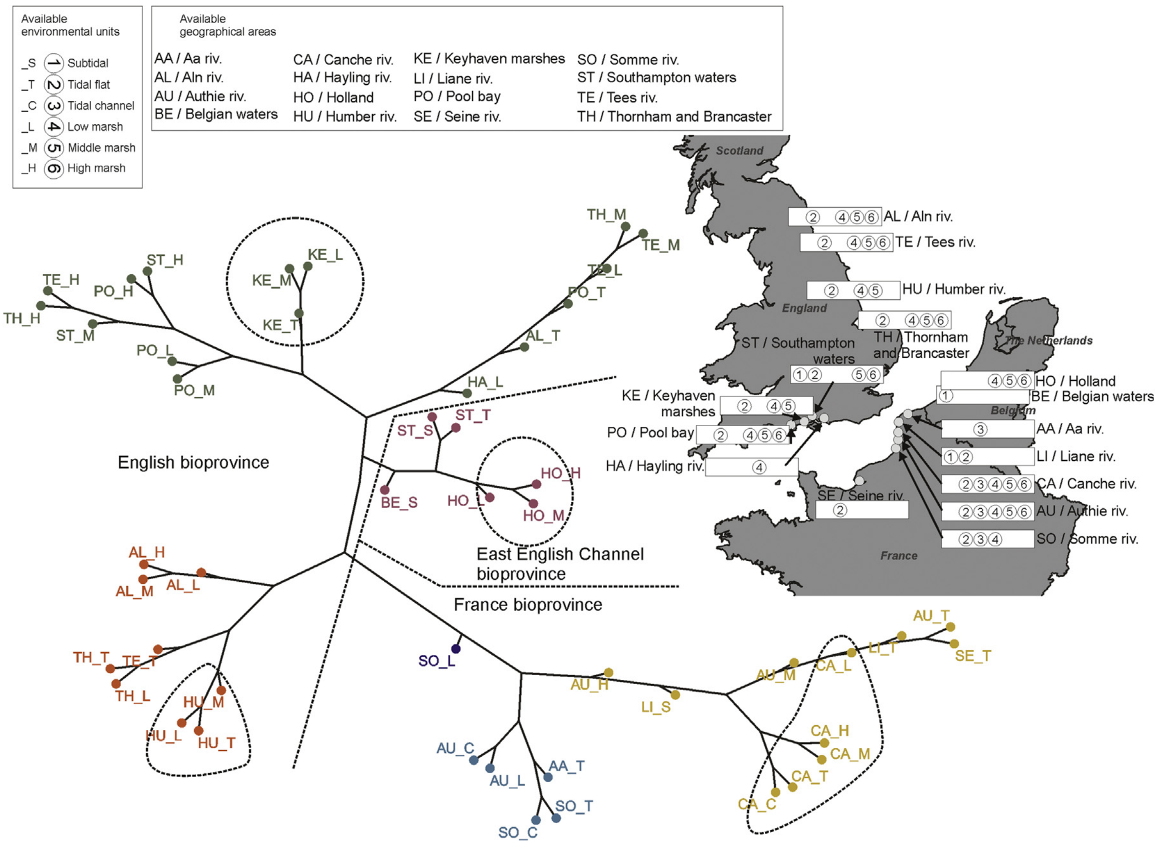

Fig. 5. Phylogenetic-like dendrogram based on dead species with the area/unit arranged in six groups (colors). For the names, the two first letters are the area (Aa: AA; Aln: AL; Authie: AU; Belgian waters: BE; Canche: CA; Hayling: HA; Holland: HO; Humber: HU; Keyhaven: KE; Liane: LI; Pool: PO; Seine: SE; Somme: SO; Southampton: ST; Tees: TE; Thornham Brancaster: TH) and the last letter represents the environmental unit (High marsh: H; Middle marsh: M; Low marsh: L; Tidal flat: T; Subtidal: S; Tidal channel: C).

industrial and urban pollution. Here, foraminiferal assemblages showed low species richness and the presence of trace-metal tolerant taxa (Armynot du Châtelet et al., 2011; Francescangeli, 2017). In the same area, Francescangeli et al. (2016) reported that human-induced stress has led to significant modifications of foraminiferal assemblages over the last 200 years. Thirty-one endemic foraminiferal species were observed in the Canche estuary that is also the location where the largest number of samples was retrieved. This positive relationship among the number of samples, the species richness and diversity is also observed in palaeontology (Murray, 2013). This is in accordance with Kim et al. (Kim et al., 2016) who, after increasing the number of samples, found 180 species that were not recorded in Korean coastal waters. The species richness may be strongly subjected to sampling effort. At last, it should be noticed that, as the calculation is based on contingency table, the effect of outliers and rare species could not be observed.

4.2. Foraminiferal based bioprovinces units

In the present paper, our statistical approach allowed us to clearly identify three foraminiferal bioprovinces:

- the English bioprovince;
- the French bioprovince;
- the East English Channel bioprovince.

Although the bioprovinces are made up of different foraminiferal communities, statistically each has its own specific characteristics in terms of regional species compositions. In the same area of the English Channel and the Southern North Sea, similar results were shown by Foveau et al. (2010) in a survey based on fish population. They identified four habitats in the area; three of which are similar to the provinces we defined using benthic foraminifera. First, an area of "*High disturbance and high scope for growth*" is located in the southern North Sea, particularly along the Dutch and German coasts. This area corresponds to Holland and Belgian area foraminiferal province. Then, Foveau et al. (2010) described an area of "*High disturbance and low scope for growth*" that is located near the eastern coasts of England that corresponds to the present study's samples taken in the area south of the Thames bay. Finally, they distinguished an area of "*Low disturbance and high scope for growth*" corresponding to the English Channel, in the vicinity of Wight Island and what we can refer to as the French coast in the present study. Even if it does not precisely fit our foraminiferal-based bioprovinces, the strong similarities suggest that some of the environmental parameters driving fish distributions might be, to some extent, similar to those conditioning foraminiferal benthic distributions. One can speculate that these parameters might

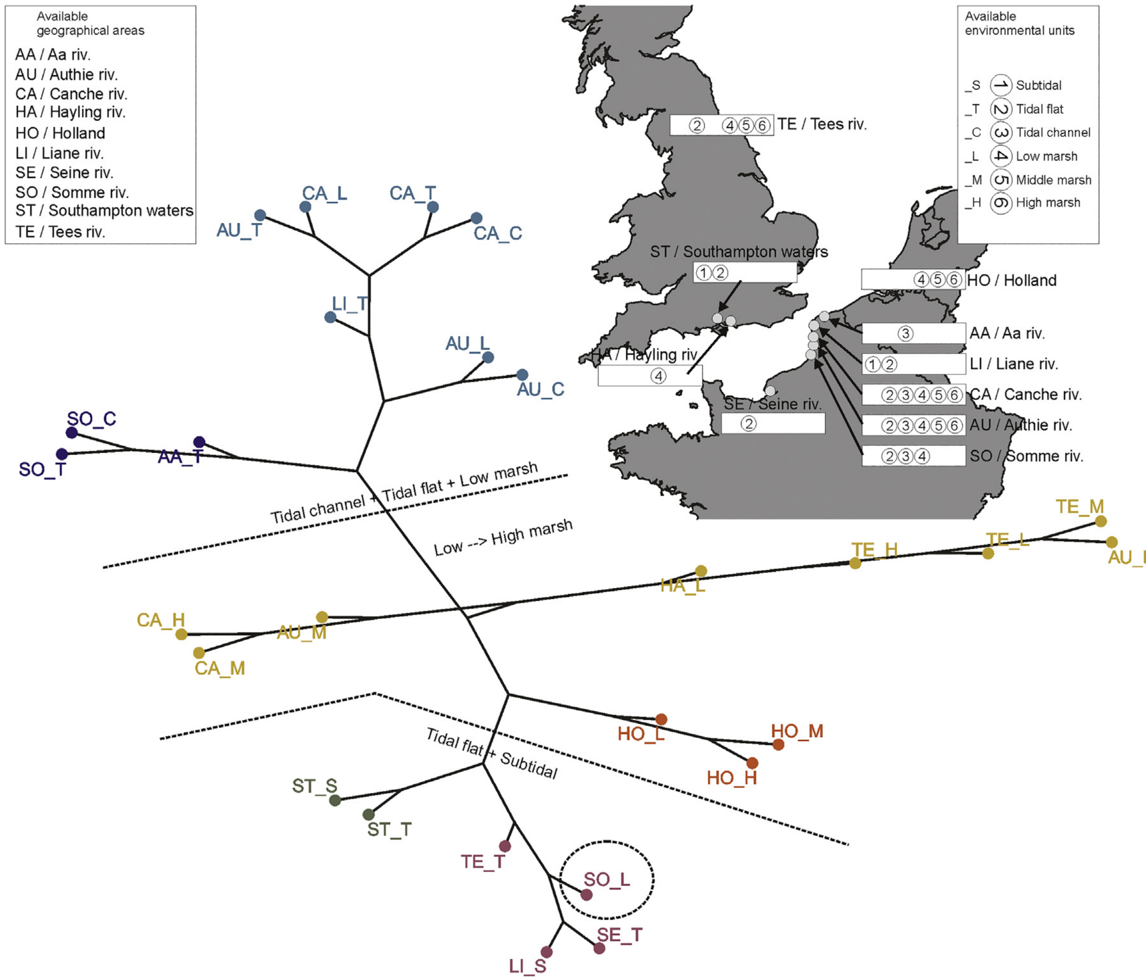

Fig. 6. Phylogenetic-like dendrogram based on living species with the area/unit arranged in six groups (colors). Legend asin Fig. 5.

be driven and constrained by different hydroclimatic conditions occurring in our bioprovinces.

Our observations also support a moderate endemic model that reveals a large similarity between the observed sites and also makes possible identification of bioprovinces. These findings match well with the observations of Sen Gupta and Smith (2010) in the Gulf of Mexico where 30% of the species are endemic. Similarly, Hayward et al. (2007) observed 10% endemism within the sub-Antarctic island compared to the nearby New Zealand mainland. Pawlowski and Holzmann (2008), with a study based on molecular global distribution of benthic foraminifera, come up to the same conclusion. Mechanisms of dispersion may be responsible for the distribution: for example, propagules (Alve and Goldstein, 2002; Hayward et al., 2007), which are easily transported by the high dynamic observed in the area, but whose distribution is also influenced by their capacity to settle, develop and reproduce. Foraminiferal distribution appears patchy at different scale levels, due to differences in food supply (Murray, 2013), water salinity (McGann, 2014), physical characteristics (i.e. sediment grain size) (Armynot du Châtelet et al., 2017b; Armynot du Châtelet et al., 2018) or biogeochemical heterogeneity (such as the presence of roots and bioturbation or the existence of depressions in the sediment) (Debenay et al., 2015).

Finally, the two communities of Belgian waters and Holland marshes appear statistically distinct. We can hypothesize that there may be some issues related to the method, date, and location of sampling, that could result in greater differences between communities. For now, this remains a hypothesis, as currently we have no statistical evidence on this point.

4.3. Dead vs. living communities

The results of our study indicate that dead foraminifera are better indicators of biogeographical provinces, whereas living ones are better correlated to environmental units. Living fauna represent a snapshot of the ecological and environmental conditions at the time of sampling, indicating short-term and very localized environmental variations (Debenay et al., 2006; Francescangeli, 2017). It is evident that for environmental studies such as local ecological characterizations, environmental biomonitoring, or environmental impact assessments, the use of living assemblages is required. In addition, the density, species richness as well as the diversity of benthic living foraminifera can vary seasonally, reflecting changes in biotic and abiotic environmental variables (Milker et al., 2015; Murray and Alve, 2000; Wilson and Dawe, 2006). Conversely, dead fauna arise

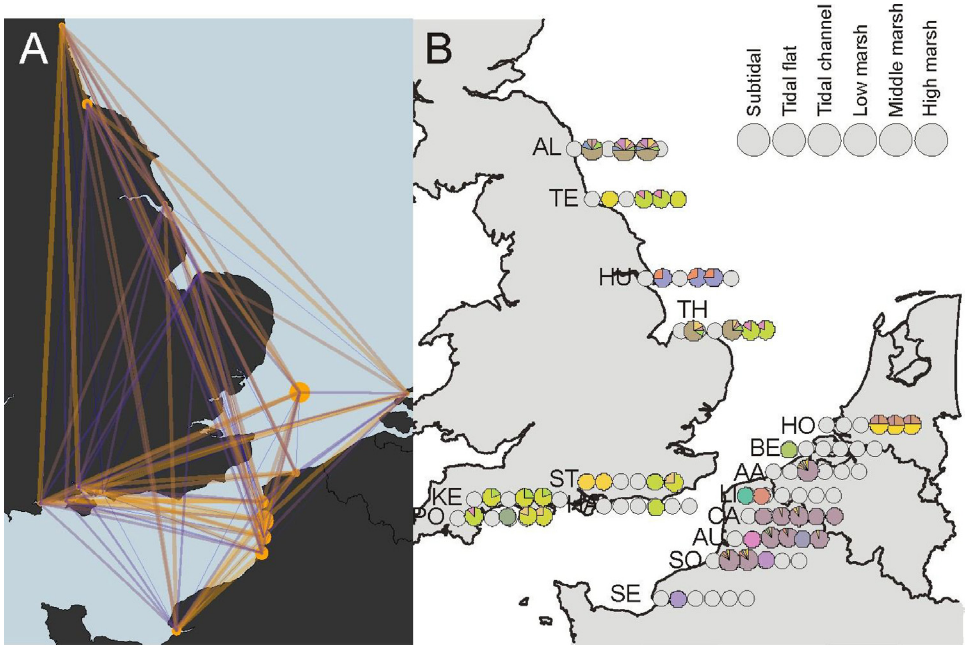

Fig. 7. Plot of the dead communities. A. The similarity matrix between geographical areas is presented on the geographical framework. The highest similarity is marked in orange and the lowest similarity in blue. B. Map plot of the edge, sorted from subtidal to high marsh for each area. The fraction of the total number of edges that a node has in each community is depicted using a pie chart. The colors in the pie indicate which statistical community is present at each location.

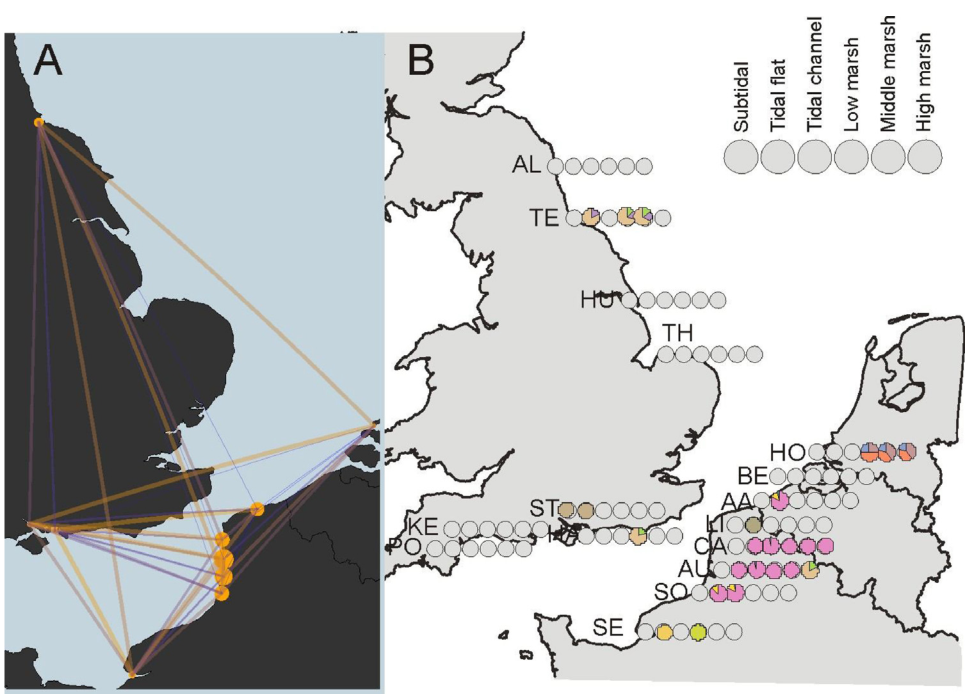

Fig. 8. Plot of the living communities. A. The similarity matrix between geographical areas is presented on the geographical framework. The highest similarity is marked in orange and the lowest similarity in blue. B. Map plot of the edge, sorted from subtidal to high marsh for each area. The fraction of the total number of edges that a node has in each community is depicted using a pie chart. The colors in the pie indicate which environmental unit is present at each location.

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from the addition of several organisms' generation over time, denoting time-averaged assemblages modified by taphonomic processes such as post-mortem transport, reworked specimens, or early diagenetic processes (Hawkes et al., 2010; Murray, 2000). Therefore, dead fauna reflects environmental characteristics and foraminiferal behavior over a greater period of time and on a larger scale. Consequently, it is not surprising that in the present study, living fauna were revealed to be structured along environmental units, whereas dead fauna was more dependent on geography. A study on endemism made it important to have knowledge of living fauna to reconstruct sea level variations based on foraminifera, but studying dead fauna on a larger scale is also important because of regional environmental evolution and potential migration of bioprovince.

5. Conclusion

In the transitional areas of the Eastern English Channel and the Southern North Sea, a total of 246 foraminiferal species have been reported. Of these, only 99 were found as living within six different environmental units along the tidal frame. Benthic foraminiferal assemblages are in large part composed of species that are widely geographically distributed, but about 30% of the species are endemic. High levels of endemism were particularly observed in Belgian waters (the oldest study included in the present paper) and in the study of the Canche estuary (the study with the greatest number of samples). Species richness may be subjected to taxonomic bias and sampling effort.

The analyses of co-occurrence and communalities allow us to define three distinct foraminiferal bioprovinces, namely the English, the French and the East English Channel bioprovinces. Dead foraminifera prove to be an optimal tool for biogeographical characterization. Living foraminifera are more indicative of purely local environmental conditions.

This data mining work and the techniques developed to analyze the assembled data might now be applied and extended to many other available datasets all over the world in a comprehensive study of biodiversity distribution.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgments

The authors deeply thank Taniel Danelian and Frédérique Eynaud the Editors in Chief of *Revue de Micropaleontologie* who gave the authors the opportunity to submit this work within the 60th anniversary issue of the journal. The authors also thank Maria Triantaphyllou and the anonymous reviewer for their constructive comments. The authors warmly thank Jennifer Morival for reviewing the American spelling. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://www.sciencedirect.com and https://doi.org/10.1016/j.revmic.2018.04.001.

References

Adl, S.M., Simpson, A.G.B., Lane, C.E., Lukes, U., Bass, D., Bowser, S.S., Brown, M.W., Burki, F., Dunthorn, M., Hampl, V., Heiss, A., Hoppenrath, M., Lara, E., Le Gall, L., Lynn, D.H., McManus, H., Mitchell, E.A.D., Mozley-Stanridge, S.E., Parfrey, L.W., Pawlowski, J., Rueckert, J., Shadwick, L., Schoch, C.L., Smirnov, A., Spiegel, F.W., 2012. The Revised Classification of Eukaryotes. The Journal of Eukaryotic Microbiology 59, 429–493.

Alve, E., Goldstein, S.T., 2002. Resting stage in benthic foraminiferal propagules: a key feature for dispersal? Journal of Micropaleontology 21, 95–96.

Alve, E., Murray, J.W., 1994. Ecology and taphonomy of benthic foraminifera in a temperate mesotidal inlet. Journal of Foraminiferal Research 24, 18–27.

Armynot du Châtelet, E., Bout-Roumazeilles, V., Coccioni, R., Frontalini, F., Francescangeli, F., Margaritelli, G., Rettori, R., Spagnoli, F., Semprucci, F., Trentesaux, A., Tribovillard, N., 2016. Environmental control on a land–sea transitional setting: integrated sedimentological, geochemical and faunal approaches. Environmental Earth Science 75, 123.

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

Armynot du Châtelet, E., Francescangeli, F., Bouchet, V.M.P., Frontalini, F., 2018. Benthic foraminifera on transitional environments in the English Channel and the southern North Sea: a proxy for regional scale environmental and paleo-environmental characterizations. Marine Environmental Research 137, 37–48.

Armynot du Châtelet, E., Gebhardt, K., Langer, M.R., 2011. Coastal pollution monitoring: Foraminifera as tracers of environmental perturbation in the port of Boulogne-sur-Mer (Northern France). Neues Jahrbuch für Geologie und Paläontologie 262, 91–116.

Armynot du Châtelet, E., Trentesaux, A., Francescangeli, F., Evrard, A., 2017a. Le port de Boulogne, une histoire enfouie dans ses sédiments. In: Le Portel, Notes et Documents., pp. 43–53.

Armynot du Châtelet, E., Frontalini, F., Francescangeli, F., 2018. Significance of replicates: environmental and paleoenvironmental studies on benthic foraminifera and testate amoebae. Micropaleontology 63, 257–274.

Becker, R.A., Wilks, A.R., 2016. Mapdata: extra map databases. In: R package version 2. 2-6. R version by Ray Brownrigg.

Becker, R.A., Wilks, A.R., 2017. Maps: draw geographical maps. In: R package version 3. 2. 0. R version by Ray Brownrigg. Enhancements by Thomas P Minka and Alex Deckmyn.

Buzas, M.A., Culver, S.J., 1989. Biogeographic and evolutionary patterns of continental margin foraminifera. Paleobiology 15, 9–11.

Conway, J.R., Lex, A., Gehlenborg, N., 2017. UpSetR: An R package for the visualization of intersecting sets and their properties. Bioinformatics 33, 2938–2940.

Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. International Journal of Complex Systems, 1695.

Cushman, J.A., 1947. Recent Belgian Foraminifera, Bruxelles.

Debenay, J.-P., 1999. Foraminifera. In: Amiard-Triquet, C., Rainbow, P.S. (Eds.), Environmental assessment of estuarine ecosystems: a case study. CRC Press, Taylor and Francis Group, Boca Raton, pp. 255–280.

Debenay, J.-P., Bicchi, E., Goubert, E., Armynot du Châtelet, E., 2006. Spatial and temporal distribution of benthic foraminiferal assemblages in the Vie Estuary (Vendée, W France). Estuarine, Coastal and Shelf Science 67, 181–197.

Debenay, J.-P., Marchand, C., Molnar, N., Aschenbroich, A., Meziane, T., 2015. Foraminiferal assemblages as bioindicators to assess potential pollution in mangroves used as a natural biofilter for shrimp farm effluents (New Caledonia). Marine Pollution Bulletin 93, 103–120.

Denis, L., Gontharet, S., Gevaert, F., Duong, G., Goulard, F., Armynot du Chatelet, E., Artigas, F., Bolhuis, H., Brotas, V., Caillaud, J., Gommeaux, M., Lefebvre, S., Philippe, S., Ribeiro, L., Trentesaux, A., Verpoorter, C., 2016. MIDIEM project: microbenthic diversity (functional & biological). In: Intertidal Estuarine Mudflats. Université de Lille, Laboratoire LOG, Wimereux.

Dimiza, M.D., Koukousioura, O., Triantaphyllou, M.V., 2016. Live and dead benthic foraminiferal assemblages from coastal environments of the Aegean Sea (Greece): distribution and diversity. Revue de Micropaléontologie 59, 19–32.

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22, 1–20.

Epskamp, S., Cramer, A.O.J., Waldorp, L.J., Verena, D., Schmittmann, V.D., Borsboom, D., 2012. qgraph: network visualizations of relationships in psychometric data. Journal of Statistical Software 48, 1–18.

Evans, T.S., Lambiotte, R., 2009. Line graphs, link partitions and overlapping communities. Physical Review E 80, 016105.

Foveau, A., Vaz, S., Kostylev, V.E., 2010. Identification of sensitive benthic habitats in the Eastern English Channel based on functional traits and the Kostylev approach. International Council for the Exploration of the Sea Copenhagen, Denmark.

Francescangeli, F., 2017. Spatio-temporal distribution of benthic foraminifera in intertidal area of Hauts-de-France: environmental applications and implications. In: Doctoral school EDSMRE. University of Lille, Villeneuve d'Ascq, pp. 202.

Francescangeli, F., Armynot du Chatelet, E., Billon, G., Trentesaux, A., Bouchet, V.M.P., 2016. Palaeo-ecological quality status based on foraminifera of Boulogne-sur-Mer harbour (Pas-de-Calais, Northeastern France) over the last 200 years. Marine Environmental Research 117, 32–43.

Francescangeli, F., Bouchet, V.M.P., Trentesaux, A., Armynot du Châtelet, E., 2017. Does elevation matter? Living foraminiferal distribution in a hyper tidal salt marsh (Canche Estuary, Northern France). Estuarine, Coastal and Shelf Science 194, 192–204.

Frontalini, F., Coccioni, R., 2011. Benthic foraminifera as bioindicators of pollution: a review of Italian research over the last three decades. Revue de Micropaléontologie 54, 115–127.

Frontalini, F., Kaminski, M.A., Mikellidou, I., Armynot du Châtelet, E., 2015. Checklist of benthic foraminifera (class Foraminifera: d'Orbigny 1826; phylum Granuloreticulosa) from Saros Bay, nothern Aegean sea: a biodiversity hotspot. Marine Biodiversity.

Fruchterman, T.M.J., Reingold, E.M., 1991. Graph drawing by force-directed placement software. Practice and Experience 21, 1129–1164.

Gehlenborg, N., 2016. UpSetR: a more scalable alternative to Venn and Euler diagrams for visualizing intersecting sets. In: R package version 1. 3. 3.

Gehrels, W.R., 1994. Determining relative sea-level change from saltmarsh foraminifera and plant zones on the coast of Maine, U.S.A. Journal of Coastal Research 10, 990–1009.

Gooday, A.J., Hori, S., Todo, Y., Okamoto, T., Kitazato, H., Sabbatini, A., 2004. Soft-walled, monothalamous benthic foraminiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. Deep Sea Research I 51, 33–53.

Gooday, A.J., Jorissen, F., 2012. Benthic foraminiferal biogeography: controls on global distribution patterns in deep-water settings. Annual Review of Marine Science 4, 237–262.

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. Quaternary International 221, 116–140.

Hawkins, S.J., Southward, A.J., Genner, M.J., 2003. Detection of environmental change in a marine ecosystem-evidence from the western English Channel. Science of The Total Environment 310, 245–256.

Hayward, B.W., Grenfell, H.R., Sabaa, A.T., Neil, H.L., 2007. Factors influencing the distribution of Subantarctic deep-sea benthic foraminifera, Campbell and Bounty Plateaux, New Zealand. Marine Micropaleontology 62, 141–166.

Hohenegger, J., 2005. Estimation of environmental paleogradient values based on presence/absence data: a case study using benthic foraminifera for paleodepth estimation. Palaeogeography, Palaeoclimatology, Palaeoecology 217, 115–130.

Horton, B.P., 1999. The distribution of contemporary intertidal foraminifera at Cowpen Marsh, Tees Estuary, UK: implications for studies of Holocene sea-level changes. Palaeogeography, Palaeoclimatology, Palaeoecology 149, 127–149.

Horton, B.P., Edward, R.J., 2006. Quantifying Holocene Sea Level change using intertidal Foraminifera: lessons from the British Isles. Cushman Foundation for Foraminiferal Research. Special Publication 40, 97.

Horton, B.P., Edwards, R.J., Lloyd, J.M., 1999a. A foraminiferal-based transfer function: implications for sea-level studies. Journal of Foraminiferal Research 29, 117–129.

Horton, B.P., Edwards, R.J., Lloyd, J.M., 1999b. UK intertidal foraminiferal distributions: implications for sea-level studies. Marine Micropaleontology 36, 205–223.

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. Marine Micropaleontology 63, 169–186.

Kalinka, A.T., Tomancak, P., 2011. linkcomm: an R package for the generation, visualization and analysis of link communities in networks of arbitrary size and type. Bioinformatics 27, 2011–2012.

Kassambara, A., Mundt, F., 2017. Factoextra: extract and visualize the results of multivariate data analyses. In: R package version 1.0.5.

Kim, S., Frontalini, F., Martins, V., Lee, W., 2016. Modern benthic foraminiferal diversity of Jeju Island and initial insights into the total foraminiferal diversity of Korea. Marine Biodiversity 46, 337–354.

Lemon, J., 2006. Plotrix: a package in the red light district of R. R-News 6, pp. 8–12.

Levin, I.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annual Review of Systematics and Ecology 32, 51–93.

Lex, A., Gehlenborg, N., Strobelt, H., Vuillemot, R., Pfister, H., 2014. UpSet: visualization of Intersecting Sets. IEEE Transactions on Visualization and Computer Graphics (InfoVis '14) 20, 1983–1992.

McGann, M., 2014. Earliest record of the invasive foraminifera Trochammina hadai in San Francisco bay, California, USA. Marine Biodiversity Records 7, 1–7.

Milker, Y., Horton, B.P., Nelson, A.R., Engelhart, S.E., Witter, R.C., 2015. Variability of intertidal foraminiferal assemblages in a salt marsh, Oregon, USA. Marine Micropaleontology 118, 1–16.

Murray, J.W., 1968. The living Foraminifera of Christchurch Harbour, England. Micropaleontology 14, 83–96.

Murray, J.W., 1991. Ecology and paleoecology of benthic foraminifera. Longman, Harlow.

Murray, J.W., 2000. The enigma of the continued use of total assemblages in ecological studies of benthic foraminifera. Journal of Foraminiferal Research 30, 244–245.

Murray, J.W., 2006. Ecology and applications of benthic foraminifera. Cambridge University Press, Cambridge.

Murray, J.W., 2007. Biodiversity of living benthic foraminifera: how many species are there? Marine Micropaleontology 64, 163–176.

Murray, J.W., 2013. Living benthic foraminifera: biogeographical distributions and the significance of rare morphospecies. Journal of Micropaleontology 32, 1–58.

Murray, J.W., Alve, E., 2000. Major aspects of foraminiferal variability (standing crop and biomass) on a monthly scale in an intertidal zone. Journal of Foraminiferal Research 30, 177–191.

Murray, J.W., Alve, E., 2016. Benthic foraminiferal biogeography in NW European fjords: a baseline for assessing future change. Estuarine, Coastal and Shelf Science 181, 218–230.

Murtagh, F., Legendre, P., 2014. Ward's hierarchical agglomerative clustering method: which algorithms implement Ward's criterion? Journal of Classification 31, 274–295.

Pawlowski, J., Holzmann, M., 2008. Diversity and geographic distribution of benthic foraminifera: a molecular perspective. Biodiversity and Conservation 17, 317–328.

Pawlowski, J., Holzmann, M., Tyszka, J., 2013. New supraordinal classification of Foraminifera: molecules meet morphology. Marine Micropaleontology 100, 1–10.

Phleger, F.B., 1970. Foraminiferal populations and marine marsh processes. Limnology Oceanography 15, 522–534.

Core Team, R., 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radicchi, F., Castellano, C., Cecconi, F., Loreto, V., Parisi, D., 2004. Defining and identifying communities in networks. PNAS 101, 2658–2663.

Raux, A., 2014. Foraminifères benthiques vivants et pollution dans le port de Boulogne-sur-Mer. Université de Lille, Villeneuve d'Ascq, pp. 25.

Rosset-Moulinier, M., 1986. Les populations de foraminifères benthiques de la Manche. Cahiers de Biologie Marine 27, 387–440.

Saad, S.A., Wade, C.M., 2016. Seasonal and spatial variations of saltmarsh benthic foraminiferal communities from North Nrfilk, England. Microbial Ecology 73, 539–555 [Springer ISSN: 0095-3628].

Scott, D.B., Medioli, F.S., 1978. Vertical zonation of marsh foraminifera as accurate indicators of former sea levels. Nature 272, 528–531.

Scott, D.B., Medioli, F.S., Schafer, C.T., 2001. Monitoring in coastal environments using Foraminifera and thecamoebian indicators. Cambridge University Press, New York.

Sen Gupta, B.K., 1999a. Chapter 1 – Introduction to modern Foraminifera. In: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, Dordrecht, p. 371.

Sen Gupta, B.K., 1999b. Foraminifera in marginal marine environments. In: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, pp. 141–159.

Sen Gupta, B.K., Smith, L.E., 2010. Modern benthic foraminifera of the Gulf of Mexico: a census report. Journal of Foraminiferal Research 40, 247–265.

Swallow, J.E., 2000. Intra-annual variability and patchiness in living assemblages of salt-marsh foraminifera from Mill Rythe Creek, Chichester Harbour, England. Journal of Micropaleontology 19, 9–22.

Wilson, B., Dawe, R.A., 2006. Detecting seasonality using time series analysis: comparing foraminiferal population dynamics with rainfall data. Journal of Foraminiferal Research 36, 108–115.

Xiao, N., 2017. ggsci: Themed Color Palettes for 'ggplot2'. R package version 2. 8. Scientific Journal and Sci-Fi.

Please cite this article in press as: Armynot du Châtelet, E., et al., Definition of benthic foraminiferal bioprovinces in transitional environments of the Eastern English Channel and the Southern North Sea. Revue de micropaléontologie (2017), https://doi.org/10.1016/j.revmic.2018.04.001