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Benthic foraminifera in transitional environments in the English Channel and the southern North Sea: A proxy for regional-scale environmental and paleo-environmental characterisations

E. Armynot du Châtelet[a,*], F. Francescangeli[a,b], V.M.P. Bouchet[b], F. Frontalini[c]

[a] Univ. Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 59 000, Lille, France
[b] Univ. Lille, CNRS, Univ. Littoral Côte d'Opale, UMR 8187, LOG, Laboratoire d'Océanologie et de Géosciences, F 62 930, Wimereux, France
[c] Univ. Urbino Dipartimento di Scienze Pure e Applicate (DiSPeA), Università degli Studi di Urbino "Carlo Bo", Campus Scientifico Enrico Mattei, Località Crocicchia, 61029, Urbino, Italy

A R T I C L E I N F O

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A B S T R A C T

On the basis of the available databases including 700 sampling stations from subtidal to salt marsh areas, the purpose of this paper is to synthesise the regional distribution of living benthic foraminifera in transitional environments along the English Channel and southern North Sea. Indicator species analyses assign 37 foraminiferal taxa to high salt marsh, middle salt marsh, low salt marsh, tidal flat, tidal channel, and subtidal environmental units. Species are indicator of a single unit (e.g., *Elphidium gunteri* for tidal flat) up to four units (e.g., *Haynesina germanica* from tidal flat to middle marsh). The outcomes of the present study enhance future high-resolution paleo-environmental interpretations based on benthic foraminifera in transitional environments.

1. Introduction

Benthic foraminifera (Rhizaria) are unicellular eukaryotes belonging to the clade that groups Stramenopiles, Alveolata, and Rhizaria (SAR) (Adl et al., 2007, 2012; Pawlowski et al., 2013). With a biodiversity of more than 10,000 species, they primarily occur in marine environments (Murray, 2006). A few specialised taxa are commonly found in marine transitional environments (TEs), such as lagoons, estuaries, marshes, and other brackish environments. Under the combined influence of marine and fresh waters, TEs are fragile ecotones characterised by strong environmental gradients and high variability of physico-chemical parameters (e.g., salinity, temperature, oxygen and pH) (Elliott and Quintino, 2007; Le Cadre et al., 2003). The concurrent overlapping of anthropogenic activities (e.g., urban sewage, industry, aquaculture, and agricultural runoff) makes TEs both naturally and anthropogenically stressed (Alve, 1995; Armynot du Chatelet and Debenay, 2010; Bouchet and Sauriau, 2008; Francescangeli et al., 2016; Frontalini and Coccioni, 2011). Therefore, TEs are much more selective to species than marine or terrestrial ecosystems, and only some benthic foraminiferal species could thrive and reproduce in these areas.

A large number of studies have dealt with the effect of natural and anthropogenic pressures on foraminiferal distributions in TEs (e.g., Albani et al., 2007; Armynot du Châtelet et al., 2004; Debenay et al., 1997; Francescangeli et al., 2017; Frontalini et al., 2009; Martins et al., 2015b). Because of the complexity of ecosystems in TEs, the working load, and/or the sampling opportunity, most of the published studies only focused on small regional areas, such as a single estuary (e.g., Debenay et al., 2003), lagoon (Martins et al., 2014), shore (e.g., Albani et al., 2010), or harbor (e.g., Frontalini et al., 2009). While syntheses covering a wider area have been undertaken (Armynot du Chatelet and Debenay, 2010; Frontalini and Coccioni, 2011), they were only aimed at demonstrating the applicability of benthic foraminifera as local environmental bioindicators.

Although benthic foraminiferal species are considered valuable environmental indicators (see Scott et al., 2001), our knowledge of the ecological requirements and behaviours of each species is hampered by the natural heterogeneity and complexity of these dynamic environments. Frequent recurring questions are: What are the physical, chemical, and biological environmental parameters driving their distributions? Which is the specific ecological niche of foraminiferal species?

The attribution of species to a peculiar environmental unit has been already attempted, such as during the foraminiferal biomonitoring initiatives (FOBIMO). The foraminiferal biomonitoring aimed at defining and standardising methods in benthic foraminiferal monitoring (Schönfeld et al., 2012). The definition of five ecological groups, according to species response to increasing organic carbon gradient, was

* Corresponding author.
E-mail addresses: eric.armynot@univ-lille1.fr (E. Armynot du Châtelet), Fabio.Francescangeli85@gmail.com (F. Francescangeli), vincent.bouchet@univ-lille.fr (V.M.P. Bouchet), Fabrizio.Frontalini@uniurb.it (F. Frontalini).

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set in the Northeast Atlantic and Arctic fjords (Alve et al., 2016). These assignments were then used for testing a biotic index (i.e., the Foram-AMBI index) (Alve et al., 2016). Similarly, a new biotic index, namely, the Foram Stress Index, based on relative abundances of tolerant-sensitive taxa to organic enrichment, was put forward and tested by Dimiza et al. (2016).

In a recent study assessing benthic macro-invertebrate species richness along the French coasts, the English Channel appeared to host the lowest number of species when compared to the Bay of Biscay or the Mediterranean Sea (Gallon et al., 2017). The authors shows the poorest diversity in the southern part of the North Sea biogeographical province and the richest one in the transition with the Atlantic province. This transitional region between the southern North-Sea and the English Channel, is a key area for meiofauna, as the high tide range (up to 9 m) offers a unique opportunity to explore a large range of transitional habitats and to explore benthic foraminiferal assemblage variations therein.

A local study in the hyper tidal estuary of La Canche (English Channel, France) showed that subaerial exposure is a key natural parameter driving the distribution of benthic foraminifera in TEs (Francescangeli et al., 2017). It suggests that the response of benthic foraminiferal communities to natural constraints is more complex than the simple grain size or total organic carbon (TOC) *vs*. species response. Hence, there is a need to quantitatively monitor the state of benthic foraminiferal communities and *in situ* environmental parameters in TEs. The aims of the present study are four-fold: 1) to synthesise data and biodiversity at a regional scale from studies dealing with benthic foraminifera in TEs in the southern North Sea and the eastern English Channel, 2) to assign the species to environmental units, 3) to identify environmental factors that trigger the distribution of benthic foraminiferal species, and ultimately, 4) to discuss the suitability of benthic foraminifera for environmental and paleo-environmental characterisations.

2. Materials and methods

2.1. Dataset selection

Throughout TEs along the eastern English Channel and the southern North Sea, suitable datasets have been strictly selected based on: 1) living foraminifera (rose Bengal stained), 2) availability of raw data, 3) georeferenced samples, at least by means of an explicit map, and, if available, 4) a description of the environmental parameters including sediment grain size, elevation, and TOC content. The foraminiferal taxonomical list has been updated by cross checking with the World Register of Marine Species (WoRMS Editorial Board, 2018) to use valid names and avoid synonyms. Sub-species were grouped under the species name. For diversity and indicator species, taxa in open nomenclature taxa (i.e., sp. or spp., classified only at genus level) were also ignored.

2.2. Definition of indicator species

The Shannon diversity index (Shannon and Weaver, 1963) and faunal density (number of specimens per cubic centimetre) for all the samples were defined and discussed in relation to the environmental characteristics of the studied areas. Across strong environmental gradients, such as elevation in the English Channel and the southern North Sea (Francescangeli et al., 2017), selected environmental units are defined as follows: subtidal; tidal flat; lower, middle and upper salt marshes; and tidal channel. The limit between the subtidal and tidal flat is defined as the lowest tide elevation. Subtidal samples are never exposed. The salt marsh limits are defined after floral limits (Jennings and Nelson, 1992). The probability for species to be an indicator of one or a combination of these environmental units was then calculated for species that occurs at least at 5%, following the procedure by Dufrene and Legendre (Cáceres et al., 2010, 1997).

The probability is composed of two components. Component 'A' is the probability that the surveyed site belongs to the target site group given the fact that the species has been found (De Cáceres et al., 2010). This conditional probability is called the *specificity* of the species as an indicator of the site group. Meanwhile, component 'B' is the probability of finding the species at sites belonging to the site group. This second conditional probability is called the *fidelity* of the species as an indicator of the target site group (De Cáceres et al., 2010).

Species with specificity and fidelity > 0.60 were considered reliable indicator species for the belonging units (Benito et al., 2016). These measurements were calculated on samples where the environmental units were defined, limited to species with a relative abundance greater than 5%. This threshold was considered the limit in the investigated studies that commonly base the counting on no more than 200 to 300 specimens, thus giving less statistical strength to minor species.

2.3. Definition of key parameters governing foraminiferal distribution

Key parameters controlling benthic foraminiferal distributions were defined via two analyses. First, the dataset was statistically processed using non-metric multidimensional scaling (nMDS) (Legendre and Legendre, 2012). The nMDS ordination was based on the relative abundance of taxa (> 5%) derived from the Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) constructed from the 673 samples where the environmental units were defined. Elevation above the mean sea level and the TOC content were used as explaining parameters.

To enhance the interpretation of the influence of the forcing factors, a multivariate regression tree (MRT) was processed. The MRT represents a constrained clustering technique introduced by De'ath (2002) that allows the partitioning of the foraminiferal dataset by a matrix of explanatory variables composed of estuary, elevation above mean sea level, the environment, and the percentages of TOC, sand, silt, and clay. The tree model was produced after three different treatments of the dataset: 1) total scaling (divided by margin total), 2) occurrence/absence, and 3) standardized values (scaled to zero mean and unit variance). The first trial assesses classical trends based on the dominating species; the second one examines the influence of assemblage composition, while the third reinforces the influence of minor species. As missing values are not permitted, calculations were only conducted on those 219 samples for which all the environmental parameters were available.

All analyses were implemented in R software (R Core Team, 2016). The packages used were as follows: base for base statistics; mvpart (De'ath, 2014) for multivariate regression trees; vegan for diversity and nMDS (Oksanen et al., 2016); and indicspecies (De Caceres and Legendre, 2009), labdsv (Roberts, 2016), and made4 (Culhane et al., 2005) for indicator species computation.

3. Results

3.1. Data mining

To our knowledge, 20 studies have investigated benthic foraminifera within the southern North Sea and the eastern English Channel region (Fig. 1). Although a total of 781 samples containing information about living foraminifera are reported, only 673 of them could be used for statistical purposes, because foraminiferal data are not fully provided or localisation of samples is missing (Appendix A).

3.2. Diversity and density

In total, 95 species were observed and indicated in the selected study. In several cases, genus names changed (e.g., *Jadammina macrescens* to *Entzia macrescens*) but the species names were preserved. In other cases, species names became synonyms (e.g., *Quinqueloculina*