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Seasonal variability in living benthic foraminifera across intertidal areas of the eastern English Channel

Fabio Francescangeli[1], **Vincent M. P. Bouchet**[2], **Yvonne Milker**[3], **Fabrizio Frontalini**[4],
Alain Trentesaux[5], **and Eric Armynot du Châtelet**[5]

[1]Department of Geosciences, University of Fribourg, Chemin du Musée 6, 1700 Fribourg/Freiburg, Switzerland
[2]University of Lille, CNRS, Univ. Littoral Côte d’Opale, IRD, UMR 8187, LOG,
Laboratoire d’Océanologie et de Géosciences, Station Marine de Wimereux,
62 930 Wimereux, France
[3]University of Hamburg, Institute for Geology, Centre for Earth System Research and Sustainability,
20146 Hamburg, Germany
[4]University of Urbino, Dipartimento di Scienze Pure e Applicate (DiSPeA), 61029 Urbino, Italy
[5]University Lille, CNRS, Univ. Littoral Côte d’Opale, IRD, UMR 8187, LOG,
Laboratoire d’Océanologie et de Géosciences, 59 000 Lille, France

Correspondence: Fabio Francescangeli (fabio.francescangeli@unifr.ch) and Vincent M. P. Bouchet
(vincent.bouche@univ-lille.fr)

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Abstract. The ecology of benthic foraminifera in tidal flats has been extensively studied at local scales, but its seasonal and spatial dynamics across broader intertidal gradients remain poorly understood. This study investigates seasonal variations in the composition and structure of living benthic foraminiferal assemblages across contrasting intertidal habitats in the eastern English Channel. We analyzed 256 surface sediment samples (192 for foraminifera and 64 for sediment properties) collected over four seasons at various sites in the Hauts-de-France region (northern France) along the eastern English Channel. Multivariate analyses revealed significant seasonal changes in the assemblage structure. Linear discriminant analysis identified two dominant seasonal groups. Opportunistic taxa, such as *Haynesina germanica* and *Ammonia confertitesta*, dominate during colder seasons, while more diverse and thermophilic species including *Elphidium selseyense*, *Quinqueloculina dimidiata*, and *Trochammina inflata* characterize warmer months. These findings provide new insights into the phenology of benthic foraminifera and contribute to a better understanding of seasonal ecological processes in temperate intertidal ecosystems.

1 Introduction

Estuarine environments are dynamic transition zones where freshwater from rivers mixes with saltwater from the sea. These areas are among the most productive ecosystems on Earth, as they receive nutrients from rivers that transport organic materials and sediments, supporting a wide range of biodiversity (Daborn and Redden, 2018). Within estuaries, intertidal areas (regions alternately exposed and submerged due to tidal fluctuations) play a crucial role in nutrient cycling, sediment trapping, and providing habitats for various organisms, including benthic communities such as foraminifera, which thrive on or within the seafloor.

Benthic foraminifera are sensitive bioindicators and are commonly used to determine past and ongoing environmental conditions (e.g., Al-Enezi et al., 2022; Bunzel et al., 2023; Nunes et al., 2023; Francescangeli et al., 2024). They live in environments ranging from intertidal to deep-sea areas (Murray 2006). The ecology of intertidal benthic foraminifera has been extensively investigated in both natural habitats like tidal marshes (e.g., de Rijk, 1995; Horton, 1999; Milker et al., 2015a; Müller-Navarra et al., 2016) and tidal flats (e.g., Alve and Murray, 1999; Debenay et al., 2000; Debenay and Guillou, 2002; Murray and Alve, 2000; Armynot du Châtelet et al., 2018a) and in coastal polluted areas (e.g., Alve, 1995; Armynot du Châtelet et al., 2004; Bouchet et al., 2007; Brunner et al., 2013). The distribution of intertidal foraminifera is mostly driven by the tidal gradient and exposure (e.g., Francescangeli et al., 2017; Horton and Murray, 2007). However, several other parameters can control their distribution, such as salinity, temperature, oxygen contents, substrate, total organic carbon (TOC), and the type of vegetation (Alve and Murray, 1999; Armynot du Châtelet et al., 2009a; Burone et al., 2007; de Rijk, 1995).

In temperate meso- to macrotidal environments in Europe, benthic foraminifera exhibit characteristic distribution patterns (e.g., Debenay and Guillou, 2002; Jorissen et al., 2023). Agglutinated species (e.g., *Trochammina inflata* and *Entzia macrescens*) tend to dominate in the upper part of the tidal marsh, whereas hyaline species (e.g., *Haynesina germanica*, *Elphidium selseyense*, and *Ammonia tepida* morphotypes) are more prevalent in the lower tidal marsh, tidal flat, and subtidal zones (Fouet et al., 2024; Francescangeli et al., 2020; Pavard et al., 2023a). However, anthropogenic influences (e.g., ditching or grazing) can alter the foraminiferal distribution in intertidal areas (Müller-Navarra et al., 2016).

Short-term temporal variations in benthic foraminiferal assemblages have been investigated in different environments, ranging from transitional to deep-sea zones (e.g., Fontanier et al., 2003; Guilhermic et al., 2024; Gustafsson and Nordberg, 2000; Morvan et al., 2006). However, research in intertidal areas is rather limited, and comparisons are commonly challenging due to the heterogenous time resolution across studies. Indeed, changes in foraminiferal assemblages have been monitored over periods of weeks (Boltovskoy and Lena, 1969), months and seasons (Debenay et al., 2005; Debenay et al., 2006; Lei et al., 2017; Mandal et al., 2023; Morvan et al., 2006; Murray and Alve, 2000; Saad and Wade, 2017), to longer than a year (Buzas et al., 2015; Fatela et al., 2014; Hippensteel et al., 2002; Horton et al., 2017; Swallow, 2000). Like other microorganisms, such as dinoflagellates (Fitt et al., 2000) and diatoms (Wang et al., 2015), the density, diversity, and the faunal turnover of intertidal foraminifera can vary seasonally in response to biotic and environmental variables (Murray and Alve, 2000; Wilson and Dawe, 2006). For instance, Fatela et al. (2014) observed a species turnover in the Caminha tidal marshes (northwestern Portugal) in an intra-decadal study and attributed the change over 5 consecutive dry years to increased salinity in sediment pore water. In the lower Guadiana Estuary (southeastern Portugal) during winter, when fluvial discharge peaks, agglutinated species represented more than 80 % of the total individuals (Camacho et al., 2015). In the same area, during summer, when marine conditions prevail, calcareous species became more dominant and expanded to higher marsh zones and upper estuarine areas (Camacho et al., 2015). Several works have pointed out that foraminifera can have one or more reproductive periods per year (for a review, see Murray 1991). For instance, in intertidal areas of Puerto Deseado (Argentina), Boltovskoy (1964) observed that *Elphidium macellum* reproduced once a year (one peak per year in the maximum abundance). Murray (1983) reported that *Nonion depressulus* (accepted as *Haynesina depressula*) can even reproduce 10 times per year. Saad and Wade (2017) documented seasonal reproductive cycles, mostly in spring and autumn, while other studies have shown that foraminiferal assemblages have peaks in maximum abundance that are not permanently controlled by a clear annual cyclicity (Morvan et al., 2006; Murray and Alve, 2000). There is, however, a high intra- and interannual variability, and the seasonality present in a year may not occur in the following one (Buzas et al., 2002).

In this context, the present study investigates seasonal changes in benthic foraminiferal assemblages over the course of 1 year across five intertidal estuarine areas in the Hauts-de-France (eastern English Channel), each exposed to varying degrees of natural and anthropogenic stress (Fig. 1). The coastal zones of the Hauts-de-France region have undergone significant human-induced changes over the past 2 centuries. Since the Second Industrial Revolution, various polluting industries – such as metallurgical, textile, and chemical factories – have emerged alongside major infrastructure, including the ports of Boulogne-sur-Mer, Calais, and Dunkirk and the Gravelines nuclear power plant. These developments have led to considerable environmental degradation (Francescangeli et al., 2016; Rolet et al., 2015). In contrast, the southern coast of the Hauts-de-France region, particularly the Picardy area, remains largely undisturbed and protected through regional parks and conservation efforts, resulting in comparatively lower pollution levels (Francescangeli et al., 2018; Henry et al., 2004). This marked contrast in anthropogenic impact makes the Hauts-de-France region a valuable natural laboratory for studying the response of living benthic foraminifera to varying environmental conditions and monitoring their temporal dynamics.

Understanding how temporal and spatial variations affect benthic organisms is essential for monitoring ecosystem health and managing coastal environments effectively.

2 Materials and methods

2.1 Study area and sampling strategy

The Hauts-de-France coastline stretches approximately 240 km along the southern North Sea and eastern English Channel, from the Belgian border to the Bay of Somme (Fig. 1a). The continental shelf here has undergone extensive erosion, resulting in limited sediment supply (Crapoulet et al., 2016). Recent sedimentation mainly occurs offshore as tidal sandbanks or coastal dunes formed by wind over macrotidal beaches (Battiau-Queney et al., 2001). Sediment transport is primarily northward and then northeastward, driven by a strong littoral drift (Anthony and Héquette, 2007). Estuaries along this path act as sediment traps, accumulating both coarse and fine materials (Turki et al., 2021). The region experiences a macro- to hyper-tidal semidiurnal regime with tidal ranges exceeding 10 m in the south and decreasing to $\sim$4 m near the Belgian border (Crapoulet et al., 2016). Limited wave action and dominant tidal forces classify the area as a tide-dominated system (Margotta et al., 2016), where estuaries are commonly closed by northward-drifting sand or gravel spits, forming broad tidal flats (Dalrymple and Choi, 2007). Five main rivers drain the region (Fig. 1a): in the north, the Aa River, modified since the 17th century, is now flowing through a 4 km artificial channel. The Liane River was significantly altered in the 18th century to accommodate the Boulogne-sur-Mer Harbor developments (Armynot du Châtelet et al., 2017a). In contrast, the Canche, Authie, and Somme rivers – flowing into Le Touquet-Paris-Plage, Berck-sur-Mer, and Saint-Valéry/Le Crotoy, respectively – have been affected by minimal modification, limited mainly to coastal fortifications (see also in Francescangeli et al., 2020).

A total of 16 sampling stations were selected from five areas along the intertidal zones of the Hauts-de-France region (Fig. 1B–F) from the most human-modified Aa Estuary, in the embanked area of Grand-Fort-Philippe (stations FP1, FP2, and FP3) and the Liane Estuary in the harbor of Boulogne-sur-Mer (stations BL1, BL2, and BL3) to the more natural Canche (stations CA1, CA2, and CA3), Authie (stations AU1, AU2, and AU3), and Somme (stations SO1, SO2, SO3, and SO4) estuaries. Four replicated surface sediment samples were seasonally (i.e., spring, April 2014; summer, July 2014; autumn, October 2014; and winter, February 2015) collected at each station (10 dm^3, the uppermost 1 cm in a surface of 1 m^2). Three replicates were used for the foraminiferal analysis, whereas the fourth one was used to measure sediment properties (i.e., grain size, TOC, and the C/N ratio). In total 256 samples (192 for foraminifera and 64 for sediment properties) were collected at low tide. It is important to mention that the samples collected during the sampling campaign in spring 2014 were previously reported in Francescangeli et al. (2020).

The foraminiferal samples were stored in transparent graduated containers with ethanol and rose bengal ($2\,\mathrm{g\,L^{-1}}$) to distinguish living from dead specimens (Walton, 1952). Sampling station positions and elevations were measured using a Trimble GeoXT dGPS instrument, allowing a precision better than 10–15 cm (in elevation). We used the WGS 84 coordinate system to position the sampling stations. Elevations were referenced to the mean sea level (MSL) calculated using the IGN69 elevation reference system (Table S1 in Francescangeli, 2025).

2.2 Sediment analyses

Grain size analyses were performed using the principle of diffraction and diffusion of a monochromatic laser beam on suspended particles (Malvern Mastersizer 2000, red He–Ne laser). The method is based on near-forward scattering of a laser beam by particles in suspension (Trentesaux et al., 2001). Measurements can range from 0.02 to 2000 µm with an obscuration ranging between 10 and 20 %. Three grain size fractions were considered: clays (< 2 µm), silt (2–63 µm), and sands (63–2000 µm).

A Flash EA 1112 elemental analyzer (Thermo Scientific) equipped with an auto-sampler was used for determining total contents of C and N. The analysis was performed on 1.5–2 mg of a sample added to approximately 5 mg of vanadium pentoxide, used as a combustion catalyst. The 2,5-Bis(5-tert-butyl-benzoxazol-2-yl) thiophene (BBOT) was used as standard. Calcium carbonate content was determined using a Bernard calcimeter. Triplicate measurements were carried out for each sample using 0.5 g of finely crushed, dry sediment. The TOC was determined by subtracting carbonate carbon from total carbon concentration (Armynot du Châtelet et al., 2009a). The C/N ratios were used to distinguish the origin of sedimentary organic matter (for details, see Meyers, 1994).

2.3 Foraminiferal treatment and species identification

In the laboratory, wet samples ($\sim 50\,\mathrm{cm}^3$) were carefully washed with tap water, through 315 and 63 µm mesh sieves, and dried at 40 °C. The foraminiferal fraction between 63 and 315 µm was concentrated by flotation in trichloroethylene (Horton and Murray, 2006; Semensatto and Dias-Brito, 2007). While heavy liquid separation is generally discouraged, it can be applied in environments with low foraminiferal abundance caused by high sedimentation rates, such as estuaries (Schönfeld et al., 2012). Only specimens containing dense, brightly (red) stained protoplasm were considered to be living (Alve and Murray, 1999; de Stigter et al., 1999). All living specimens from the replicates were counted and taxonomically identified, using the generic classification of Loeblich and Tappan (1987) and the specific classifications of Debenay et al. (2001). The list of taxa is available in Table S4 (Francescangeli, 2025). The observations were carried out with a binocular microscope (model Olympus SZX16). The foraminiferal density (FD) (the total number of living specimens per cubic centimeter of sediment) was determined for each sampling station. The diversity index $\mathrm{H}'_{\mathrm{bc}}$ (Shannon index bias-corrected by Chao and Shen, 2003) and the relative abundances of living taxa were also calculated.

2.4 Data analysis

A nonparametric Kruskal–Wallis rank sum test was used to reveal any significant influences of seasonality (p value

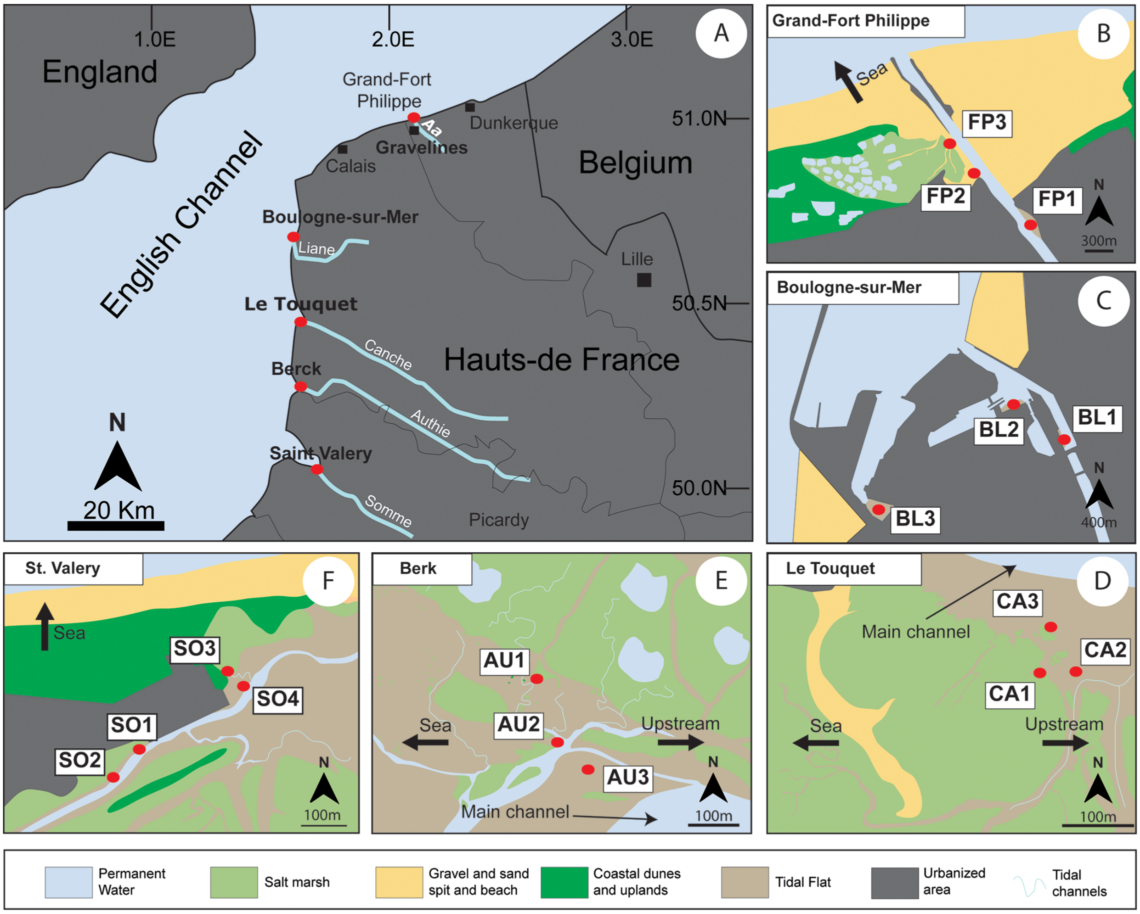

Figure 1. **(A)** Position of the five sampling areas and the 16 sampling stations in the Hauts-de-France region: **(B)** Grand-Fort-Philippe – Aa River (FP); **(C)** Boulogne-sur-Mer Harbor – Liane River (BL); **(D)** Le Touquet – Canche Estuary (CA); **(E)** Berck – Authie Estuary (AU); **(F)** Saint-Valery-sur-Somme – Somme Estuary (SO). Figure modified from Francescangeli et al. (2020).

< 0.05) on the environmental variables, on the foraminiferal densities (FD), on foraminiferal diversity (H'_{bc}), and on the major foraminiferal species (relative abundance of $> 5\,\%$ in at least one sample).

A linear discriminant analysis (LDA) was run to examine seasonal differences in benthic foraminiferal assemblages' composition. Replicated data from benthic foraminifera (relative abundances of benthic foraminifera of $> 2\,\%$ in at least on sample) were pooled. To better implement the LDA, data were transformed (Hellinger transformation). To assess the overall seasonal variations in foraminiferal species compositions, a permutational multivariate analysis of variance (PERMANOVA) was performed (p value < 0.05). PERMANOVA was used to compare groups of objects and test the null hypothesis that the centroids and dispersion of the groups as defined by measure space are equivalent for all groups. This nonparametric test was based on Bray–Curtis similarity, and 9999 permutations were run.

The R software (version 4.2.1) was used for the calculations and imaging by employing the following packages: vegan (for PERMANOVA and data transformation; Oksanen et al., 2016), lawstat (for Kruskal–Wallis; Gastwirth et al., 2015), entropy (for diversity calculation; Hausser and Strimmer, 2014), MASS (for LDA; Ripley et al., 2013), and ggplot2 (for data plotting; Wickham, 2016).

3 Results

3.1 Sediment characteristics

Silt was the dominant fraction in all samples (71 % on average) (Fig. 2A; https://doi.org/10.5281/zenodo.17046792, Francescangeli, 2025), contributing from 26 % to 86 % to the sediment. Sand content varied between 9 and 71 % and was the second most dominant fraction (24.5 % on average) (Fig. 2A, Table S2 in Francescangeli, 2025). Clay (4.5 % on average) ranged from 1.5 to 8 % (Fig. 2A, Table S2 in Francescangeli, 2025). The highest percentages of mud (silt + clay) were found in Grand-Fort-Philippe (86 % on average), while the samples from the Somme Estuary had the highest sand (34 % on average) contents. Grain size fractions did not show any clear visible seasonal pattern. In contrast, seasonal variation in the clay content was significant (Kruskal–Wallis, p value < 0.05); however there was no significant seasonal variation for silt or sand.

The TOC ranged between 0.02 and 3.8 % (Fig. 2B, Table S2 in Francescangeli, 2025). The highest values were recorded in the Canche Estuary (2.4 % on average). Different peaks in TOC were observed, such as in the Canche Estuary in spring (CA1) and autumn (CA2 and CA3) and in the harbor of Boulogne-sur-Mer in summer. Overall TOC did not show a clear seasonal trend; seasonal variations were not significant (Kruskal–Wallis, p value > 0.05).

The C/N ratio ranged from 0.38 to 19.5 (6.1 on average) (Fig. 2C, Table S2 in Francescangeli, 2025). The highest values were recorded in the Somme Estuary. The C/N ratio exhibited the highest values in spring and summer. Seasonal variations were significant (Kruskal–Wallis, p value < 0.05).

3.2 Living foraminiferal analysis

3.2.1 Foraminiferal density and diversity

A total of 48 benthic living species were found after the identification of ca. 46 000 specimens (Tables S3–S4). A total of 35 of them were hyaline, 8 were agglutinated, and 5 were porcelaneous. A total of 5 samples out of 192 replicates were devoid of living foraminifera.

The FD ranged between 0.1 and 32.1 (individuals cm^{-3}) with an annual average of 3.89 (individuals cm^{-3}) (Fig. 3A, Table S5 in Francescangeli, 2025). There were significant seasonal variations in the FD (Kruskal–Wallis test, $p < 0.05$), although it did not follow a common seasonal trend. In the Canche and Authie estuaries, the FD increased in the cold seasons, while in Boulogne, the FD showed an opposite trend. The variations in the FD across the sampling areas were significant as well (Kruskal–Wallis, p value < 0.05). The highest FD values were encountered in the Authie Estuary, whereas the lowest values were observed in Grand-Fort-Philippe (with 6.75 and 1.34 individuals cm^{-3} on average, respectively). The distribution of the FD for seasons (Fig. 4A) was mostly unimodal for all of the seasons with similar modes (i.e., the values with the highest frequency), while the distribution of the FD for sampling (Fig. 4B) was from unimodal in Grand-Fort-Philippe to multimodal in the other estuaries.

The $\mathrm{H}'_{\mathrm{bc}}$ varied between 0.6 and 3.0 (Fig. 3B, Table S5 in Francescangeli, 2025). The variations in the diversity across the sampling areas were significant (Kruskal–Wallis, p value < 0.05). The highest values of $\mathrm{H}'_{\mathrm{bc}}$ were found in Grand-Fort-Philippe, whereas the lowest values were observed in Boulogne-sur-Mer Harbor (with values of 2.2 and 1.2 on average, respectively). Seasonal variations in diversity were significant (Kruskal–Wallis test, $p < 0.05$). The highest values of $\mathrm{H}'_{\mathrm{bc}}$ were commonly found during spring and summer except in Grand-Fort-Philippe, where diversity peaked in spring and winter. The diversity's distribution for seasons (Fig. 4C) was mostly bimodal, with higher modes moving from 0.8 in winter to 2.2 in spring. The diversity's distribution for sampling (Fig. 4D) was from bimodal in Grand-Fort-Philippe to multimodal in the other studied areas.

3.2.2 Spatial distribution and seasonal variations in benthic foraminifera

The living benthic foraminiferal assemblages were dominated by calcareous taxa. Agglutinated specimens occurred only in areas adjacent to tidal marshes, although constantly with low percentages. Among the most abundant species, *Haynesina germanica* and *Elphidium selseyense* largely dominated the living assemblages (44 % and 11 % of the total assemblages on average over the sampling period, respectively) and were associated with a dozen accessory species with a relative abundance > 1 % of the total assemblages on average over the sampling period: *Ammonia confertitesta, Bolivina pseudoplicata, Bolivina variabilis, Buliminella elegantissima, El. gerthi, El. margaritaceum, Cribroelphidium magellanicum, El. williamsoni, En. macrescens, Quinqueloculina dimidiata,* and *Trochammina inflata* (Fig. 5; Tables S3–S4).

H. germanica was the most abundant taxon, with an overall abundance of 2.37 individuals cm^{-3} on average, and its highest abundances were found in the Authie Estuary (20.01 individuals cm^{-3} as maximum) (Fig. 6). *El. selseyense* was the second most abundant species (0.38 individuals cm^{-3}, on average), with the highest densities occurring in the harbor of Boulogne-sur-Mer (maximum of 9.33 individuals cm^{-3}). The highest abundances of *El. williamsoni* (10.16 individuals cm^{-3}, as maximum) were registered in the Authie and Somme estuaries. The distributions of *El. williamsoni* were similar to *El. margaritaceum* (1.38 individuals cm^{-3}, as maximum) and *El. gerthi* (0.54 individuals cm^{-3}, as maximum). *Bolivina variabilis* and *B. pseudoplicata* were the dominant species in Grand-Fort-Philippe (1.04 and 1.22 individuals cm^{-3} as maximum, respectively). *Quinqueloculina dimidiata* mainly occurred as the dominant species in the Canche Estuary (CA3) (1.20 individuals cm^{-3}, as maximum). *Ammonia confertitesta* was present in low abundance in the harbor of Boulogne-sur-Mer and in the Authie Estuary (with maximal 1.15 individuals cm^{-3} in the Authie Estuary). *Buliminella elegantissima* (0.42 individuals cm^{-3}, as maximum), *En. macrescens* (0.17 individuals cm^{-3}, as maximum), and *T. inflata* (0.28 individuals cm^{-3}, as maximum) were the least abundant among the most frequent species. *Buliminella elegantissima* was associated with *B. variabilis*, while *En. macrescens* and *T. inflata* (Table S3 in Francescangeli, 2025) were present only in upper tidal flat areas close to tidal marshes.

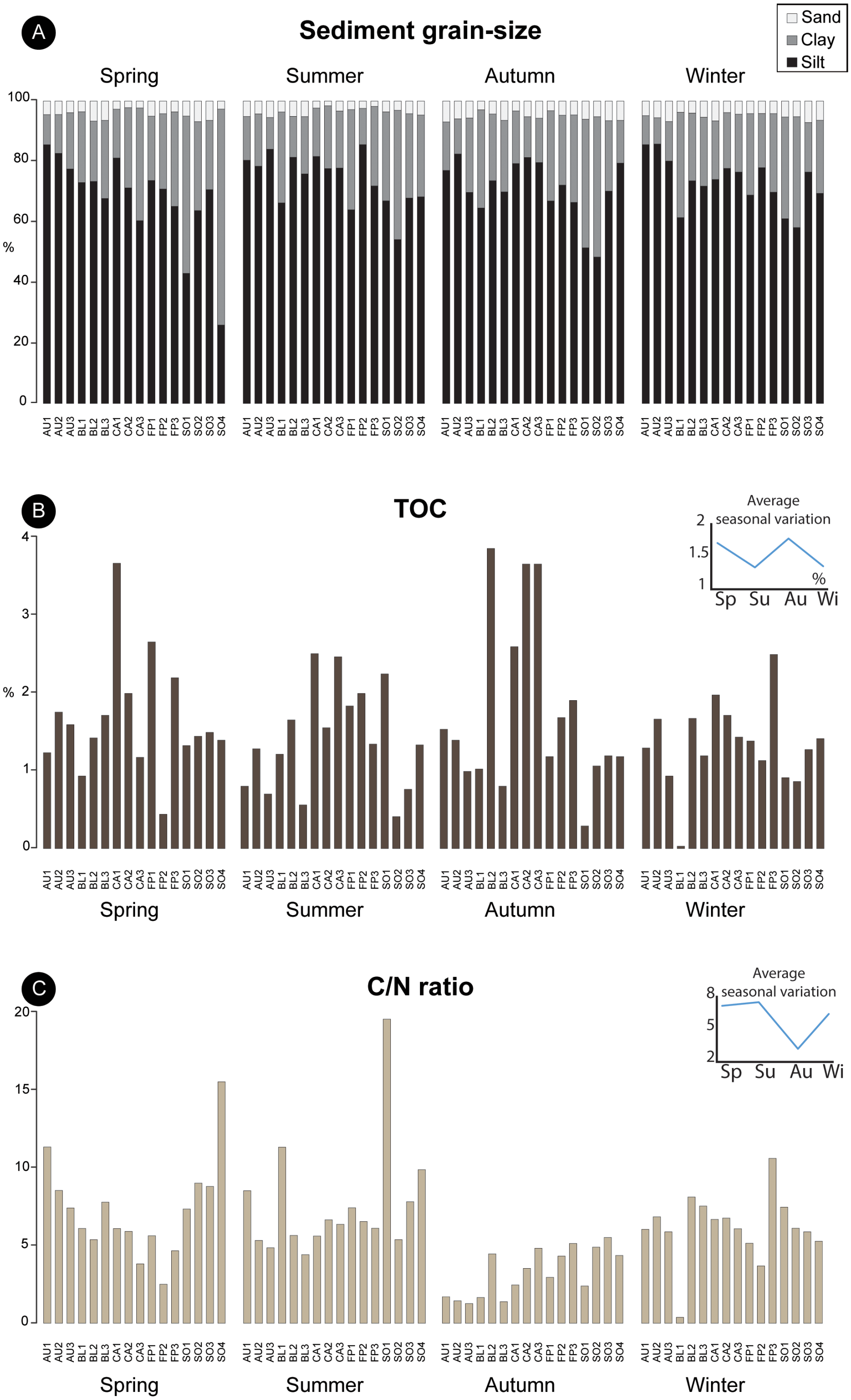

Figure 2. Seasonal variations in (**A**) sediment grain size, (**B**) TOC, and (**C**) C/N ratio for the 16 sampling stations within the five sampling areas. The averaged values measured in spring (Sp), summer (Su), autumn (Au), and winter (Wi) for TOC and C/N ratio are also provided.

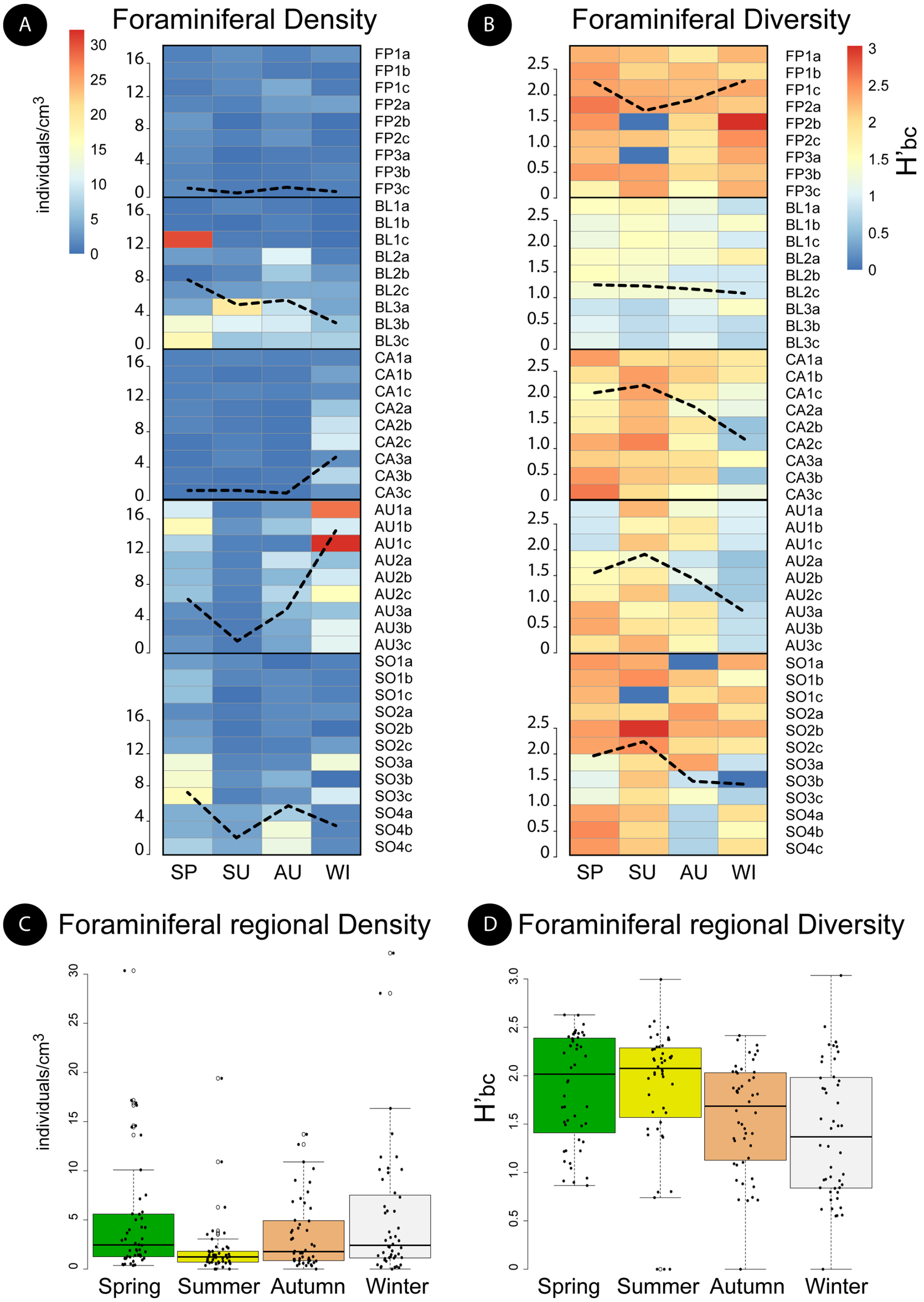

Figure 3. Heat maps of the seasonal variations in the benthic foraminiferal density (individuals cm^{-3}) **(A)** and diversity (H'_{bc}) **(B)** at the 16 sampling stations (replicated) within the five sampling areas. For each sampling area, the seasonal average trends in the density and diversity are reported (dash black lines). Box and whisker plots show the regional variations in the densities **(C)** and diversities **(D)** across seasons.

Overall, there were significant differences in the compositions and abundances of benthic foraminifera in the samples from different seasons (PERMANOVA, p value < 0.05). The LDA revealed distinct seasonal patterns in benthic foraminiferal assemblages, with the first two linear discriminants axes accounting for 91.6 % of the total between-group variance (LD1 = 55.0 %, LD2 = 36.6 %) (Fig. 7, Table S6 in Francescangeli, 2025). The LD1 primarily separated winter and autumn samples from those in summer and spring. The LD2 clearly separated spring and summer, while autumn and winter partially overlapped. Species with strong positive contributions to LD1 include *B. dilatata* (18.7), *A. confertitesta* (18.6), *Arenoparella mexicana* (7.1), and *B. variabilis* (4.5), while negative contributors include *El. oceanensis* (−17.6),

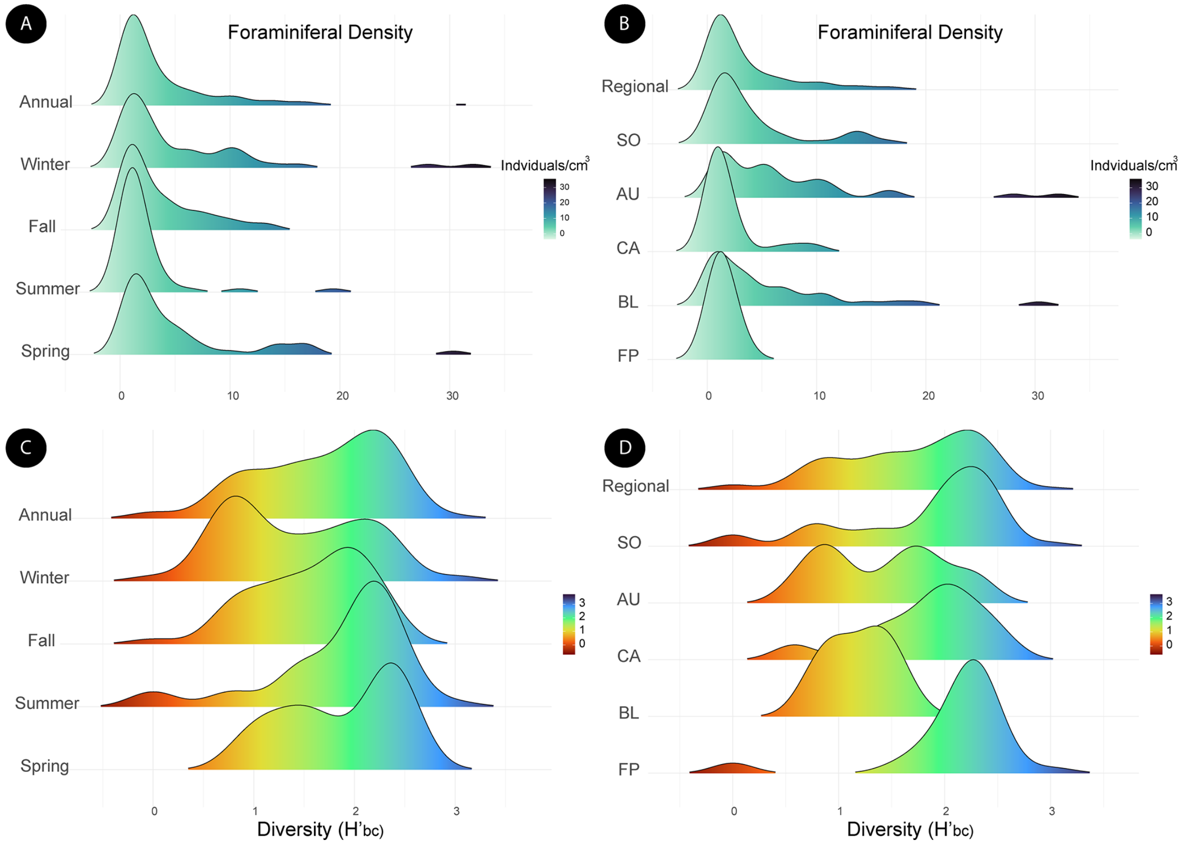

Figure 4. Density plots of the benthic foraminiferal density for seasons **(A)** and sites **(B)** and density plots of diversity (H'_{bc}) for seasons **(C)** and sites **(D)**.

B. robusta (−15.4), *T. inflata* (7.9), *Miliammina fusca* (7.5), *El. selseyense* (−4.2), *Cornuspira involvens* (−4.1), and *B. elegantissima* (−3.7). The LD2 highlights contrasts driven by high positive coefficients for *Discorbis vilabordeanus* (24.9), *El. magellanicum* (12.1), and *A. mexicana* (7.1), with negative contributions from *C. involvens* (−14.4), *El. oceanensis* (−11.9), *Rosalina bradyi* (−8.2), and *T. inflata* (−6.6).

In terms of group means, *H. germanica* consistently dominated across all seasons, peaking in winter (72.6 %), although its relative abundance did not significantly vary during the sampling periods (Kruskal–Wallis p value > 0.05). *Elphidium selseyense* was more abundant in summer (37.2 %) and spring (36.5 %) and varied significantly during the sampling periods (Kruskal–Wallis p value < 0.05). *Bolivina pseudoplicata* showed highest values in autumn (23.3 %). Species such as *B. variabilis*, *Q. dimidiata*, *B. elegantissima*, *El. magellanicum*, and *En. macrescences* showed clear seasonal shifts, with increased relative abundances in spring and summer. Amongst these species only *Q. dimidiata* and *B. elegantissima* varied significantly during the sampling periods (Kruskal–Wallis p value < 0.05). In contrast, species such as *A. confertitesta,* showed a clear and significant increase in autumn and winter (Kruskal–Wallis p value < 0.05).

4 Discussion

4.1 Reproduction over the year

The foraminiferal densities and diversities were in the range of values previously observed in marginal and coastal marine areas (e.g., Armynot du Châtelet et al., 2018b; Francescangeli et al., 2021; Murray, 2006). Overall, living foraminiferal assemblages showed a significant seasonal variability, as already observed in other studies (Buzas et al., 2015; Duchemin et al., 2008; Fontanier et al., 2003, 2006; Gustafsson and Nordberg, 2000; Horton and Murray, 2006; Kawahata et al., 2002; Murray and Alve, 2000). Conversely, Milker et al. (2015b) documented a lack of significant interannual variations in live populations in the coastal salt marshes of Oregon (USA).

Although foraminiferal density significantly varied across seasons, no clear pattern emerged at either the regional (considering the average densities recorded in the Hauts-de-France region) or local (e.g., the Gironde Estuary; Pavard et al., 2023b) scales. The results of this study fail to identify a preferential reproduction period, which is an issue that has been previously reported (Basson and Murray, 1995). In fact, several foraminiferal reproductive phases can occur through

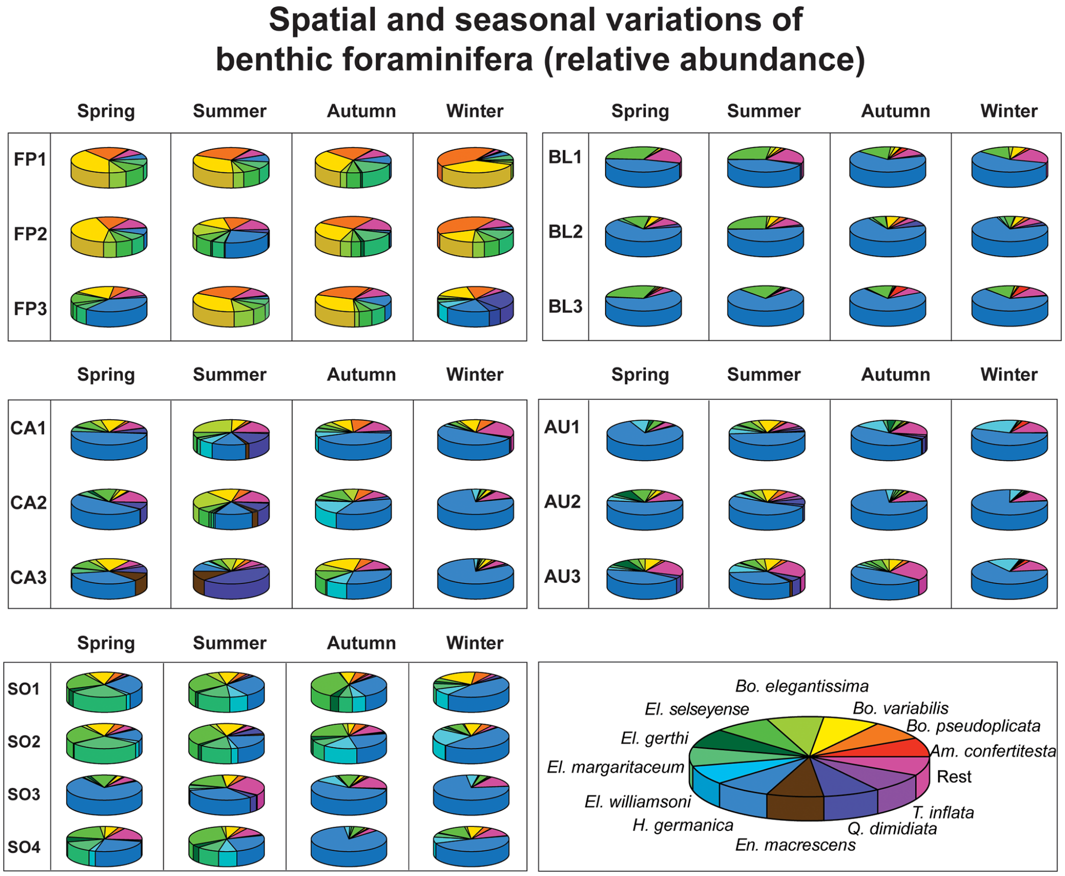

Figure 5. Seasonal variation in the abundance of main benthic foraminiferal species in the Hauts-de-France region.

the year (Cearreta, 1988; Murray, 1983). Population dynamic studies, involving the measurement of several species, are required to determine the preferred period of reproduction of foraminifera. Accordingly, different peaks and declines were observed in the five studied areas in relation to the seasonal variations recorded during the sampling period. In the intertidal zone of North Norfolk (UK), Saad and Wade (2017) documented (1) peaks in total foraminiferal densities in autumn (between September and October) and in late spring and (2) a decline during summer and winter. Similarly, a decline was observed in summer by Swallow (2000) in Chichester Harbor (UK). In our study, a similar pattern could only be observed in the Authie and Somme estuaries. An unclear annual cycle in total foraminiferal densities, although a more evident cycle in species diversity, was found in the intertidal area of the Hamble Estuary in the UK (Murray, 2000). Similarly, our study shows that regional species diversity exhibited a clear cyclicity, with the highest values occurring in spring and summer, and the lowest values occurring in autumn and winter. This pattern is more evident in the less impacted estuaries of the Canche, the Authie, and the Somme, but it is less observable in the areas of the harbor at Boulogne-sur-Mer and Grand-Fort-Philippe that are more heavily influenced by human activities. This suggests the possibility that human influences may not only diminish foraminiferal diversity but also disrupt their natural cyclical processes.

A general observation is that benthic foraminifera seem to reproduce rapidly during the spring and autumn months, with a general increase in abundance, while the occurrence of stressful environmental conditions reduces the number of individuals during the summer and winter months (Saad and Wade, 2017). However, we did not observe the same clear cyclicity in our study region. This could be ascribed to different reasons:

1. *Sampling frequency*. Considering that some species reproduce from 1 to 10 times per year (Murray, 1991), a seasonal survey might not be sufficient to capture the full extent of reproductive variability. A more frequent sampling survey (e.g., weekly or monthly) would have been more effective. However, given the spatial extent of the study area, this would enormously increase the time and cost of analyses.

2. *Sampling period*. Foraminifera may reflect seasonal oscillations in environmental parameters as observed by Fatela et al. (2014) during an intra-decal study in the Caminha tidal marshes (northwestern Portugal). To ob-

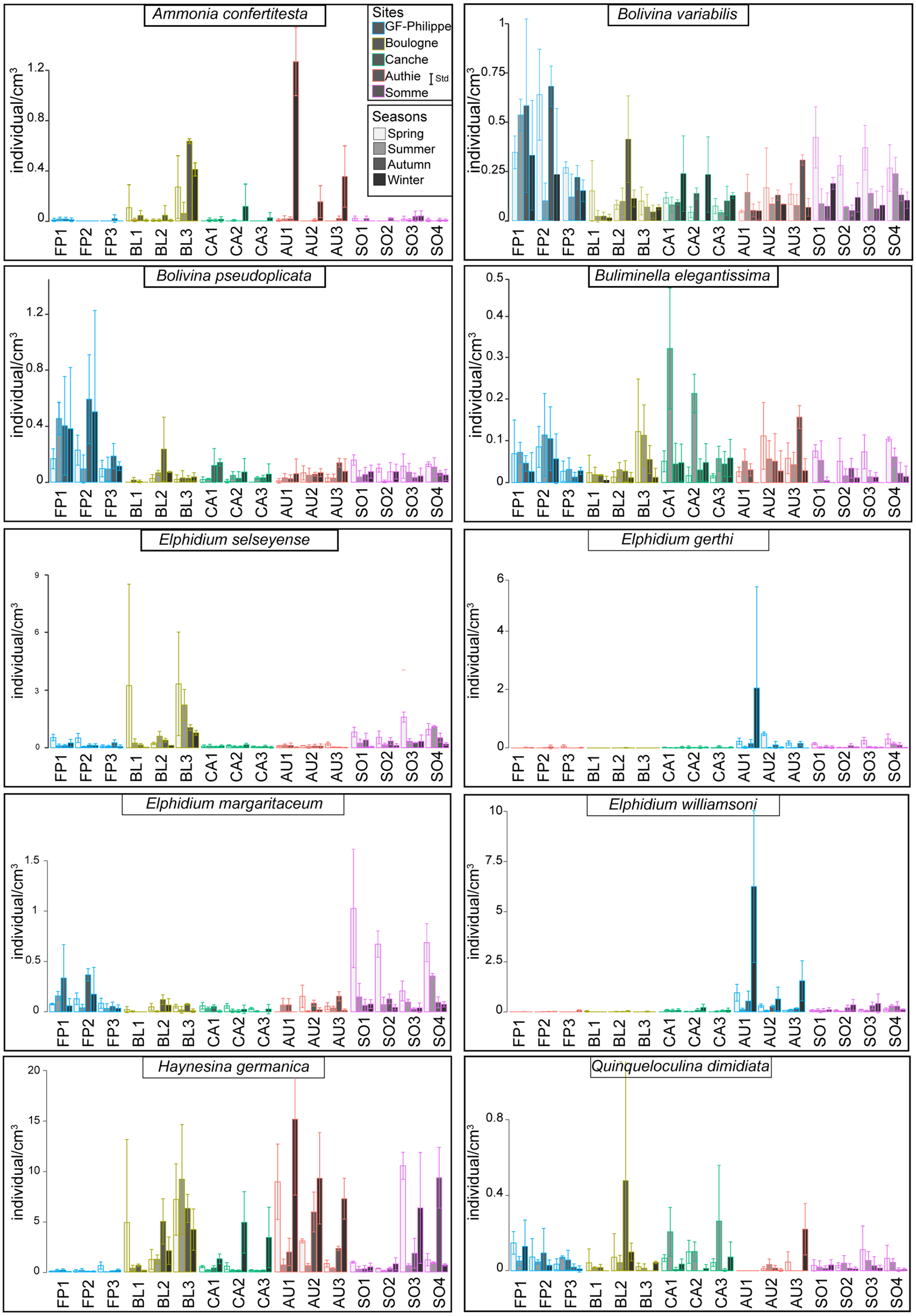

Figure 6. Seasonal variation in total abundance (individuals cm^{-3}) of the 10 most abundant and frequent foraminiferal species in the Hauts-de-France region.

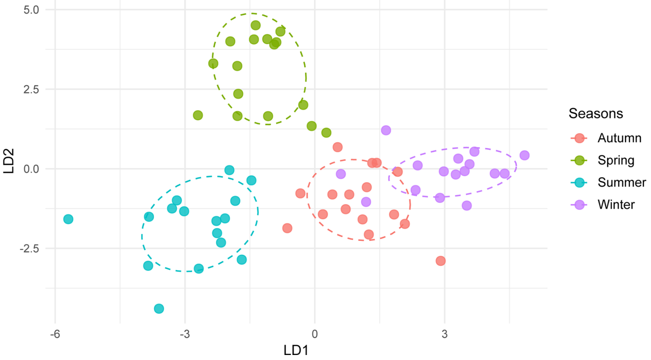

Figure 7. Linear discriminant analysis based on the relative abundance of benthic foraminiferal species from the five sampling areas in the Hauts-de-France region.

serve cyclicity in benthic assemblages, sampling should therefore include observation periods longer than 1 year. Indeed, rather than fixed seasonal peaks, living populations show shifts in abundance and diversity on an annual basis – likely linked to reproduction, food availability, or disturbance (Buzas et al., 2015).

3. *Spatial distance*. In most cases, the reproduction period, namely the maximum abundance of the standing crop, is related to seasonal fluctuations in food supply (Murray, 2000). For instance, Myers (1943) and Schönfeld and Numberger (2007) observed that peaks in abundance of *Elphidium crispum* occurred in spring, corresponding to the phytoplankton bloom. The distance among our sampling areas is about 30–40 km. Hence, it might be speculated that blooms (e.g., diatom blooms) occur at different times. Local hydrodynamics, temperature, salinity, and grain size may slightly change as a complex equation to trigger the bloom. Coastal benthic foraminifera may not have reproducible annual life cycles, and living assemblages may provide different or even contradictory results, depending on whether the sampling is done during an increase in food supply for foraminifera (Morvan et al., 2006).

4. *Patchiness*. Foraminifera show irregular spatial distribution at the seafloor, in relation to environmental heterogeneity (e.g., sediment type, organic matter, and oxygen level), disturbance (e.g., storms and bioturbation), and biological interaction (Buzas er al., 2002). For instance, in intertidal areas, Armynot du Châtelet et al. (2017b) showed that the minimum number of replicates required to significantly capture the total variability in foraminiferal density within 1 m^2 was 26 replicates. Therefore, although the number of replicates used in this study is comparable to that used in other studies (summary in Schönfeld et al., 2012), it may not be sufficient to account for the effect of patchiness.

4.2 Seasonal variations in foraminifera

4.2.1 Seasonal shift

The observed seasonal variation in benthic foraminiferal assemblages may reflect ecological responses to environmental fluctuations. In our study, sediment grain size is relatively consistent across seasons and, therefore, did not appear to be a key factor controlling the seasonal changes in benthic foraminiferal assemblages. Although TOC varied notably over the sampling period, neither local nor regional trends accounted for the observed changes in foraminiferal density, diversity, or species composition. The C/N ratio consistently remained below 10 – indicative of predominantly algal organic matter – and showed no clear response to wetter periods (typically in autumn in the study area), during which the C/N ratio would ordinarily be expected to increase due to greater terrestrial input (Meyers, 1994). Therefore, other parameters such as temperature, salinity, food availability, and oxygenation and nitrate availability were likely responsible for the temporal foraminiferal variations (Murray, 2006). The results of the LDA reveal a seasonal structuring of benthic foraminiferal assemblages, distinguishing those of the warm seasons (spring and summer) from those of the colder seasons (autumn and winter).

4.2.2 Cold assemblages

The cold seasons are characterized by less diverse assemblages. The dominance of *H. germanica* across all seasons, particularly in winter, supports its ecological inference as an euryhaline and opportunistic species (Armynot du Châtelet et al., 2009b; Murray and Alve, 2000). Similarly, this species was more abundant in colder seasons in the intertidal zones of the Yellow Sea (Lei et al., 2017) and in a small river along the French Atlantic coast (Morvan et al., 2006). *Ammonia confertitesta*, an alien species from Asia (Pavard et al., 2023a; Pavard et al., 2023b), peaks only during winter. In the Gironde Estuary, *A. confertitesta* was the dominant taxon, although its temporal variation over the 1-year survey was not clearly defined (Pavard et al., 2023a). This species is morphologically similar to *A. aberdoveyensis* and *A. veneta*, and these species have commonly been grouped together under the *A. tepida* morphogroup in the literature (Richirt et al., 2019). *A. tepida* was reported to be more abundant in warmer seasons (Debenay et al., 2006; Morvan et al., 2006), but it is unclear which morphotype was found in these studies. *Bolivina variabilis* and *B. dilatata* are more abundant in colder months as well; however, information about their temporal variations in the literature is scarce. For example, Mandal et al. (2023) reported that *Bolivina* spp. occurrence peaks during monsoon, possibly due to lowered salinity and increased of nutrients. These taxa are generally regarded as reliable indicators of low-oxygen conditions, and their abundance would therefore be expected to increase during warmer months when hypoxic conditions are more likely to develop.

As the opposite pattern is observed in this case, it may be hypothesized that nitrate availability is higher in winter, consistent with their ability to perform denitrification (Glock et al., 2013). Although not directly correlated with nitrate levels, the study area generally showed higher nitrogen concentrations during the cold seasons than during the warm ones (Table S2 in Francescangeli, 2025).

4.2.3 Warm assemblages

The seasons are characterized by the occurrence of more diverse assemblages. *Elphidium selseyense* was more abundant during warm months. Accordingly, a temporal study of the intertidal areas of Rivedoux-Plage (France) found an increase in *El. selseyense* in spring and summer (Bouchet, 2007). This taxon was similarly correlated with higher temperatures, being more abundant in summer along the coast of the Yellow Sea (Gustafsson and Nordberg, 2000; Lei et al., 2017). However, Debenay et al. (2006) reported this species to be more abundant in colder seasons. Indeed, in other studies, species belonging to the *Elphidium* and *Cribroelphidium* groups have been found to peak in both colder and warmer seasons, meaning that they are more sensitive to food supply than temperature. (Mandal et al., 2023; Morvan et al., 2006). Other species that are more related to warm conditions include *Q. dimidiata*, *T. inflata*, *B. elegantissima*, *El. gerthi*, and *En. macrescens*. Accordingly, *Quinqueloculina* spp. occurred mainly in spring and summer in the Vie Estuary (France), consistent with its preference for higher salinity and oxygen (Debenay et al., 2006). Similarly, *T. inflata* was reported to be more abundant during spring and summer months in the salt marshes of North Norfolk (Saad and Wade, 2017), in the Bandon Marsh (Milker et al., 2015b), and in the Chichester Harbor (Swallow, 2000).

A possible explanation for the observed higher abundance of species belonging to the genera *Haynesina*, *Ammonia*, and *Bolivina* in colder months is their relatively low respiration rate, which translates into a reduced overall energy demand compared to other benthic foraminiferal genera such as *Elphidium* and *Quinqueloculina* (Glock et al., 2019). Lower respiration rates are generally associated with slower metabolic activity, allowing these species to survive and maintain physiological functions even under conditions of limited food supply. This physiological trait could provide a competitive advantage during the colder months, when primary productivity and the input of organic matter to the sediment are typically reduced. Moreover, species with lower metabolic demands may be better able to withstand periods of environmental stress, such as low temperatures or hypoxia, which can further limit the availability of high-quality food sources. In contrast, genera with higher respiration rates, like *Elphidium* and *Quinqueloculina*, require more energy to sustain their metabolic processes and may therefore experience greater population declines under food-limited conditions. The predominance of *Haynesina*, *Ammonia*, and *Bolivina* in colder months could thus reflect an ecological strategy geared towards energy conservation, which allows these taxa to exploit temporal niches that are less favorable for more energetically demanding species.

In addition, differences in trophic ecology among genera may also contribute to this pattern. For example, some species of *Bolivina* and *Ammonia* are known to utilize a wider range of organic matter sources, including detrital material and refractory carbon compounds, which are still available when labile food sources are scarce (e.g., Langer et al., 1989; Murray 2006). Such flexibility, combined with a low metabolic rate, likely reinforces their resilience during the winter months, leading to their seasonal dominance in the benthic foraminiferal assemblages.

5 Conclusions

Our study confirms that benthic foraminiferal assemblages in temperate estuarine environments exhibit marked seasonal variability in density, diversity, and species composition. However, unlike patterns observed in other European and global intertidal ecosystems, we were unable to identify a consistent annual cyclicity across all the studied sites. Instead, the response of the foraminiferal assemblages appeared to be site-specific and varied over time, likely due to local environmental heterogeneity, reproductive cycles, and nutrient dynamics.

Opportunistic taxa, such as *H. germanica* and *A. confertitesta*, dominated during colder seasons, while more diverse assemblages and thermophilic species, including *El. selseyense*, *Q. dimidiata*, and *T. inflata*, characterized the warmer months. These trends broadly align with previous studies, but they also highlight the limitations of a seasonal sampling approach in capturing the full dynamics of living foraminiferal populations. The observed spatial patchiness and intra-annual variability underscore the need for higher-frequency, multiyear monitoring to robustly assess foraminiferal responses to environmental forcing. This has important implications for their use in ecological monitoring and paleoenvironmental reconstructions.

Data availability. The supplementary materials (Tables S1–S6) are available from Zenodo: https://doi.org/10.5281/zenodo.17046792 (Francescangeli, 2025), Francescangeli et al_2025_supplementary. This file contains the station positions (Table S1), environmental parameters (Table S2), species counts (Table S3), a list of taxa (Table S4), the density and diversity (Table S5), and the LDA results (Table S6).

Sample availability. All the samples are stored at the Department of Earth Science, University of Lille, France.

Author contributions. FF: conceptualization, data curation, formal analysis, investigation, validation, visualization, and writing (original draft preparation); VB: conceptualization, methodology, funding acquisition, supervision, and writing (original draft preparation); YM: data curation, formal analysis, and writing (original draft preparation); FF: conceptualization, validation, and writing (original draft preparation); AT: investigation, funding acquisition, supervision, and writing (original draft preparation); EAdC: conceptualization, investigation, methodology, funding acquisition, supervision, and writing (original draft preparation).

Competing interests. The contact author has declared that none of the authors has any competing interests.

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