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### ► **To cite this version:**

Jean-Charles Pavard, Camille Hennion, Apolyne Courleux, Françoise Henry, Armelle Riboulleau, et al.. Moving beyond the overrated perception of harbors as polluted ecosystems : unexpected high diversity of meio- and macro-benthic communities in the Port of Dunkirk, France. *Journal of Environmental Management*, 2026, 408, pp.129893. <10.1016/j.jenvman.2026.129893>. <hal-05619763>

**HAL Id: hal-05619763**

**<https://hal.science/hal-05619763v1>**

Submitted on 13 May 2026

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## Research article

# Moving beyond the overrated perception of harbors as polluted ecosystems: unexpected high diversity of meio- and macro-benthic communities in the Port of Dunkirk, France

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## ARTICLE INFO

## Keywords:

Industrial harbor  
Pollution  
Productivity  
Benthic foraminifera  
Benthic macrofauna  
Biodiversity hotspot  
Transitional waters

## ABSTRACT

Harbors are often regarded as highly degraded ecosystems, yet their benthic biodiversity remains poorly documented. This study investigated environmental conditions, organic matter sources, pollutants and benthic assemblages over two seasons in the Port of Dunkirk, France, an industrialized and heavily modified transitional water body. Seven subtidal stations were sampled in spring and fall 2020 for water parameters, sediment geochemistry (including trace metals and molecular biomarkers), benthic foraminifera and macrofauna. Species richness and diversity were quantified and multivariate analyses performed to relate faunal patterns to environmental gradients. The industrial basin showed severe enrichment in trace metals (Cd, Cu, Pb, Hg) and high inputs of petroleum and combustion-derived compounds whereas the marina displayed lower metal enrichment but clear signature of fresh sewage. Despite these pressures, faunal assemblages exhibited high and spatially heterogeneous richness and diversity, comparable to or exceeding those of nearby and less industrialized transitional waters. Macrofaunal diversity was higher in fall whereas foraminiferal diversity remained steady over seasons. Redundancy analyses indicated that species distributions were driven by sediment grain size, chlorophyll *a*, organic matter content and cadmium, though macrofaunal assemblages were more influenced by seasonal features (water temperature and sand). Assemblages were dominated by typical stress-tolerant species from transitional waters of North-East Atlantic, though several non-indigenous species were also observed, confirming harbors as gateways for bioinvasion and peculiar biodiversity hotspots. These findings challenge the perception of industrial harbors as sacrificed ecosystems and underline their importance for biodiversity assessment and preservation, biomonitoring and management of non-indigenous species. Our study further underscores the robustness and relevance of benthic foraminifera and macroinvertebrates for biodiversity monitoring in harbor environments, and calls for further research and targeted conservation efforts to better understand and mitigate their ecological impacts while assessing their potential as habitats.

## 1. Introduction

Maritime transport accounts for ~90% of international trade by volume (Christiansen et al., 2020). Over the last decades, international sea shipping underwent significant increase in cargo volume and fleet size (Lau et al., 2024), with harbors serving as the primary gateway of this rapidly growing industry. These coastal urban ecosystems facilitate the access to the sea for human population and provide protection to

coastal population from wave action; their strategic location at the interface of land, rivers and seas, i.e. deltas and estuaries, offering ideal conditions for the development of both land and sea anthropic activities and then to benefit from coastal goods and services (French, 2002). However, for the sake of economic growth, industries, fishing, tourism or recreational activities, harbors are also the source of various anthropogenic pressures on coastal waters such as shipping, yachting, dredging, industrial sewage, eutrophication or trace metals pollution

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<https://doi.org/10.1016/j.jenvman.2026.129893>

Received 19 December 2025; Received in revised form 15 April 2026; Accepted 5 May 2026

Available online 12 May 2026

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(Marin et al., 2008), potentially impacting these human-modified ecosystems and their associated biodiversity. In this context, a national strategy was implemented in France in 2021 to set economic and environmental transition objectives, essentially for commercial harbors, by 2050 (CIMer, 2021). Its 11th objective is to ensure a better protection of the biodiversity using plans and projects aiming to manage, protect and restore biodiversity for each commercial harbor which differs from the objectives settled by European legislations.

Considering the sheltered nature of most harbors, preventing a regular renewal of water and the release of anthropogenic pollutants, benthic species communities are particularly exposed to these peculiar environmental constraints due to their naturally sedentary feature (Balsamo et al., 2012; Desrosiers et al., 2013; Orani et al., 2018; Riera et al., 2011). Surprisingly, these communities revealed themselves to be adapted to harbor disturbances, though they are not very resilient (Vassallo et al., 2013). International harbors of Sydney, Australia (Johnston et al., 2015) or San Pedro Bay in Los Angeles, USA (Stolzenbach et al., 2021) even recorded their highest biodiversity ever, suggesting that the statement of a ‘sacrificed’ harbor diversity is not obvious. In India, the benthic functioning of the harbor of Mumbai even resembles that of the nearby Malvan Marine Protected Area due to similarity in dominant trait profiles in their respective macro-invertebrate communities (Dias et al., 2023). However, there are only a handful of studies dealing with the understanding of the harbor ecosystem, the majority of them indeed focused either on monitoring these pressures (e.g. Baldrighi et al., 2023; Ferraro et al., 2006; Moreno et al., 2008; Sánchez-Moyano et al., 2010; Witt et al., 2004) or reporting introduction and invasion of Non-Indigenous Species (NIS; e.g. Bouchet et al., 2023; Fossile et al., 2021; Megina et al., 2016; Tempesti et al., 2020), at the expense of harbor biodiversity studies.

Consequently, it becomes urgent to reconsider the harbor habitat as a fully functional ecosystems and to further understand the structure of faunal communities in such an overlooked ecosystem. Indeed, although harbors mostly lead to habitat degradation, increased pollution, and the introduction of non-indigenous species, they can host unexpectedly high biodiversity, with species richness or functional diversity comparable to nearby pristine habitats (Madon et al., 2023). This seemingly contradictory phenomenon underscores the need for further research and targeted conservation efforts to better understand and mitigate the ecological impacts of harbors while exploring their potential as key ecosystems in highly urbanized coastal areas. Therefore, a better knowledge of harbor ecosystems, intrinsic pressures, biodiversity and how species communities deal with harbors peculiar features can help guide sustainable development, conservation and management efforts in harbors. In this context, the present study used two types of benthic organisms, benthic macrofauna and foraminifera, widely recognized bioindicators of various anthropogenic pressures (e.g. Alve, 1995; Frontalini and Coccioni, 2011; Martins et al., 2019; Ryu et al., 2011; Souza et al., 2013), to fill the lack of knowledge of species composition, diversity and their environmental drivers (either natural or anthropogenic) in harbor habitats. Noticeably, this study focused on the Port of Dunkirk (southern North Sea, France), known as France's third-largest international trade harbor. It is influenced by numerous artificial freshwater canals draining the Flemish plain in the northern part of France (SDES, 2024). As such, the harbor can be considered as transitional waters (TWs; McLusky and Elliott, 2007), corresponding to a Heavily Modified Water Body type (European Commission, 2003, p.5). Therefore, seven stations were sampled in the Port of Dunkirk, France, to: (i) characterize the environmental conditions occurring in the harbor and source(s) of pollution and (ii) understand the environmental drivers constraining the distribution patterns of the main foraminiferal and macrofaunal species. This work will contribute (i) to fill the knowledge gap on the ecology of benthic species in harbor ecosystems and (ii) to evaluate the potential of harbors to serve as hotspots of biodiversity.

## 2. Material and methods

### 2.1. Site of study, stations sampled and oceanographic framework and physical drivers

The study was conducted in the Eastern Port of Dunkirk (“Port Est”; southern North Sea, France; Fig. 1), a lock gated industrial harbor connected to the open sea by deep draft sea locks and to the hinterland by the Dunkirk-Scheldt network and canalized reaches of the river Aa and regional “Wateringues” drainage system (Port Environmental Review System. Environmental Report, 2019). These canals, such as the Bourbourg and Exutory channels (Fig. 1), and drainage sluices deliver freshwater, fine sediments and associated contaminants into inner docks, where low hydrodynamic energy promotes trapping and vertical accumulation.

The port comprises several industrial basins and inner channels (e.g. Bourbourg channel and its derivation), hosting large steel, petrochemical and energy facilities, bulk terminals and logistics platforms (PERS, 2019), together with three urban marinas (Port du Grand Large, Bassin de la Marine, Bassin de Commerce; ~550-600 berths; Fig. 1). Grand Large lies near the outer harbor with direct sea access, whereas the two latter marinas are reached via the Trystram lock and inner channels and are therefore more weakly flushed (<https://www.dunkerque-marina.com/en/locks>). Main anthropogenic pressures include intensive handling of ores, coal, minerals, fuels and chemicals, industrial cooling water and process water discharges, municipal wastewater and stormwater inputs from the Dunkirk conurbation, heavy cargo traffic (~48-50 Mt and several thousand ship calls per year, dominated by bulk carriers, tankers, Ro-Ro and container/general cargo), and frequent maintenance dredging of fine, sometimes contaminated, sediments in low energy basins and approach channels (PERS, 2019). In May (spring) and September 2020 (late summer/fall), seven subtidal stations were sampled using the R/V SEPIA II and Celtic Warrior along the main access channel and inner industrial basins, from the outer, more marine influenced approach to the more enclosed industrial docks (Fig. 1, Table 1). In the industrial basin, D1-D3 are situated in deep inner docks (Table 1) in the derivation of the Bourbourg channel while D4 and D5 occupy intermediate-depth inner docks. This basin, receiving a mixture of marine inflow through locks and freshwater inputs from the Bourbourg channel and its derivation, is characterized by restricted exchanges, longer water residence times and stronger exposure to industrial and urban discharges, dredging plumes and stormwater runoff from adjacent facilities. D6 and D7, respectively located in the Grand Large marina and in the access channel close to the sea locks, undergo stronger tidal forcing and a direct influence of North Sea waters. However, D7 is also located at the mouth of the Exutory channel and therefore receives freshwater inputs.

Dunkirk lies in a semi diurnal macrotidal regime with typical spring tidal ranges of about 5-5.5 m and strong alongshore tidal currents where flood currents are generally stronger than ebb currents and oriented east northeast, producing a flood dominated asymmetry and net landward sediment transport past the harbor entrances. Offshore nearshore sand banks and marine dunes modulate waves and currents and favor fine sediment deposition in the approach channel (Durand et al., 2025), while, inside the lock gated basins, water levels and circulation are controlled by lock operations and canal inflows (PERS, 2019), leading to multi day water residence times in inner docks and marinas. Lock operations for marinas (e.g. Trystram) follow fixed daily schedules with two to four openings depending on season, and sea locks for commercial vessels operate around high water, creating episodic flushing interspersed with stagnation periods. The region experiences predominantly southwesterly to northwesterly winds and recurrent winter storms; major storm surges in the Dover Strait have produced elevated sea levels and skew surges of several tens of centimeters at Dunkirk, enhancing resuspension in entrance channels and interacting with dredging and sluice management (Giloy et al., 2019).

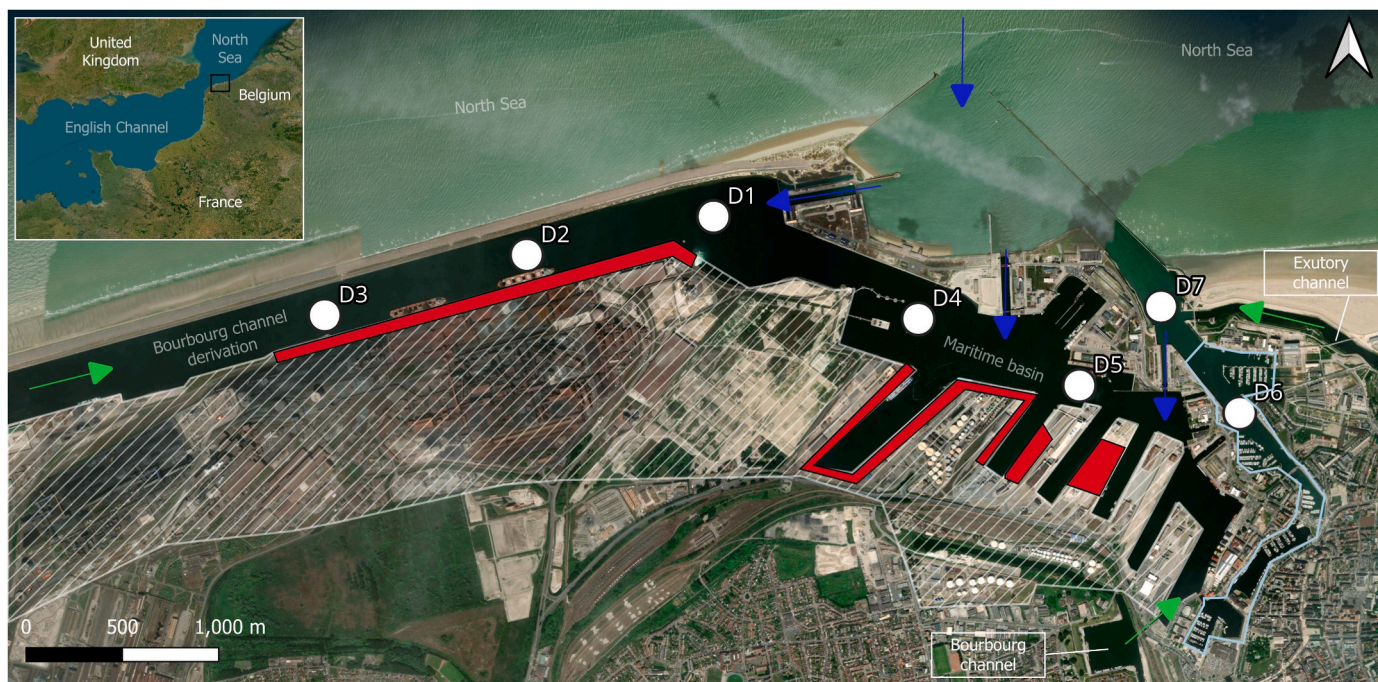


Fig. 1. Maps of localisation of Dunkirk and stations sampled in the harbor.

Table 1

Stations sampled in Dunkirk harbor, their associated coordinates and depths of sampling.

Station	Latitude	Longitude	Water depth (m)
D1	51°3'14.5080" N	2°19'58.5480" E	16.4
D2	51°3'8.1000" N	2°19'8.7600" E	16.6
D3	51°2'58.0200" N	2°18'14.9400" E	15.4
D4	51°2'57.4080" N	2°20'53.0880" E	13.0
D5	51°2'46.2480" N	2°21'36.0360" E	11.0
D6	51°2'41.6400" N	2°22'18.7680" E	5.4
D7	51°2'59.4600" N	2°21'57.7800" E	5.7

## 2.2. Sampling and analyses of environmental parameters

### 2.2.1. Water parameters

Temperature and salinity were measured by sampling the bottom water with a Niskin bottle at each station and then using a CTD probe (Alec Electronics Co Ltd, Kobe, Japan). Water depth at sampling stations was obtained with the boat sounder.

### 2.2.2. Grain size, organic matter and chlorophyll *a* in sediment

At each station, a hand corer (56 cm<sup>2</sup> surface) was used to subsample, from the same Van Veen grab, three pseudo-replicates of surface sediment (0-1 cm) for total organic carbon (TOC) and total nitrogen (TN) analyses, three others for chlorophyll *a* (Chl *a*) analysis, one for grain size analysis, another for molecular analysis of the organic matter and a final one for trace elements analysis. Percentages of sand (grains >63 μm), silt (grains ranging between 2 and 63 μm) and clay (grains <2 μm) were obtained by diffraction and diffusion of a monochromatic laser beam on suspended particles (Trentesaux et al., 2001). The percentage of clay was studied but not used for this study as clay content was <1 % and considering this, we only used silt and sand percentages. The three pseudo-replicates of sediment samples for TOC and TN analyses were first frozen and then lyophilized. They were subsequently crushed and pre-acidified. Then, TOC and TN content (weight %) were determined by high-temperature combustion of dry samples (60 °C, 48 h). Measurements of CO<sub>2</sub> and N<sub>2</sub> were finally done by thermal conductivity using an elemental analyzer (FlashEA, Thermo Electron Corporation).

The C:N ratio was calculated as follows:

$$C:N = (TOC / TN) \times M_C / M_N$$

Where  $M_C = 12.01 \text{ g mol}^{-1}$  and  $M_N = 14.01 \text{ g mol}^{-1}$  and are molar mass of carbon and nitrogen, respectively.

For measurement of Chl *a* concentration in sediment, 0.3 g of previously freeze-dried sediment were subsampled and 3 mL of acetone was added as a solvent. Subsamples were then preserved in a fridge during minimum 12 h to extract pigments of chlorophyll and protect samples from natural light. Samples were then centrifuged at 4099×g and 4 °C for 15 min. Finally, subsamples were analyzed using a mass spectrophotometer and UVProbe software. Chlorophyll *a* concentrations were calculated following (SORE/UNESCO):

$$\text{Chl } a \text{ (}\mu\text{g mL}^{-1}\text{)} = 11.64D_{663} - 2.16D_{645} - 0.1D_{630}$$

Where  $D_x$  is the absorbance at a wavelength X (nm).

### 2.2.3. Sediment organic matter molecular analysis

Five to 20 g of freeze-dried sediment samples were Soxhlet extracted for 24 to 48 h with a 9:1 (v:v) mixture of dichloromethane (DCM) and methanol (MeOH). The recovered extract was concentrated through rotary evaporation, and an aliquot was fractionated by liquid chromatography on a column of silica activated at 100 °C for 24 h after removal of elemental sulfur with activated copper. The "apolar" fraction, containing saturated and aromatic compounds, was eluted with a mixture cyclohexane:DCM (8:2), the "oxygenated" fraction, containing alcohols and ketones, with a mixture DCM:ethyl-acetate (8:2), finally, the "polar" fraction, containing acids and macromolecules was eluted with DCM:MeOH (1:1). The oxygenated fraction was acetylated with acetic anhydride/pyridine, and the polar fraction was esterified with methanol/acetyl chloride prior to injection in GC-MS.

The three fractions were analyzed by gas chromatography coupled to mass spectrometry in the laboratory METIS (UMR 7619, CNRS-Sorbonne Université, Paris). Briefly, a 1 μL of each fraction was injected into a Trace 1310 gas chromatograph equipped with an RSH autosampler and coupled with an ISQ 7000 mass spectrometer (ThermoFisher Scientific). A Restek RXI-5 Sil MS silica column (60 m × 0.25 mm, i.d. 0.25 μm film thickness) was used with He as the carrier gas at 2 mL/min. The GC oven

program was: 100 °C for 1 min, then from 100 to 300 °C at 4 °C/min, then at 300 °C for 20 min. Samples were injected in split mode (20 mL/min) and the injector was set at 250 °C. Mass spectrometry was performed with electron impact at 70 eV, with a source temperature of 250 °C, in full scan mode from  $m/z$  50 to 550. Compound identification was based on the comparison with NIST mass spectra database and/or on the comparison with retention times of standards and published data. The semi-quantification of compounds and calculation of biomarker ratios was achieved by measuring peak area of selected ion chromatograms. Semi-quantification of sterols was based on peak areas on the characteristic mass chromatogram multiplied by a correction factor, in order to account for the variable intensity of the characteristic fragment in the mass spectrum of the different compounds. The correction factor for each family of compounds was determined from the NIST mass spectral database. Values of biomarkers are available in [Table S1](#).

#### 2.2.4. Sediment trace metals analysis and enrichment factor (EF)

To determine concentrations of selected metals (Al, Cd, Cr, Cu, Fe, Hg, Mn, Ni, Pb, V and Zn) samples of surface sediments were dried at 40 °C to constant weight. About 300 mg of ground sediments were digested with a mixture of 7 mL HF 22.6 M (Suprapur Merck) and 2.5 mL HNO<sub>3</sub> 14.6 M (sub-boiling, Merck) at 125 °C for 48 h. Samples were again digested with 6 mL 6M (HCl, sub-boiling, Merck) and 3 mL HNO<sub>3</sub> 14.6 M (sub-boiling, Merck) at 125 °C for 48 h and was repeated once. After evaporation, samples were diluted to 2% HNO<sub>3</sub>, then filtered out using polyethylene syringes equipped with cellulose acetate filter (0.2 µm). Except for mercury, metal analysis was performed by ICP-AES (Agilent 5110 VDV). For quality assurance, reagents blanks, sample replicates and standard reference materials (MESS-3 and PACS-2, National Research Council Canada) were used to assess the accuracy and precision of the analyses. Recovery efficiencies ranged between 83 and 107 %. The limits of quantification were 0.3 mg kg<sup>-1</sup> for Cd, Cr, Cu and Zn and 0.8 mg kg<sup>-1</sup> for Al, Fe, Mn, Ni, Pb and V. Total Hg was measured in dry and ground sediment samples (without any treatment) by means of atomic absorption spectroscopy (AAS) using an AMA 254 solid phase Hg- Analyzer (Altec). Mean recovery for total Hg was 88 ± 2 % for certified estuarine sediment MESS-3. The limit of quantification was 0.002 mg kg<sup>-1</sup> dw.

The extent of sediment contamination was determined using the enrichment factor (EF). Commonly, normalization of the metals to a conservative and abundant element on the earth such as Al is employed to differentiate the metal source between anthropogenic and naturally occurring. The EF is defined as  $EF = (X/Al)_{\text{sample}} / (X/Al)_{\text{background}}$  where  $(X/Al)_{\text{sample}}$  is the metal to Al ratio in the samples of interest and  $(X/Al)_{\text{background}}$  is the natural background value of the metal to Al ratio. The background values were the median concentrations obtained on deep horizons of soils sampled on the French Coastal plain (the Watriques marine plain) supposed to be preserved from potential contamination sources (Sterckeman et al., 2004). According to previous studies (Birth, 2003; Chen et al., 2007), different categories based on EF values could be reported: EF < 1 indicates no enrichment, EF < 3 minor enrichment, EF = 3 - 5 moderate enrichment, EF = 5 - 10 moderately severe enrichment and EF > 10 severe enrichment. Enrichment values are available in [Table S2](#).

#### 2.3. Benthic foraminifera, macrofauna and descriptors of species assemblages

Sampling and sediment sample processing for benthic foraminiferal analyses followed the routine biomonitoring protocol FOBIMO (Schönfeld et al., 2012). Three replicate samples from three different deployments (Reineck corer) were taken at each station for foraminiferal sampling. The 0-1 cm layer was subsampled for foraminiferal analysis using a hand corer (56 cm<sup>2</sup> surface). We added a solution of ethanol (70%) and Rose Bengal (2 g L<sup>-1</sup>) to samples to distinguish living benthic foraminifera from dead ones. Samples were sieved, after about

two weeks, with a 63 µm mesh and dried at 50 °C for 24 h. Then, they were separated by density with a solution of trichloroethylene ( $d = 1.46$ ). The floating sediment was collected and analyzed under a stereomicroscope. A minimum of 300 benthic foraminifera were collected and identified in each replicate for statistical robustness (Bouchet et al., 2012). If the threshold of 300 individuals was not reached in a sample, all individuals were collected. Species belonging to the morphogroup *Ammonia tepida* were identified following Pavard et al. (2021). Raw counts of individuals were normalized to a surface of 50 cm<sup>2</sup> ([Table S3](#)) to perform further comparisons and statistical analyses.

Foraminiferal analyses were restricted to the 0-1 cm surface layer, which generally hosts the highest densities of living benthic foraminifera and best reflects recent environmental conditions in soft sediments (Schönfeld et al., 2012). All sedimentary environmental parameters (grain size, TOC, TN, C:N, Chl *a*, trace metals and molecular markers) were measured on the same 0-1 cm interval to ensure direct comparability between biological and abiotic data. Although deeper layers were not sampled here, previous studies in similar transitional environments show that most living foraminiferal biomass is confined to the upper centimeter of sediment.

Concerning the macrozoobenthos, three replicates were also sampled at each station, using three deployments of a 0.1 m<sup>2</sup> Van Veen grab. Samples were directly sieved on board with a 1 mm-mesh sieve and fixed and preserved in a 5% formaldehyde-seawater solution until they were sorted and preserved again in a 70% ethanol-water solution. Macro-invertebrate organisms were morphologically identified and counted, using taxonomic keys and literature. Then, raw counts were normalized to a surface of 1 m<sup>2</sup> ([Table S4](#)).

Mean normalized abundances of both foraminiferal and macrofaunal were determined from triplicated sediment samples ([Tables S3 and S4](#)) for each station and by season and mean relative abundance of species were used for further multivariate analyses. Species richness, and Exp ( $H'_{bc}$ ) index were finally calculated (mean ± standard deviation) at each station for foraminifera and macrofauna and their values are available in [Table S5](#), respectively. We applied an exponential function on the corrected index of Shannon index  $H'$  to give the effective number of species in a sample (Chao and Shen, 2003; Hill, 1973) which was then used as a measure of diversity. Mean total abundance (± standard deviation) was not shown in this study but is also available in [Table S5](#).

#### 2.4. Statistical and multivariate analyses

Only mean values of environmental (TOC, TN, C:N and Chl *a*) and biological parameters that were replicated (species richness and the Exp ( $H'_{bc}$ ) index) were used for the statistical analyses. Following tests of normal distribution (Shapiro-Wilk) and homogeneity of variance of data (Levene), either a two-way ANOVA (2w ANOVA) or an Aligned Rank Transform ANOVA (ART) was performed to detect statistical differences between stations, season or the interaction of the two variables. If significant ( $p < 0.05$ ), a post-hoc test was performed, respectively a Tukey HSD or an Estimated Marginal Mean (EMM) test, to detect pairwise differences for each variable or interaction. Details for statistical results of these tests are available in [Table S6](#).

Prior to further multivariate analyses, variables with at least once a correlation value > 0.90 with other variables (Silt, Mn, Zn) were removed from dataset to decrease the possible effect of collinearity and improve the clarity of graphic analyses. Their values are available in [Table S7](#). Significant correlation values between environmental variables and values of removed variables are available in [Fig. S1](#). A Principal Component Analysis (PCA) on standardized environmental data (mean centered) was performed ([Fig. S1](#)) on the selected environmental variables (TN, Chl *a*, Sand, Cr, Cu, Fe, Hg, Mn, Ni, V, Temp, Salinity). A subsequent Hierarchical Ascendant Classification (HAC) based on the outputs of this PCA to determine clusters of environmental similarity of stations according to the season of sampling, using the Euclidean distance and following the method of Ward. The three first dimensions of

the PCA explained respectively 31.9%, 26.5% and 18.5% of the environmental parameters' variability among stations (Fig. S2). Correspondence Analyses (CAs) were performed using relative abundances of the main species of foraminifera and macrofauna (species comprising at least >5% of the species assemblages at least in one sample) to analyse their distribution in the harbor. As for environmental parameters, two HACs were performed to discriminate how stations were similar in terms of fauna.

For the species community data, initial detrended correspondence analyses indicated that the gradient is short (<3 SD) in the foraminiferal relative abundance dataset while the gradient was intermediate for the macrofaunal dataset (i.e. included between 3 and 4 SD). Consequently, Redundancy analyses (RDAs) were applied to find which environmental variables were most clearly related to the species communities. Prior to both RDAs, Variance Inflation Factor (VIF) tests have been made step-by-step to remove highly colinear variables (i.e. VIF >10) from the models (Fe, TOC, CN, Salinity, Hg and Cr). Forward selections of remaining environmental variables by permutation tests have then been performed to build automatic stepwise RDA models only based on the variability explained by variables and their significance. For the foraminiferal RDA, Sand, Chl *a* and Cd have been selected while only the first two parameters have been chosen by the analysis for the macrofaunal one. A final VIF analysis was performed to check for collinearity between the selected variables. Significance of axes and environmental parameters fitted for RDAs was tested (Legendre et al., 2011). Forward sections have been performed using the "ordiR2step" function from the *vegan* package (Oksanen et al., 2013). Ordination representations, HACs and statistical tests were performed using R software version 4.2.2 (R Core Team, 2022).

### 3. Results

#### 3.1. Environmental parameters

##### 3.1.1. Hydrography and sediment properties

Both water salinity and temperature were higher in fall than in spring (Table 2). The sand content followed an opposite seasonal pattern, being generally higher in spring than in fall (Table 2). Despite this seasonality, the water salinity and temperature were respectively higher and lower at both D6 and D7 compared to all the stations of the main basin of the harbor (D1-D5).

Sediment grain size, TOC, TN C:N, Chl *a*.

No clear spatial pattern was observed for the sand content. The contents of TOC and TN as well as chlorophyll *a* in the sediment (Table 2) were higher in fall than in spring (EMM,  $p < 0.05$ ). More specifically, TOC content was significantly higher in fall at D3, D4 and D6 (EMM,  $p < 0.001$ ). In addition, the TOC content significantly varied among stations within season (EMM,  $p < 0.001$ ). In fact, maximal values

observed at D3 in spring and fall were higher than D4 for both seasons as well as D2 and D6 in fall (Table 2). The TN content also varied significantly between stations where D3, D6 and D7 had higher values than other stations, except D1 (EMM,  $p < 0.001$ ). However, the content of TN in sediment did not vary either from one station to another within each season or at the same station between the two seasons (EMM,  $p > 0.05$ ). Oppositely to the other parameters, there was no seasonal variation for C:N (ART,  $p > 0.05$ ). Indeed, this ratio only differed spatially (EMM,  $p < 0.001$ ) where D3 had a higher value than both D6 and D7 (Table 2). Finally, the chlorophyll *a* content was significantly higher in D6 and D7 than in D2, D3 and D4 (EMM,  $p < 0.001$ ). The interaction of season and station was significant for this parameter and, the post hoc test revealed that the sediment from both D1 and D6 contained more chlorophyll *a* in spring (EMM,  $p < 0.001$ ).

##### 3.1.2. Trace metals, enrichment factors and environmental parameter clustering

Severe enrichment factors (EF > 10) were observed only at main-basin stations (D1-D5) and concerned.

Cd, Cu, Fe, Hg, and Pb (Table 3). Oppositely, no severe enrichment was observed in the two marina stations (D6, D7). During spring, D2, D3 and D5 were severely enriched in Cd, Cu, and Zn. The same pattern was observed for D4, though it was not highly enriched in Zn. At this season, D2 and D3 were the only stations with a Fe contamination. The same spatial distribution of metal contamination was observed in fall for D3, D4 and D5. This season, D2 did not show any severe contamination in Cu and Fe. Finally, both stations D4 and D5 exhibited a high enrichment in Pb during the fall sampling campaign.

The Hierarchical Ascendant Clustering (Fig. 2) based on the outputs of PCA of environmental parameters (Fig. S2) discriminated the combination of stations and seasons into four clusters. The first cluster included D1, D6 and D7 in both seasons and was characterized by high chlorophyll *a*, low C:N and concentrations of Cu, Cd, Hg and Pb in the sediment (Fig. 2, Table S2). Stations D4 and D5, at both seasons, were clustered together for having the highest concentrations of Cu and Pb in the sediment as well as low content of TN. The station D3 during fall formed a cluster by itself by having the highest concentrations of TOC, Cd, Hg and Ni in the sediment. Finally, the fourth cluster was only composed of D2 during both seasons and D3 during spring. It was mainly influenced by high concentrations of Fe and a high C:N ratio.

##### 3.1.3. Sedimentary molecular markers

Molecular markers were analyzed for both seasons at stations D2 to D6. At stations D1 and D7, only the fall sample was analyzed (Table 4). The distribution of *n*-alkanes is generally bimodal, with a first maximum in  $nC_{17}$  or  $nC_{18}$  (Table S1), and *n*-alkanes with a chain length higher than 22 carbon atoms show a predominance of compounds with an odd carbon number. The Terrestrial to Aquatic Ratio (TAR, Bourbonniere

**Table 2**

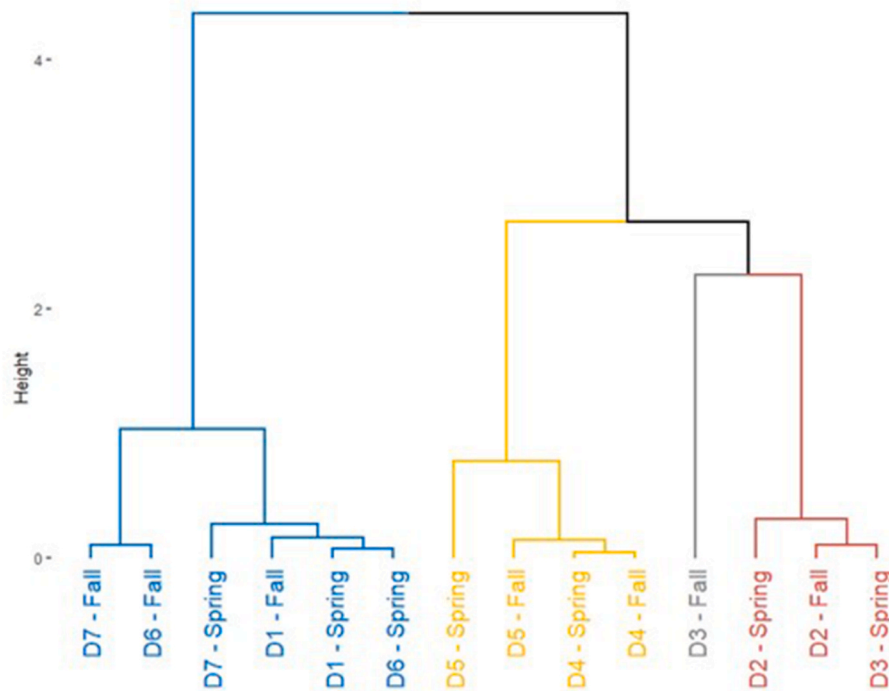
Values (mean  $\pm$  standard deviation) of environmental parameters (water salinity, water temperature, content of Sand, Silt, TOC, TN, C:N, Chl *a* in the sediment) by station. Water temperature is expressed in °C while Silt, Sand, TOC, TN are expressed in weight %, Chl *a* in  $\mu\text{g g}^{-1}$ .

Season	Station	Salinity	Temperature	Sand	Silt	TOC	TN	C:N	Chl <i>a</i>
Spring	D1	26.5	17.2	11.5	88.4	2.4 (0.4)	0.2 (0.1)	16 (2.8)	28.5 (4)
	D2	26.7	17.0	9.3	90.0	4.1 (1.7)	0.2 (0.1)	23.3 (1.6)	7.2 (1.1)
	D3	26.9	17.0	13.1	86.7	6.3 (1.3)	0.3 (0.1)	28.7 (1.1)	7.1 (1.3)
	D4	27.0	17.1	11.5	88.3	3.1 (0.5)	0.2 (0.0)	17.9 (2.4)	7.8 (1.6)
	D5	27.1	17.2	20.5	79.3	1.5 (0.3)	0.1 (0.0)	17.4 (3.3)	7.1 (1.6)
	D6	30.4	16.1	14.8	85.1	3.3 (0.5)	0.3 (0.0)	13.4 (0.4)	35.5 (9.7)
	D7	30.8	16.1	8.7	91.2	2.9 (0.4)	0.3 (0.0)	12.5 (0.2)	47.4 (12.9)
Fall	D1	31.6	20.9	10.4	89.5	4.1 (0.1)	0.3 (0.1)	11.7 (0.9)	18.5 (5.7)
	D2	31.7	21.0	15.6	84.3	4.1 (1.2)	0.2 (0.1)	24.2 (3.1)	16.4 (7.4)
	D3	32.0	20.8	9.8	90.0	10.7 (0.4)	0.4 (0.0)	28.6 (7.8)	17.6 (0.9)
	D4	31.0	21.6	11.1	88.8	3.4 (0.5)	0.2 (0.1)	17.3 (1.3)	9.5 (0.7)
	D5	31.0	21.6	14.6	85.3	3.4 (0.1)	0.2 (0.1)	15.1 (1.5)	20.6 (9.6)
	D6	32.1	19.1	4.7	95.0	3.8 (0.1)	0.3 (0.0)	11.7 (1.1)	16.2 (4.7)
	D7	33.5	18.9	5.8	94.1	4.2 (0.1)	0.4 (0.0)	10.7 (0.4)	70.0 (21.9)

**Table 3**

Concentrations of trace metals and metal, i.e. Cd, Cr, Cu, Fe, Hg, Pb, Zn in sediment by station. Concentrations of trace metals are expressed in mg.kg-1 and in g.kg-1 for Fe. Bold values of trace metals significant that Enrichment Factor were higher than 10 (i.e. corresponding to, at least, a severe enrichment - see Table S2 for details).

Season	Station	Cd	Cr	Cu	Fe	Hg	Pb	Zn
Spring	D1	<b>0.85</b>	43.4	<b>18.7</b>	20.5	0.08	22.6	<b>110.2</b>
	D2	<b>2.93</b>	32.4	<b>49.2</b>	<b>100.8</b>	<b>0.11</b>	<b>42.1</b>	<b>286.5</b>
	D3	<b>1.81</b>	57.7	<b>41.4</b>	<b>49.7</b>	<b>0.19</b>	<b>80.2</b>	<b>368.4</b>
	D4	<b>2.68</b>	57.9	<b>132.6</b>	24.5	<b>0.22</b>	<b>129.9</b>	<b>274.3</b>
	D5	<b>1.00</b>	52.1	<b>303.9</b>	16.7	<b>0.13</b>	<b>102.5</b>	<b>350.6</b>
	D6	<b>0.77</b>	46.4	<b>23.4</b>	19.9	0.07	23.4	96.6
	D7	<b>0.38</b>	33.8	<b>16.9</b>	12.2	0.05	15.4	81.5
Fall	D1	<b>1.54</b>	47.5	<b>30.9</b>	31.8	0.05	29.7	<b>198.9</b>
	D2	<b>2.06</b>	35.0	<b>36.0</b>	<b>59.8</b>	0.10	<b>42.7</b>	<b>340.2</b>
	D3	<b>6.56</b>	67.6	<b>93.0</b>	<b>60.2</b>	<b>0.31</b>	<b>91.8</b>	<b>756.1</b>
	D4	<b>2.64</b>	53.7	<b>133.3</b>	22.9	<b>0.27</b>	<b>167.3</b>	<b>286.9</b>
	D5	<b>1.55</b>	77.0	<b>269.1</b>	19.4	<b>0.17</b>	<b>144.4</b>	<b>295.0</b>
	D6	<b>0.41</b>	55.6	<b>24.7</b>	27.0	0.10	28.0	107.5
	D7	<b>0.42</b>	49.8	<b>18.2</b>	21.5	0.09	22.4	92.9



**Fig. 2.** Hierarchical Ascendant Clustering based on PCA outputs of measured environmental parameters.

**Table 4**

Molecular markers content in sediment by season and station. D1 and D7 during Spring were not analyzed.

Season	Spring						Fall						
	D2	D3	D4	D5	D6	D1	D2	D3	D4	D5	D6	D7	
TAR	0.5	0.7	2.6	2.0	4.3	4.1	1.3	1.3	1.8	1.7	6.4	2.2	
Paq	0.7	0.6	0.3	0.4	0.3	0.3	0.4	0.5	0.3	0.4	0.2	0.4	
CPI (B&E)	1.6	2.2	3.5	2.1	4.7	4.9	3.4	3.0	5.5	3.0	6.4	2.1	
Pr/Ph	3.0	3.6	0.7	0.7	0.5	0.6	1.6	1.7	0.4	0.7	0.5	0.7	
hopanes/alkanes	0.8	2.2	6.7	6.6	0.4	1.1	1.5	1.2	0.4	6.6	0.4	7.0	
HAP/alkanes	10.2	27.4	58.0	163.8	2.5	11.5	24.6	16.3	4.0	68.7	2.7	35.8	
stanones	0.4	0.4	0.4	0.3	0.4	0.4	0.3	0.3	0.3	0.4	0.4	0.4	
dinostenone	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	
Sterols Δ5 C27	56.4	68.7	50.3	53.8	62.5	45.3	38.2	46.2	57.1	35.9	55.3	30.8	
Sterols Δ5 C28	18.3	11.3	18.3	14.0	14.3	28.1	16.8	16.3	25.0	23.9	19.2	26.8	
Sterols Δ5 C29	25.3	20.1	31.4	32.2	23.2	26.7	45.0	37.5	17.9	40.1	25.4	42.5	
(Cp + epi-Cp)/(Cp + epi-Cp + Chln)	0.2	0.7	0.6	0.4	0.9	0.8	0.9	0.9	1.0	0.1	1.0	0.6	
(β-sti + epi-β-sti)/(β-sti + epi-β-sti + sti)	0.3	0.7	0.7	0.9	0.9	0.9	0.9	0.9	0.2	0.6	1.0	0.6	
Cp/(Cp + β-sti)	0.7	0.7	0.6	0.8	0.8	0.7	0.7	0.7	0.6	0.5	0.8	0.5	
epi-Cp/Cp	0.4	0.5	0.5	0.2	0.2	0.3	0.5	0.4	0.7	0.6	0.2	0.6	

and Meyers, 1996), and the Carbon Preference Index (CPI, Bray and Evans, 1961) are generally higher than 1. The highest values are observed at station D6 for both seasons and at station D1 in fall (Table 4). Stations D4, D5 and D7 have values of the TAR close to 1 for both seasons while TAR values lower than 0.7 are observed at stations D2 and D3 for both seasons. For all stations, the CPI values are higher in fall than in spring (Table 4). Although the Paq is generally low at most of the stations (Table 4), stations D2 and D3 show higher values, particularly in spring.

The pristane to phytane ratio (Pr/Ph) presents values higher than 1 at stations D2 and D3 for both seasons, but with a marked decrease in fall compared to spring (Table 4). A similar seasonal evolution is observed at the other stations, though the values of the Pr/Ph ratio are lower than 0.8.

Sterols were characterized by both the presence of dinosterol and C<sub>29</sub> sterols. These latter even observed an increase in September for most stations (Table 4). The ratio of stanol to sterols, i.e. indicator of the freshness of the organic matter, is generally lower in spring compared to fall.

Hopanes and polycyclic aromatic hydrocarbons (PAHs) are present in all the samples, and their relative abundance fluctuates in parallel. The highest proportions of hopanes and PAHs are observed at station D7 (fall only), D5 for both seasons, and D4 in spring (Table 4). The lowest proportions of hopanes and PAHs are observed at station D6 for both seasons and D4 in fall. Fecal contamination from omnivores ((Cp + epi-Cp)/(Cp + epi-Cp + Chln)) and herbivores ((β-sti + epi-β-sti)/(β-sti + epi-β-sti + sti)) are detected at station D6 for both seasons, and at stations D1 to D4 in fall (Table 4). It is likely at stations D3 and D4 in spring, and possible at station D5 in spring. In general, at a given station, the relative abundance of fecal sterols is lower in spring than in fall, except at station D5. The presence of fresh human sewage (i.e. Cp/(Cp + β-sti), Table 4) is particularly marked at station D6 for both seasons while the animal manure is best expressed at station D5 for both seasons.

### 3.2. Biological assemblages

#### 3.2.1. Benthic foraminifera: diversity and composition

Species richness and diversity index  $\text{Exp}(H'_{bc})$  values for both benthic foraminifera and macrofauna assemblages per station are reported in Table S5. Foraminiferal richness and diversity did not undergo seasonal influence (respectively 2w ANOVA and ART,  $p > 0.05$ ). Spatially, the lowest values of richness and diversity for both types of organisms were always observed at D6 (Tukey HSD and EMM,  $p < 0.001$ ). Indeed, the foraminiferal richness and diversity at this station went down to  $12 \pm 3$  species and  $3.4 \pm 0.3$  (Fig. 3). Oppositely, maximal values of foraminiferal richness and diversity followed a different pattern. In fact, richness reached  $22 \pm 2$  species at D1 but was not different from all the other stations, except for D6 (Table S6). The foraminiferal diversity was statistically higher at D1, D2 and D7 (Table S6), reaching respectively  $11.5 \pm 4.2$ ,  $9.0 \pm 1.8$  and  $9.0 \pm 1.8$  (Fig. 4). No interaction between season and station influenced the foraminiferal richness (2w ANOVA,  $p > 0.05$ ). Though no difference of foraminiferal diversity was observed between stations within each season, the diversity index  $\text{Exp}(H'_{bc})$  at D3 and D7 observed a difference between seasons (EMM,  $p < 0.05$ ). Indeed, the former station had a higher diversity during spring than in fall while the latter was less diversified in spring compared to the second season.

At both seasons, foraminiferal species *Elphidium selseyense* and *Ammonia* species were generally the most abundant species in assemblages (Fig. 4). Indeed, the former ranged from 4.7% to 66.3% while abundance ranges of *A. aberdoveyensis* and *A. confertitesta* were of 0.8–20.9% and 0.2–29.6%, respectively (Fig. 4). Except at D3 and at D7 in fall, *Elphidium selseyense* was highly abundant in almost all stations and reached its abundance peak at D6 in fall (Fig. 4). The highest abundances of *E. selseyense*, together with high abundances of *Elphidium* spp. explained cluster gathering D6 and D7 during spring and D1 and D6 during Fall (Fig. 4). The species composition at D1 in spring was similar to this cluster but the higher abundances of *E. magellanicum* and *E. pulvereum* at this season clustered this station by itself (Fig. 4). Stations D2, D4 and D5 were seasonally clustered together. More precisely, *A. confertitesta* and *Ammonia* spp. (mainly composed of juveniles and

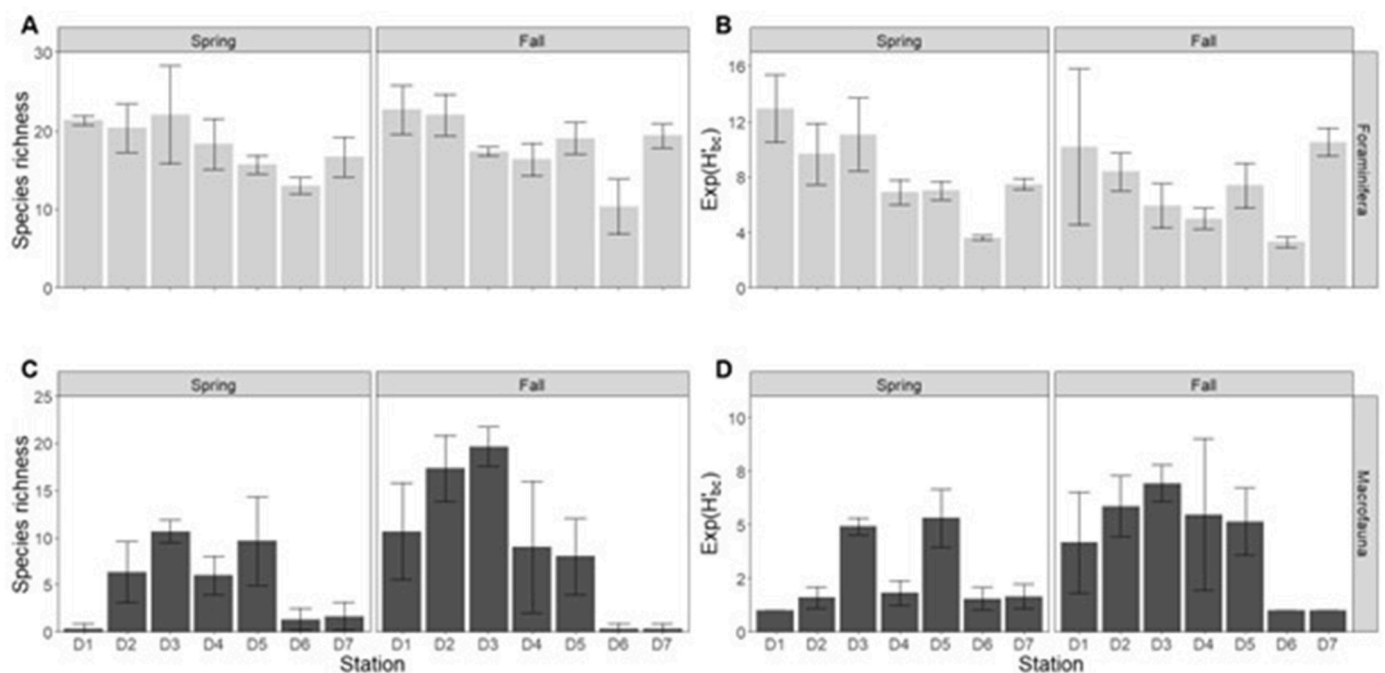
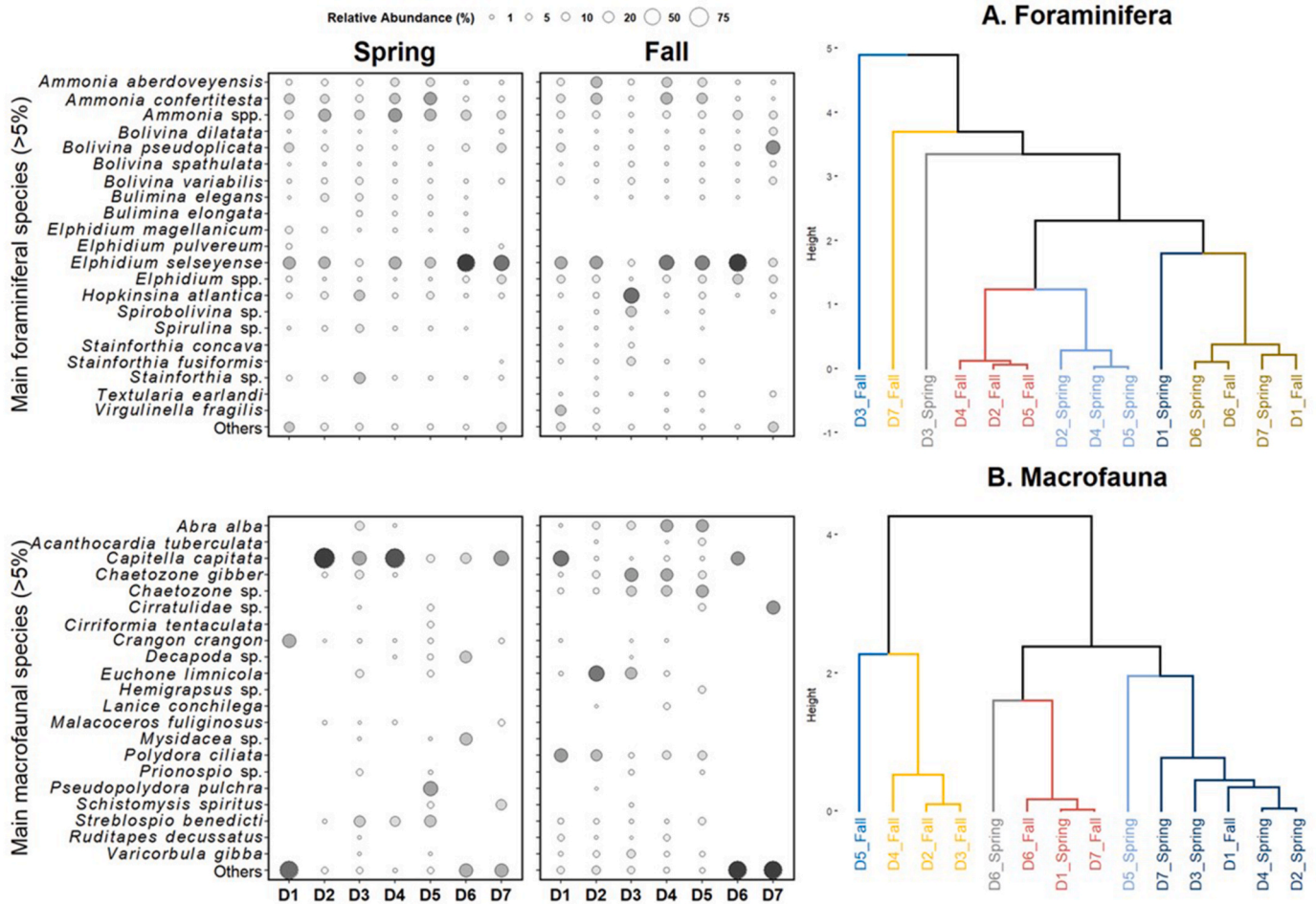


Fig. 3. Mean  $\pm$  sd of species richness and  $\text{Exp}(H'_{bc})$  values per station for benthic foraminifera (respectively A, B) and benthic macrofauna (respectively C, D). Letters on top of each bar represent statistical differences or similarities between each station among one season. If there are no letters in common between bars, values are statistically different ( $p < 0.05$ ).



**Fig. 4.** Bubble plots of relative abundances of main species (>5%) of benthic foraminifera during spring (top left) and fall (top mid) and benthic macrofauna during the same seasons (respectively bottom left and bottom mid) and clusters dendrograms based on Correspondence Analyses outputs using relatives abundances of main species of benthic foraminifera (top right) and macrofauna (bottom right). In the four bubble plots, the bigger and darker the bubble is, the more abundant in a station the species is. In the two dendrograms, a different color means a statistical different cluster.

small individuals) were more abundant in spring while, in fall, *A. aberdoveyensis* equally accompanied *A. confertitesta* (Fig. 4). Finally, D3 during spring and fall as D7 during fall formed a cluster each (Fig. 4). In spring, D3 was less influenced by the presence of *E. selseyense* and was mainly composed of *Hopkinsina atlantica*, *Stainforthia* sp., *Spirulina* sp. as well as *Ammonia* species (Fig. 4). In addition, both *Bulimina elegans* and *B. elongata* were also present at this station during spring. In fall, *H. atlantica* became the most abundant species, followed by a species absent in spring, *Spirobolivina* sp., and were accompanied by *Stainforthia concava*, *S. fusiformis* and *Bolivina spathulata* (Fig. 4). The last station D7 during fall observed higher abundances of *Bolivina* species, with *B. pseudoplicata* as the main species (36.4%), as well as the presence of *Textularia earlandi* (Fig. 4). Surprisingly, the large but highly variable abundance of *Virgulinea fragilis* (18.7 ± 29.1%; Fig. 4) did not cluster the assemblage of D1 in fall by itself, though it was its only occurrence in the study. No clear conclusion on its ecological requirements can be therefore stated.

### 3.2.2. Macrofauna: diversity and composition

Unlike foraminifera, macrofaunal richness and diversity were statistically higher in fall than in spring (respectively Tukey HSD and EMM,  $p < 0.001$ ). Indeed, the macrofaunal richness reached 9 ± 8 species in fall and 5 ± 4 species in spring while the macrofaunal diversity was equal to 4.2 ± 2.7 and 2.6 ± 1.8, respectively. The lowest values of macrofaunal richness and diversity were always observed at D6 (EMM,

$p < 0.001$ ). Indeed, they were respectively equal to 1 ± 1 species and 1.3 ± 0.4 (Fig. 3), though, D7 was not statistically different from D6 in terms of macrofaunal richness (Table S6). In opposition, D3 was significantly the richest and most diversified station (Table S6), reaching 15 ± 5 species and 5.9 ± 1.2 (Fig. 3). In comparison to foraminifera, the effect of the interaction between seasons and stations on macrofaunal assemblage descriptors was more accentuated (EMM,  $p < 0.001$ ). First, D1 and D2 were poorer in spring than in fall (Fig. 3). Within each season, station D3 was consistently the richest station in terms of species. However, the second richest was D5 during spring and D2 during fall. Oppositely, D1 was the poorest station during spring while both D6 and D7 replaced this last station in fall. Secondly, only D2, D6 and D7 were statistically different from one station to another regarding diversity. Indeed, while D2 observed a lower diversity during spring than in fall, D6 and D7 were more diversified in fall.

Macrofaunal species *Capitella capitata* and *Chaetozone* spp. group were generally the most abundant species in macrofaunal assemblages (Fig. 4). A seasonal pattern is well distinguishable in terms of clustering (Fig. 4). Indeed, D2, D3, D4 and D7 during spring were clustered altogether with D1 during fall. This cluster was represented by high abundance of *Capitella capitata*, ranging from 37.0 to 91.1% (Fig. 4). This cluster is also driven by low abundances of *Malacoceros fuliginosus*, though only present in spring. The cluster represented only by D5 during spring was still slightly influenced by *Capitella capitata*, though in lower abundance (Fig. 4). However, *Malacoceros fuliginosus* was absent at this

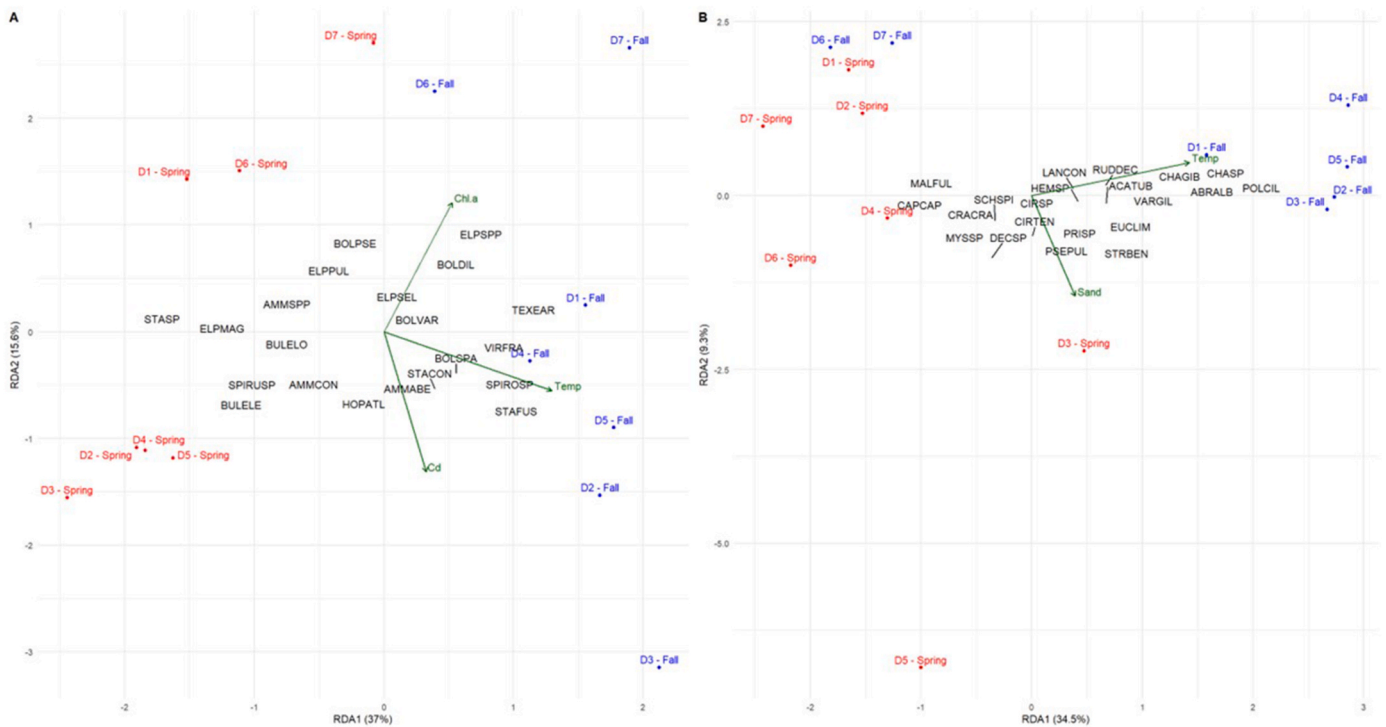
station and *Streblospio benedicti*, *Prionospio* sp., *Cirriiformia tentaculata*, *Pseudopolydora pulchra* were present instead (Fig. 4). D1 during spring and both D6 and D7 during fall were clustered together due to the scarce abundances of some species (i.e. one to two individuals of a single species, Table S4) and non-identified organisms, either broken or too damaged. Despite being clustered quite close to the previous cluster, D6 contained slightly more species during spring, including *Mysidacea* sp., *Decapoda* sp. as well as *C. capitata* (Fig. 4) but each was still represented by only a few individuals (Table S4). Finally, all the stations from the main basin of the harbor were almost all clustered together (Fig. 4). Stations D1, D2, D3, and D4 during fall formed a cluster mainly represented by *Varicorbula gibba*, *Polydora ciliata*, *Ruditapes decussatus*, *Chaetozone gibber* and *Euchone limnicola*, species being either absent or slightly abundant during spring (Fig. 4). *Euchone limnicola*, together with *Ruditapes decussatus* were not present any more in D5 at the same season. Instead, this cluster was defined by the two main species, *Abra alba* and *Chaetozone* sp. as well as *Acanthocardia tuberculata*. In addition, this station observed the only occurrence of the crab *Hemigrapsus* sp. through the whole study (Fig. 4).

### 3.2.3. Multivariate analyses (redundancy analyses)

The RDA representing how environmental variables constrained relative abundances of foraminiferal species (Fig. 5) was significant ( $p < 0.001$ ) and its two first dimensions explained 37.0 and 15.6% of assemblages' variability (Fig. 5). Temperature (Temp), chlorophyll *a* (Chl *a*) and cadmium (Cd) contents within the sediment were the selected environmental parameters which explained most the variability of

species abundances and statistically fitted the representation of the RDA (Fig. 5A). *Elphidium selseyense* and *Elphidium* spp. were positively correlated with Chl *a*, especially, while being negatively correlated with Cd. However, the central position of *E. selseyense* showed that its abundances were only influenced by the highest values of measured environmental variables. Being present only in spring, *E. magellanicum* and *E. pulvereum* were logically influenced negatively by the Temp. *Elphidium magellanicum* was not correlated either with Cd or Chl *a* while *E. pulvereum* was slightly influenced positively by the Chl *a* and negatively by Cd. *Ammonia confertitesta* had a negative correlation with Chl *a* and a slightly positive one with Cd (Fig. 5). The same pattern was observed for *A. aberdoveyensis*, though it had a stronger positive correlation with Cd. On the other hand, *Ammonia* spp. were influenced by the lower water temperature in spring and were not correlated by Cd and Chl *a*. Species present at D3 in spring, i.e. *Hopkinsina atlantica*, *Stainforthia* sp., *Spirulina* sp. and *Ammonia* species, were influenced by colder waters, positively correlated with Cd and negatively with Chl *a*. During fall, *H. atlantica*, *Spirobolivina* sp., *Stainforthia concava*, *S. fusiformis* and *Bolivina spathulata* (Fig. 4) were logically influenced by the warmer waters and positively correlated with the Cd content (Fig. 5). Only *H. atlantica* did not undergo the seasonality by being highly abundant at both seasons (Fig. 5). *Bolivina pseudoplicata* and *B. dilatata* were driven by Chl *a* while *B. spathulata* was indifferent to this environmental variable and has even been influenced by Cd. Though *Textularia earlandi* showed a weak correlation with Chl *a*, it was also driven by the water temperature.

The first two dimensions of the RDA (Fig. 5) respectively explained



**Fig. 5.** Redundancy Analyses (RDAs) of main species of (A) benthic foraminifera and, (B) macrofauna (scaling 2) as constrained variables and the green triplot as chosen environmental constraining variables. Stations sampled during spring and fall are respectively represented in blue and red dots. The two first dimensions of the foraminiferal RDA explained 37.0% and 15.6%, respectively, while the two first dimensions of the macrofaunal RDA explained 34.5% and 9.3% of the species variability. Main foraminiferal and macrofaunal species are respectively represented by their shortened species names. Foraminiferal species names are shortened as: AMMABE = *A. aberdoveyensis*, AMMCON = *A. confertitesta*, AMMSPP = *Ammonia* spp., BOLDIL = *B. dilatata*, BOLPSE = *B. pseudoplicata*, BOLSPA = *B. spathulata*, BOLVAR = *B. variabilis*, BULELE = *B. elegans*, BULELO = *B. elongata*, ELPMAG = *E. magellanicum*, ELPPUL = *E. pulvereum*, ELPSEL = *E. selseyense*, ELPSP = *Elphidium* spp., HOPATL = *H. atlantica*, SPIROSP = *Spirobolivina* sp., SPIRUSP = *Spirulina* sp., STACON = *S. concava*, STAFUS = *S. fusiformis*, TEXEAR = *T. earlandi*, STASP = *Stainforthia* sp., VIRFRA = *V. fragilis*. Macrofaunal species names are shortened as: ABRALB = *A. alba*, ACATUB = *A. tuberculata*, CAPCAP = *C. capitata*, CHAGIB = *C. gibber*, CHASP = *Chaetozone* sp., CIRSP = *Cirratulidae* sp., CIRTEN = *C. tentaculata*, CRACRA = *C. crangon*, DECSP = *Decapoda* sp., EUCLIM = *E. limnicola*, HEMSP = *Hemigrapsus* sp., LANCON = *L. conchilega*, MALFUL = *M. fuliginosus*, MYSSP = *Mysidacea* sp., POLCIL = *P. ciliata*, PRISP = *Prionospio* sp., PSEPUL = *P. pulchra*, RUDDC = *R. decussatus*, SCHSPI = *S. spiritus*, STRBEN = *S. benedicti*, VARGIL = *V. gibba*.

34.5 and 9.3% of the macrofaunal species variability ( $p < 0.001$ ). Macrofaunal species communities have mainly been driven by the water temperature and secondly by the sand proportion in the sediment (Fig. 5). *Capitella capitata* and *M. fuliginosus* were seasonally influenced by colder waters. Though *Streblospio benedicti*, *Prionospio* sp., *Cirriiformia tentaculata*, *Pseudopolydora pulchra* were influenced by a sandier sediment, only the main species at this station, *P. pulchra*, and *C. tentaculata* did not undergo a seasonal effect (Fig. 5). Both *Mysidacea* sp. and *Decapoda* sp. were negatively correlated with the temperature of water, though the latter was slightly correlated with sandier sediments while the former had no relationship with the sand content. By being absent during spring, the distribution of *Varicorbula gibba*, *Polydora ciliata*, *Ruditapes decussatus*, *Chaetozone gibber* and *Euchone limnicola* is logically driven by the warmer water temperature of fall. *Euchone limnicola* was also correlated with sandier sediment. *Euchone limnicola*, *R. decussatus*, *A. alba*, *Chaetozone* sp. and *A. tuberculata* were positively influenced by the water temperature, except *Hemigrapsus* sp. located in the centre of the RDA because of its single occurrence (Fig. 5).

#### 4. Discussion

##### 4.1. Terrestrial and marine origin of organic matter confirm the transitional water status of the port of dunkirk

The combined information from bulk sediment parameters (TOC, TN, C:N, Chl a) and molecular biomarkers clearly shows that the Eastern Port of Dunkirk receives a complex mixture of terrestrial and marine organic matter from different sources and qualities (i.e. freshness), with pronounced spatial and seasonal variability. For instance, the organic matter in the harbor had a dominant terrestrial origin in D2 and D3 (i.e. C:N > 20) while, in other stations, it had a mixed origin with both terrestrial and marine origin ( $12 > \text{C:N} > 15$ ), with a slightly more marine origin at D6 and D7 (Meyers, 1994). The bimodal n-alkane distributions, with a first maximum in nC17 - nC18 and a second maximum in nC29, are typical of mixed inputs from phytoplankton, aquatic macrophytes and higher terrestrial plants. High values of both TAR and CPI, indices of organic matter freshness (Bourbonniere and Meyers, 1996; Cooper and Bray, 1963), particularly observed at the marina station D6 at both seasons and D1 in fall, indicates a better quality or a faster turnover of the OM, synonym of a strong and relatively fresh terrestrial contribution at these stations, consistent with inputs from the canal and urban drainage in the harbor. Also, an increase of sterols from terrestrial origin was observed in fall for most stations. This follows planktonic blooms happening during spring to early summer which undergo degradation in the sediment during late summer as well as seasonal inputs of terrestrial OM during fall due to riverine discharge and terrestrial runoff (Bodineau et al., 1999). This is further supported by the stanols:sterols ratio (Nakakuni et al., 2017), indicating a fresher OM in the harbor during spring in the harbor, as well as the pristane - phytane ratio (Pr:Ph), an indicator of oxygen conditions (Powell, 1988), which showed relatively well oxygenated conditions at D2 and D3 in spring, though there was a net decrease during fall in most of stations. This oxygen decrease after summer could be explained by microbial activity enhanced by the detritus and degradation occurring after blooms of phytoplankton and dinoflagellates (Broman et al., 2019), which dominate the contribution of sterols, noticeably the dinosterol (Amo et al., 2008; Cao et al., 2023), at all stations. On the other hand, the relative contribution of lipid biomarkers from macrophytes and C:N values at D2 and D3, particularly during spring, suggest high abundances of macrophytes at these stations (Pedersen et al., 2010; Sheppard et al., 2023), possibly favored by calmer hydrodynamic conditions.

Sedimentary chlorophyll a concentrations were generally higher in fall than in spring, reflecting the accumulation of late-summer phytoplankton and microphytobenthic production in surface sediments (Jacobs et al., 2021; Spilmont et al., 2006). The highest Chl a values at the marina stations D6 and D7 indicate a highly productive environment

where marine water from the North Sea meets waters from the Exutory channel loaded in nutrients supporting at the entrance of the marina supporting substantial primary production. At the same time, seasonal increases in TOC and TN, especially at D3, D4 and D6, show that fresh organic matter continues to settle throughout the growing season and is differentially trapped among sub-basins.

Taken together, these patterns confirm that the Port of Dunkirk meets the definition of transitional waters *sensu* the Water Framework Directive, being strongly influenced by both riverine and marine inputs, subject to hydrodynamic confinement, and characterized by high productivity. Such semi-enclosure of harbors as the industrial basin of Dunkirk of the industrial basin is prone to limiting exchanges with the sea, preventing the water renewal, and to the accumulation of organic matter and contaminants (Armynot du Châtelet et al., 2011; Ferraro et al., 2006; Francescangeli et al., 2016; González-Fernández et al., 2011; Mostafa et al., 2004) enhanced by terrestrial inputs (Mann and Lazier, 2013) from canals surrounding the city (e.g. Bourbourg, Furnes, Moëlles, Watteringues). On the other hand, the marina is directly connected to the North Sea, and thus, experiences more dynamic conditions but receives urban and sewage-related inputs. These physical and biogeochemical contrasts underpin the productivity and environmental gradients that shape observed benthic communities.

##### 4.2. The Port of Dunkirk hosts a cocktail of pollutants: contamination patterns and sediment quality

The Port of Dunkirk exhibited a steady and severe enrichment (following classification from Chen et al., 2007) in several trace metals (Cd, Cu, Fe, Hg, and Pb) mostly in the industrial basin of the harbor (D2 - D5) while the marina remains weakly enriched. The enrichment of Cd and Cu was particularly high in both seasons, especially at D5, whereas D6 and D7 in the marina show EF close to 1, indicative of near-background conditions for trace metals and elements. In line with previous observations (Geffard et al., 2002), this spatial distribution matches the functional organization of the harbor, with heavily industrial activities and chronic metal inputs concentrated in the Bourbourg channel, and predominantly recreational use in the marina.

When compared qualitatively with the Effect Range Low (ERL) and Effect Range Median (ERM) sediment quality guidelines of Long et al. (1995, 2000), metal levels in the industrial basin frequently fall within the range where the probability of biological effects increases (above ERL for Cd, Cu and sometimes Pb) and locally approach ERM, especially for Cd at some stations in fall. In contrast, sediments from the marina remain largely below effect ranges for these metals. This suggests that sublethal effects and community-level changes can be expected in the most contaminated sectors, while the risk associated with metals is comparatively lower in the marina, where organic and fecal contamination represent more prominent issues.

For instance, molecular markers related to petroleum products (hopanes, PAHs) and fecal sterols refine this picture by distinguishing different sources of organic pollution. Hopanes and PAHs, with particularly high relative abundances at D4-D5 and at D7 in fall, located either close to bulk terminals or the marina, indicate a strong influence of petroleum products and combustion residues derived from shipping, industrial activities and port discharges as well as boating. The presence of marine traffic-related pollution as well as combustion products is a common pattern worldwide (e.g. Bortali et al., 2023; Dorleon et al., 2025; Moreira et al., 2017). The distribution of fecal sterols reveals human sewage contamination, especially at the marina station D6 and at industrial stations in fall, along with a contribution from livestock or manure-derived inputs more marked at D5. The harbor of Dunkirk, located at the mouth of six canals, could be the endpoint of water runoffs from sewer systems and industrial activities, explaining why the fecal contamination is highest at D6 located in front of a canal. Moreover, commercial harbors such as Dunkirk suffer from toilet waste unloaded from ships, vessels and boats, i.e. black water, and could also explain the

presence of such contamination in the industrial basin. In addition, the harbor of Dunkirk is acknowledged to host colonies of sea birds (Caloin, 2015). These seabird colonies are an important driver of nutrients (Otero et al., 2018) and could explain the presence of animal manure in the industrial basin of harbor, where no animal-related industry exists. Overall, the sedimentary record integrates long-term industrial contamination and more recent urban and agricultural inputs, in line with other European harbors where similar mixtures of metal and organic pollutants have been reported (e.g. de Boer et al., 2001; Pérez-Fernández et al., 2019; Sprovieri et al., 2007) By integrating chemical and molecular diagnostics with quantitative benthic indicators, this study not only allows to assess the contamination intensity but also the benthic community responses.

#### 4.3. The dual nature of the Port of Dunkirk: an industrialized environment harboring high benthic diversity

Benthic foraminiferal assemblages in the Port of Dunkirk exhibit high species richness and diversity, with living densities reaching several hundred to more than one thousand individuals per 50 cm<sup>2</sup> (Table S5) at many stations. These values are comparable to, or even higher than those reported for less industrialized transitional waters of the NE Atlantic, e.g. Auray, Vie (Fouet et al., 2022) Canche, Authie, and Somme estuaries, France (Armynot du Châtelet et al., 2009; Francescangeli et al., 2020), or in the Elbe estuary, Germany (Francescangeli et al., 2021). Richness and diversity in Dunkirk were also higher than a smaller and less polluted harbor of the region, i.e. Boulogne-sur-mer, with respectively 5-10 living species and values of diversity of 5 (Armynot du Châtelet et al., 2011; Francescangeli et al., 2020). Note that all these locations were not only sampled in subtidal environments. Therefore, it indicates that foraminiferal communities are not numerically depressed by the surrounding contamination documented before. In fact, this high diversity in the harbor of Dunkirk appeared to be promoted by the high productivity in this anthropized ecosystem. Indeed, TOC values ranging from  $\approx$  3 to 4% through both seasons with a peak between 6 and 10%, is likely to enhance richness and diversity of benthic communities up to a threshold (Nilsson and Rosenberg, 2000). In fact, TOC values observed in other natural or moderately industrialized areas of the region, e.g. Somme and Canche estuaries (Armynot du Châtelet et al., 2011; Francescangeli et al., 2020) but lower than in other moderately or highly industrialized harbors of the NE Atlantic (Armynot du Châtelet et al., 2004; Daief et al., 2014; Debenay et al., 2001; Pérez-Fernández et al., 2020), suggesting that TOC never reached limiting values for benthic communities in Dunkirk harbor. Furthermore, the constant content of *Chl a* could reinforce the hypothesis of the Dunkirk harbor being a productive area as the sediment generally contained more *Chl a* than in many areas in the English Channel (Pavard et al., 2023a) or the Gironde estuary (Pavard et al., 2023b).

However, high diversity does not imply undisturbed communities. Indeed, assemblages are dominated by species widely recognized as tolerant or opportunistic, typically associated with eutrophic, organically enriched and sometimes oxygen-depleted environments. More specifically, analyses highlight the importance of seasonality (water temperature), productivity (*Chl a*), organic load, and metallic pollution (Cd) on their distribution. For instance, *Elphidium selseyense*, and *Ammonia aberdoveyensis*, the most abundant foraminiferal species in most of the stations enriched in trace metals and moderately enriched in TOC, are commonly reported in harbors and polluted areas (Armynot du Châtelet and Debenay, 2010; Francescangeli et al., 2020; Sharifi et al., 1991), though it exhibits a greater tolerance against TOC in Dunkirk than its assignment as a sensitive species in Bouchet et al. (2021). As *E. selseyense* may be a complex of cryptic species (Darling et al., 2016), it could explain discrepancy between observations of its tolerance to TOC. Being lumped into the *Ammonia tepida* morphogroup for decades (Richirt et al., 2019), little is still known about environmental drivers of *A. aberdoveyensis*. Though it is characteristic species of more natural TWs

(Pavard et al., 2023a), this species seems tolerate metal and organic enrichment consistently with previous studies (Pavard et al., 2023a, 2023b). and the ecology of the *A. tepida* morphogroup (Armynot du Châtelet et al., 2004; Bouchet et al., 2021; Francescangeli et al., 2020; Frontalini and Coccioni, 2008; Martins et al., 2015)

The highest content of TOC in sediment at D3 both in spring and fall favored the more opportunistic species, *Hopkinsina atlantica*, *Stainforthia* sp., and *S. fusiformis*. Indeed, *H. atlantica* is a low-opportunistic species responding to a fresh OM input (Diz and Francés, 2008; Goineau et al., 2012; Mojtahid et al., 2009) generally associated with freshwater discharge (Mendes et al., 2012), and therefore, highly probably to terrestrial organic matter inputs as in D3. Likewise, *S. fusiformis* presents also highly opportunistic features against organic matter enrichment, in addition to tolerating a wide range of water oxygenation (Alve, 2003; Bernhard and Bowser, 1999; Gooday and Alve, 2001). Looking at the high abundances of *S. fusiformis* in the harbor and a pattern of adult recruitment in fall after phytoplankton blooms (Filipsson et al., 2004), small individuals of *Stainforthia* sp. in spring could highly be considered as juveniles of *S. fusiformis*.

In addition to *E. selseyense*, station D7 was mainly characterized by species the *Bolivina* genus, *Bolivina pseudoplicata*, *B. variabilis*, *B. dilatata*, especially in fall. This genus is generally associated with oxygen-depleted environment and high content of mud (Armynot du Châtelet and Debenay, 2010; de Nooijer et al., 2008). Moreover, these species are described from 'indifferent' to 'tolerant' species against TOC enrichment (Bouchet et al., 2021) and sensitive to some metals contamination such as Pb, Cu or Ni (Martins et al., 2013), Consistently to environmental conditions of the marina The high *Chl a* content suggests a high primary productivity and reflects an input of fresh phytodetritus, consistent with the C:N indicating dominantly phytoplanktonic organic matter in the sediment. Such conditions are favorable to oxygen depletion or even anoxia, which is confirmed by the low Pr/Ph ratio, and explain the high abundances of *Bolivina* species, generally responding rapidly to organic fluxes and phytodetritus deposition (Alve, 1990; Debenay et al., 2001; Murray, 1991).

Rare species are present (Table S3) and contribute to species richness but occur at low densities and do not control the main community patterns. Therefore, the high diversity observed in the Port of Dunkirk should not be interpreted as evidence of an undisturbed hotspot, but rather as the result of a high number of species co-occurring in a structurally impacted ecosystem where tolerant species numerically dominate. For environmental assessment and management, this implies that simple diversity metrics may overestimate ecological quality and should ideally be complemented by sensitivity-weighted or trait-based indices for foraminifera (e.g. ForAMBI; Bouchet et al., 2021).

Macrofaunal assemblages show a similar pattern of relatively high richness and diversity compared to other natural and moderately anthropized TWs of NE Atlantic, i.e. 5-15 species (Boutoumit et al., 2022; Rolet and Luczak, 2014; Sánchez-Moyano et al., 2010; Zettler et al., 2017). though, with a clear seasonal signal. Richness and Exp ( $H'_{bc}$ ) are significantly higher in fall than in spring, potentially reflecting the influence of water temperature, sediment conditions and life cycles of macrofaunal communities such as the recruitment periods of juveniles in spring and early summer in NE Atlantic TWs (Reiss and Kröncke, 2004; van der Wal et al., 2008). The almost azoic samples collected at D6 and D7 in fall for macrofauna can be explained by frequent dredging in the marina to unclog navigation channels for ships and boats (PERS, 2019), which is a known anthropic pressure on benthic communities (Guerra-García et al., 2003; López-Jamar and Mejuto, 1988; Thrush and Dayton, 2002). Conversely, benthic foraminifera were less affected as they are known to recolonize the nearest ambient seafloor in a shorter transit time in high energy environments (i.e. within days, Alve, 1999), thus explaining the foraminiferal presence but with a lower diversity compared to the inner stations.

As for foraminifera, almost all main species of benthic macrofauna assemblages described at both seasons appeared to be commonly

observed in the English Channel in stressed environments. Indeed, *Abra alba*, *Capitella capitata*, *Chaetozone gibber*, *Ruditapes decussatus*, *Streblospio benedicti*, *Varicorbula gibba* are widely reported across the area (Beck et al., 2015; Dauvin et al., 2017, 2003; Rolet and Luczak, 2014). Additionally, faunal assemblages were sometimes characterized by species more or only present at one season, the macro-invertebrate species *Malacoceros fuliginosus*, *Schistomysis spiritus* and *Cirriiformia tentaculata*, a pattern commonly observed in TWs (Camacho et al., 2015; Debenay et al., 2006; Rodil et al., 2008; Ysebaert and Herman, 2002).

The seasonality, assessed by measuring water temperature, explained most of the variability of macrofaunal species' distribution in the harbor of Dunkirk, and was followed by the sand content in the sediment. For instance, the complex of polychaetes *Capitella capitata* is widely observed in disturbed environment (Méndez et al., 1997; review in Tsutsumi, 1987; Warren, 1977). In addition, its highest abundance peak in literature has always been reported in spring or early summer (Martin and Bastida, 2006; Méndez et al., 1997; Tsutsumi, 1987) congruently to this study. Likewise, another polychaete, *Streblospio benedicti*, has been reported to be highly tolerant to several types of pollution in transitional waters, e.g. OM enrichment, metallic pollution or PAH (Chandler et al., 1997; Ferrando and Mendez, 2011; Kihlslinger and Woodin, 2000), but is also positively correlated to the percentage of sand, negatively correlated with reducing conditions as well as observing recruitment in spring (García-Arberas and Rallo, 2004). This was verified in the harbor of Dunkirk, where this species was more abundant in spring, in more oxygenated conditions than fall, and was positively influenced by the sand content. More sparsely occurring species as *Acanthocardia tuberculata* and *Ruditapes decussatus* are also typical bioindicators for trace metal enrichment (Esposito et al., 2018; Grassle and Grassle, 1974). These species, mostly present during fall in the harbor, have both a recruitment period occurring from summer to fall (Matias et al., 2013; Tirado et al., 2017), which fits with observations from this study. *Abra alba*, *Polydora ciliata*, *Chaetozone gibber*, as well as *Varicorbula gibba* are all characteristic species of an OM enrichment in polluted areas (Borja et al., 2000; Hily and Le Bris, 1984; Hrs-Brenko, 2006), especially the two latter species, present at D3 during fall, the most TOC-enriched station of this study. All of them also had a better affinity with the temperature of the water and subsequently to the fall season.

Overall, both foraminifera and macrofauna demonstrate that the Port of Dunkirk supports rich and abundant benthic communities despite severe environmental constraints. This resilience, however, is largely mediated by the success of opportunistic and disturbance-tolerant species and therefore should not be equated with high ecological quality in the conventional sense.

#### 4.4. Non-indigenous species (NIS) occurrences support the high harbor diversity and the need to better monitor these highly urbanized ecosystems

In addition to observations of typical stress tolerant species, the occurrence of several non-indigenous or cryptogenic species never observed either in Europe, France or in the English Channel - Southern North Sea area in both foraminiferal and macrofaunal assemblages confirms the role of the Port of Dunkirk as a gateway for NIS introductions. For instance, macrofaunal NIS observed in this study, i.e. *Hemigrapsus* sp., *Euchone limnicola* and *Arcuatula senhousia*, are not their first report in the region. Indeed, the two NIS of *Hemigrapsus* known in Europe, *H. takanoi* and *H. sanguineus* are established in the English Channel since they were introduced in 1999 (Breton et al., 2002; Dauvin et al., 2009; Gothland et al., 2014), while the two other species originating from the Pacific Ocean have been previously reported in Dunkirk in 2015 and 2018 (Guyonnet and Borg, 2015; Massé et al., 2022), respectively, and may have settled following observations from the present study.

On the other hand, the benthic foraminifera *Virgulinitella fragilis* is a common species in Asia, has been recorded in New-Zealand, Namibia

and Peru (review in Tsuchiya et al., 2009) and only a few individuals have been recorded in Italy very recently (D'Onofrio et al., 2025), which makes it here its first observation in the NE Atlantic. This species typically occurs in oxygen-depleted environments (Cardich et al., 2015; Leiter and Altenbach, 2010; Takata et al., 2005), in line with observations at D1 in Fall where it reaches its maximal abundance (Table S3), though it is a shallow water environment. This study is the first report of the foraminifera *Spirobolivina* sp., in Europe and therefore could be considered as NIS. Indeed, the genus *Spirobolivina* has been reported only once alive in Tunisia (Martins et al., 2017). Though it is impossible to enquire about the origin of this species, our results suggested that it presents tolerance characteristics to eutrophication as it occurred together with *S. fusiformis* and *H. atlantica*.

The presence of the NIS *A. confertitesta* is particularly noteworthy but must be interpreted with caution. This species has been lumped into the cryptic complex of *A. tepida* and is morphologically very similar to the native species *A. veneta* and *A. aberdoveyensis*, and a more reliable discrimination generally requires detailed SEM and molecular data (e.g. Richirt et al., 2019, 2021; Hayward et al., 2021). In this study, identification was based mainly on light-microscope morphology (Pavard et al., 2021), and we therefore acknowledge that some uncertainty inherent to the stereomicroscope method remains regarding the exact taxonomic status of the *Ammonia* morphotypes. However, the presence of this species has been well documented in Europe since the last few years (Bird et al., 2020; Hayward et al., 2021; Pavard et al., 2023a; Richirt et al., 2021; Saad and Wade, 2016) and has been often found in or close to harbors (Pavard et al., 2023a), suggesting that it can cope with the peculiar environmental features of these artificial ecosystems. For instance, recent records of *A. confertitesta* in the Baltic Sea indicate that it thrives under low pH, low oxygen and metal-polluted conditions (Szymańska et al., 2025), which closely resemble conditions encountered in the harbor of Dunkirk, though it was less abundant at high levels of organic and metal pollution. Moreover, this species possesses the ability to accumulate intracellular phosphate and use it as an energetic compound in oxygen depletion settings, which can favor its fitness in such impacted environments as the harbor of Dunkirk (Glock et al., 2025). Thus, its presence is consistent with its known ecology and may simply reflect the spread of stress tolerant species through shipping rather than a new management issue specific to this harbor. Moreover, given its pseudo-cryptic character, it cannot be excluded that the species has been historically overlooked in the region and misidentified in earlier studies, further arguing for a prudent interpretation of its biogeographic and conservation significance.

We therefore consider the NIS evidence as an additional illustration of the role of large harbors as hubs for the dispersal of tolerant benthic taxa, and as an argument for including advanced taxonomic tools within harbor monitoring schemes, rather than as a standalone driver of new management measures in the Port of Dunkirk. Moreover, this study could serve as baseline for future NIS surveys to monitor plausible settlements of those species over time.

#### 4.5. Assessment of benthic community patterns: a first step to align the Port of Dunkirk with biodiversity conservation

Several limitations should be acknowledged when interpreting our results in an environmental management context. First, we did not include an external reference site outside the harbor area; instead, we compared Dunkirk assemblages with published datasets from other North-East Atlantic transitional waters sampled at comparable depths and seasons. Second, sampling was restricted to two seasons in a single year and to the 0-1 cm surface layer, providing a snapshot of the present-day communities rather than a full multi-annual or vertical perspective. For these reasons, our conclusions should be regarded as preliminary evidence that industrial harbor basins can host diverse and resilient benthic communities under chronic contamination, and as a starting point for designing longer-term monitoring programs that incorporate

reference sites and deeper sediment intervals.

Harbors such as the Port of Dunkirk are routinely dredged to maintain navigation (4,000,000 m<sup>3</sup> of sediment every year; Herman et al., 2014), raising questions about safe disposal and beneficial use of contaminated sediments. Our combined chemical and biological dataset provides a baseline for classifying dredged material from different sub-basins (e.g. Cd- and Cu-enriched industrial sites versus the relatively less contaminated marina) and supports an assorted approach in which sediments from hotspots such as D3 are prioritized for confined disposal or treatment, whereas material from D6 and D7 could be candidates for less restrictive uses, provided organic and fecal contamination are addressed. This is consistent with risk-based sediment management frameworks applied in the Seine estuary, Dunkirk and other French harbors (Carpentier et al., 2002; Junqua et al., 2006; Montigny et al., 2025), where occurrence of adverse biological effects is weighed against guideline exceedance before authorizing disposal.

From a conservation perspective, the coexistence of high macro and meio-benthic diversity, though species are considered tolerant, with significant metal and organic pollution challenges the perception of industrial harbors as sacrificed ecosystems devoid of ecological value. In the context of the French national strategy for commercial harbors (CIMer, 2021) emphasizing biodiversity protection and restoration, our results indicate that harbor basins cannot be managed solely as industrial infrastructures but should also be recognized and monitored as biodiversity reservoirs that support ecosystem functions and services. Integrating benthic indicators, such as foraminiferal and macrofaunal metrics, into existing environmental monitoring strategies would improve the ability of port authorities to track both contamination and biological resilience over time. In fact, by deploying adequate benthic diversity monitoring, industrial harbors can gain a deeper understanding of their benthic habitats, drive effective management strategies, and promote sustainable practices that benefit both local ecosystems and broader conservation goals. In urban ecosystems such as ports, the use of robust bioindicators like benthic foraminifera and macro-invertebrates is essential for harbor stakeholders to assess the effectiveness of different conservation approaches and encourage good practices, for example, through the certification “Clean Harbors active in biodiversity” (AFNOR Certification, 2024) aiming to align harbor operations with biodiversity conservation. The harbor of Dunkirk, like all harbors in the eastern English Channel, does not currently hold this certification. This study provides a baseline assessment aimed at defining a reference state that could support future certification efforts.

The occurrence of putative non-indigenous taxa, including *Ammonia confertitesta*, further highlights harbors as gateways for species introduction (e.g. Ferrario et al., 2017; Floerl et al., 2009; Katsanevakis et al., 2013), even when local communities remain dominated by stress-tolerant native species and cryptogenic species. However, given the pseudo-cryptic nature of *A. confertitesta* and the reliance on morphology alone in the present study (following Pavard et al., 2021), the management message is less about a single NIS and more about the need to implement routine and integrative surveillance (e.g. combining morphological, SEM and molecular tools) in harbor monitoring programs. Such approaches would allow early detection of genuinely invasive foraminiferal species and better evaluation of their contribution to local biodiversity and ecosystem functioning.

## 5. Conclusion

This study shows that the Port of Dunkirk functions as a highly productive transitional water ecosystem, where mixed terrestrial-marine organic inputs, strong seasonal phytoplankton dynamics and localized faecal contamination coexist with severe enrichment in organic matter, trace metals and petroleum-derived compounds in the industrial basin. Despite these multiple anthropogenic pressures, benthic foraminiferal and macrofaunal richness and diversity were comparable to, or even higher than, those reported from less

industrialized transitional waters of the NE Atlantic, indicating that diverse assemblages can persist in heavily modified harbor ecosystems, even though dominating species are stress tolerant and opportunistic species. Species distribution was primarily controlled by sediment grain size, chlorophyll *a*, organic matter content and cadmium, with foraminifera tightly linked to pollution gradients and macrofauna more responsive to seasonal features, underscoring the value of combining both groups for ecosystem assessment.

The dominance of typical coastal and transitional-water taxa, together with the presence of several non-indigenous species in both meio- and macro-benthic compartments, highlights harbors as simultaneously important and peculiar biodiversity reservoirs and key gateways for bioinvasion. These findings support the view that industrial harbors should no longer be regarded as sacrificed ecosystems but as priority sites for integrated monitoring that couple contaminant metrics, organic matter characterization and faunal indicators to inform science-based dredging practices, biodiversity conservation and NIS management. In this perspective, Dunkirk provides a robust baseline for evaluating long-term ecological trajectories in heavily modified water bodies and for designing environmental management strategies that reconcile economic activities with the preservation of benthic biodiversity.

## CRedit authorship contribution statement

**Jean-Charles Pavard:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Camille Hennion:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Apolyne Courleux:** Writing – review & editing, Data curation. **Françoise Henry:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Armelle Riboulleau:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Vincent M. P. Bouchet:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jean-Charles Pavard reports financial support was provided by Water Agency Artois-Picardie. Jean-Charles Pavard reports was provided by Regional Water Agency Seine-Normandie. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

Thanks to the crew of the Oceanographic Vessels Sepia II and Celtic Warrior for their help during sampling, Romain Abraham for grain size analyses and Gwendoline Duong for the organic matter data. Jean-Charles Pavard thanks the Agence de l'Eau Artois-Picardie and the University of Lille for funding its PhD fellowship. This work is part of the Foram-INDIC project funded by the “Agence de l'Eau Artois Picardie” and the “Agence de l'Eau Seine Normandie” (Grants No. 58183 and No. 1082222)2019, respectively). This work benefited from the technical support of the EMIMA experimental platform and CHEVREUIL Institute from the University of Lille.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2026.129893>.

## Data availability

The authors are unable or have chosen not to specify which data has been used.

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