



Comparison of Living and Historical Benthic Foraminifera: Environmental Factors and Anthropogenic Impacts in a Northern Adriatic Lagoon (Italy)

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Abstract

Lagoons are transitional ecosystems characterized by high natural variability in terms of salinity, oxygenation, and nutrient availability, which creates complex ecological conditions and a delicate biological balance. This variability often results into low ecological quality indices, therefore discriminating between natural and anthropogenic stress remains a challenge, particularly when using benthic foraminifera as bioindicators. The Marano and Grado Lagoon (northern Adriatic Sea, Italy) is a shallow coastal system generally considered well preserved, despite long-standing human activities and historical mercury contamination in its eastern sector. This study presents investigations of living benthic foraminifera and integrates modern assemblage analysis with sediment core data. The assemblage is dominated by *Ammonia tepida*, *Haynesina germanica*, *Aubignyna perlucida*, and *Criboelphidium gunteri*, which are positively correlated with total organic carbon, while *Ammonia parkinsoniana*, *Quinqueloculina* spp., and agglutinated taxa are mainly related to salinity. Shell deformities, especially in *Ammonia* spp. and *C. gunteri*, are widespread. Cluster analysis evidenced three main assemblages: **urban** (*Haynesina germanica* dominant), **inner** (*H. germanica* with *Aubignyna perlucida* dominant) and the **outer lagoon** (*A. parkinsoniana* dominant) biotopes, with reduced ecological quality in the inner sectors. A sediment core was used to explore the potential impact of recent anthropogenic disturbances. The deformation index exhibits increasing trend since the mid-18th century, before the major anthropogenic impacts, suggesting a predominantly natural control. Overall, results indicate that the moderate ecological status of the inner lagoon is mainly driven by natural stress, in agreement with the ‘estuarine quality paradox’, although intensified anthropogenic use may have influenced sensitive species distributions.

Introduction

Lagoons are unique ecosystems whose ecological equilibrium supports a wide range of organisms. They represent transitional water environments including fjords, deltas, and estuaries, where strong variability in salinity, oxygen, nutrients, and other factors create complex patterns of confinement that reflects the influence of both marine and

freshwaters exchanges (McLusky & Elliott, 2007). These high dynamic transitional environments (TEs) are of major ecological and economic importance and are regulated internationally under the European Water Framework Directive (WFD) (2000/60/EEC) within the category of transitional waters with the objective to achieve ‘good ecological status’ by 2027.

Lagoons and other coastal marine habitats have been heavily exploited in recent decades, causing negative effects on the aquatic ecosystem. By examining the biological responses of animal and plant species is possible to identify biological indicators (or bio-indicators) that detect human-induced alterations. Among these, benthic foraminifera, single-celled protists with rapid growth, small size and fossilisable test, are well-established indicators of anthropogenic stress in marine ecosystems (see for example Frontalini & Coccioni, 2011; Romano et al., 2016; Bouchet et al., 2018, 2023; Francescangeli et al., 2020; Franzo et al.,

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2023; Tavera Martinez et al., 2023; Joshi et al., 2025). In recent decades, interest in benthic foraminifera as bioindicators in marine environments has gradually increased.

Although the dispersal of foraminifera in modern environments is limited by several factors, including salinity and sediment texture (e.g., Horton & Murray, 2007; Armynot du Châtelet et al., 2009), their interaction with organic matter - and thus the trophic state - is deemed crucial for assessing the ecological quality of the environments (EcoQS) (e.g., Bouchet et al., 2021; O'Brien et al., 2021; Fouet et al., 2022). The FOBIMO (Foraminiferal Bio-Monitoring) international working group attempts to determine the ecological response of foraminifera to total organic carbon (TOC), defining their sensitivity and tolerance levels by assigning species to ecological groups (EGs) (see Alve et al., 2016; Jorissen et al., 2018).

The increasing knowledge of this group has allowed the establishment of several biotic indices based on the degree of sensitivity of certain species to diverse contaminants affecting marine and transitional environments (Alve et al., 2016; Dimiza et al., 2016; Jorissen et al., 2018; Fouet et al., 2022, and review papers by O'Brien et al., 2021 and Parent et al., 2021). Notably, Bouchet et al. (2021) conducted key studies on species from European intertidal environments.

In TEs, the use of these indices remains debated because strong natural environmental variability can generate stress signals and low-quality indices even when the ecosystem is actually healthy. This phenomenon is known as 'estuarine quality paradox' (e.g., Elliott & Quintino, 2007). The challenge is to identify the stress induced by the natural environment, distinguishing it from that resulting from anthropic influence. Historical data on sediments prior to local anthropogenic activity may help resolve this issue. The distribution of foraminifera is particularly useful for detecting alterations associated to both contemporary or historical human activities (see discussion in Bouchet et al., 2021; O'Brien et al., 2021).

Accurate application of foraminifera-based biotic indices requires a solid understanding of their natural distribution, as highlighted for example by Elliott and Quintino (2007) and Fouet et al. (2022). This study examines living foraminifer assemblages from seventeen stations in the two sectors of the Marano and Grado Lagoon (northern Adriatic Sea). This work represents one of the first investigations of the living foraminiferal fauna of this lagoon, as previous studies have focused exclusively on the thanatocoenosis (Melis & Covelli, 2013). The main objectives of this study are:

i) to describe the distribution of the dominant living foraminiferal species in two lagoon sectors with different degrees of confinement to the sea;

ii) to assess how fluctuations in bottom water parameters (salinity, temperature, dissolved oxygen, pH), sediment composition, total organic carbon (TOC), redox potential (Eh) and total mercury (THg) concentrations affect species distribution, abundance, and possible deformities in foraminiferal tests;

iii) to provide new information into the ecological group (EG) assignments of key species in comparison with Bouchet et al. (2021), and to evaluate the ecological quality status (EcoQS) of the sampled environments using biotic indices based on the foraminiferal biocenosis;

iv) to compare present-day—though partly anthropised—conditions with historical settings preceding the industrial impact. For this purpose, a sediment core (G3) collected from the eastern sector of the lagoon (Grado) was studied, as part of broader sets of cores analysed within the MIRACLE project (Covelli, 2012), which investigated the Hg biogeochemical cycle and the possible coexistence of clam farming with sediment contamination.

Study Area

The Marano and Grado Lagoon (hereafter MGL) is a lentic micro-tidal lagoon (*sensu* McLusky & Elliott, 2007), and is part of the extensive system of transitional environments of the northern Adriatic Sea (Italy). Covering an area of 160 km², the MGL extends for almost 32 km between the deltas of the Tagliamento and Isonzo Rivers, with an average width of 5 km. It features a complex system of tidal flats, tidal channels and subtidal zones (Triches et al., 2011). Except for the main channels, the average depth is 1.1 m. The lagoon is divided into two geomorphologically distinct sub-basins. The Marano Lagoon, located to the west, is a semi-enclosed tidal basin with few emergent areas that receives freshwater from several spring-fed rivers (Stella, Turgnano, Zellina, Cormor, and Aussa-Corno). To the east, the Grado Lagoon includes numerous islands and tidal marshes and is fed solely by the Natissa River. Salinity in the MGL varies with freshwater inputs, tides, and wind. The western Marano sector shows lower salinity (17.0 ± 8.65 PSU) than the eastern Grado sector (29.3 ± 4.63 PSU) because of higher river inflow in Marano (Pittaluga et al., 2022). Salinity in the Grado sector is also more stable over short- and long-term periods (Ferrarin et al., 2010).

The MGL connects to the Adriatic Sea through six tidal inlets (Lignano, S. Andrea, Buso, Morgo, Grado, and Primero), which enable tidal-driven water circulation. The lagoon has a semi-diurnal tidal regime with a mean range of 0.65 m, exceeding 1 m during spring tides (Dorigo, 1965).

Tides and E–NE winds (Bora) are the main drivers of internal circulation. The sedimentary contribution of the rivers flowing into the lagoon consists of fine suspended matter originating from material washed out from the groundwater table (Piani et al., 2005). However, the sea, through the tidal inlets, is an important supply of sediment, transporting silty and clayey particles from the two main river deltas and sand from the erosion of the barrier islands (Brambati, 1970). Weather and high tides often slow downflow, moreover, dry times cause thermohaline stratification, displaying a net salt-wedge tip.

The MGL is a well-preserved Mediterranean wetland protected by the Ramsar Convention since 1971 and designated as a Site of Community Importance (SCIs-IT3320037) within the ‘Natura 2000’ network. Although considered an area where conservation coexists with activities such as fishing, clam harvesting, shipping, and industry, the lagoon—especially the eastern Grado sector—is known to be contaminated by Hg. This contamination mainly originates from the transport of Hg-enriched material by the Isonzo River from the Idrija Hg mining district (Slovenia), active for more than 500 years until 1995. A second and less relevant Hg source was represented by past uncontrolled wastewater discharges from the chlor-alkali plant of the Torviscosa (Italy) chemical complex into the Aussa River from 1949 to 1984. Sediment analyses show a decreasing east-to-west gradient of total Hg, present mostly as cinnabar (α -HgS) in the central and eastern zones and with increasing amounts of non-cinnabar forms bound to fine sediment and organic matter in the western sector of the lagoon (Acquavita et al., 2012; Covelli et al., 2012; Bettoso et al., 2023).

Additional anthropogenic pressures include tourism, fishing and aquaculture. In recent years, new marinas have been created near the mouths of rivers flowing into the lagoon and along its perimeter. Increased motorboat traffic has caused erosion, reduced oxygen saturation, and further environmental stress.

Sampling strategy and Methods

Seventeen stations were sampled in the MGL by means of a pontoon boat for the collection of the main physico-chemical water column parameters and bottom sediments. Thirteen samples were collected during the late spring and summer of three years (2020, 2021 and 2022) to cover a transect from the Natissa River to the Morgo inlet of the Grado sector. Four samples were added in spring 2023 in front of the Stella River (Marano sector, Fig. 1; Table 1). Given the average tidal range of 0.65 m, two stations are located in the intertidal zone (GR5 and GR7), and the remaining stations in the subtidal zone (Table 1).

At each station, a multi-parameter probe (HI98194, Hanna Instruments) was employed to assess the physico-chemical parameters of the surface and the bottomwater, including temperature, salinity, pH, and dissolved oxygen. Temperature and salinity were measured throughout the water column at six stations (MA1, MA3 and MA4 – Marano sector; GR1, GR6 and GR11 – Grado sector) selected to exemplify the environmental variability of the lagoon using a CTD probe (H₂O multiprobe, Hydrolab).

A 5-litre Van Veen grab was used to collect bottom sediments. Avoiding mixing the sediment, it was carefully placed in a tray for subsequent sampling to study both foraminifera and sediment properties. The sediment from each station was sampled twice inserting perpendicularly to the surface a Perspex pipes (inner $\varnothing = 5.3$ cm) for microorganisms and sediment characteristics, respectively. The first two centimetres from each core were extruded from the pipe and immediately sliced on board into 1 cm thick layers (0–1 and 1–2 cm) using a thin metal plate. At each station, the presence of a thin layer of more oxidized sediment on the surface (2–3 mm thick) was observed. Since the 0–1 cm layer includes the transition from oxidized to more reduced conditions, which is difficult to measure, Eh was determined by inserting a specific probe (Crison pH 25) directly at a depth of 1–2 cm.

The samples for benthic organisms were stored in plastic bottles, filled in with 20 ml of preservative solution (2 g of Rose Bengal per litre of ethanol at 95%), and marked to calculate the sediment volume. They were gently shaken to obtain a homogeneous mixture and transported to the laboratory for further processing.

Aliquots of 15–20 g of fresh sediment samples were used for grain-size determinations after a 24 h treatment with hydrogen peroxide (H₂O₂, 10%) to remove most of the organic matter. Samples were then wet-sieved to 2 mm and the passing fraction was analysed using a laser granulometer (Malvern Mastersizer 2000, Malvern Panalytical Ltd.). Sand and mud classes were determined using the Udden-Wentworth (Wentworth, 1922) grain-size classification. The samples were then classified according to Shepard (1954). Sample aliquots for sediment chemical analysis were frozen and freeze dried (CoolSafe 55–4 SCANVAC), sieved from 2 to 0.42 mm to remove organic debris and finely ground in an agate mortar for an optimal homogenisation. Total organic carbon (TOC) and total nitrogen (TN) contents were determined as the mean value of 2 subsamples from the same core using an Elemental Analyser (ECS 4010 CHNSO) and acetanilide as a standard for calibration. Before the analysis, the samples were progressively acidified with HCl 0.1–1.0 N (Hedges & Stern, 1984).

Total Hg (THg) concentrations were determined by means of atomic absorption spectrophotometry using a

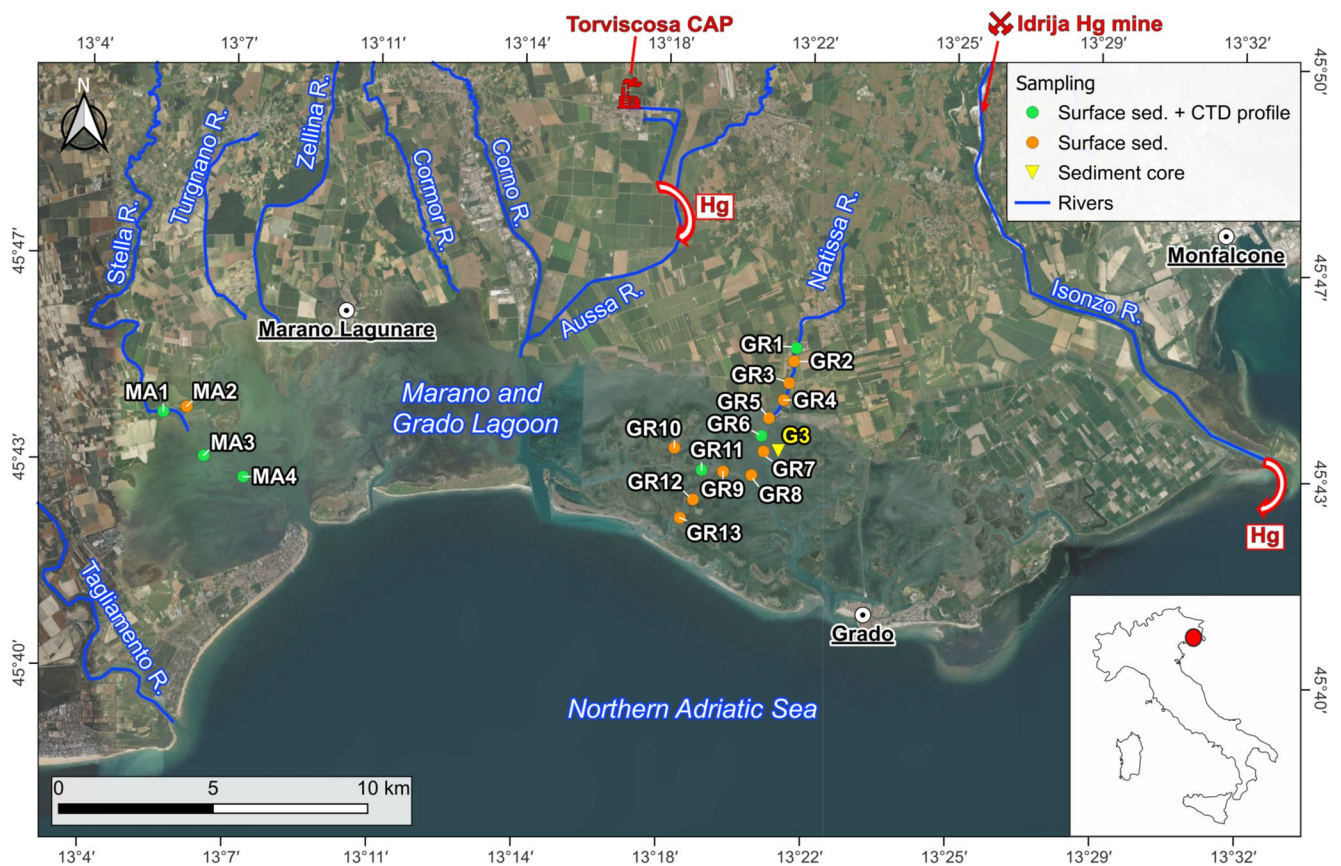


Fig. 1 Study area in the Marano and Grado Lagoon (MGL), showing surficial sediment sampling stations (dots) and sediment core G3 (triangle). GR samples are from the Grado sector, whereas MA samples

are from the Marano sector. The main sources of anthropogenic inputs of total Hg are shown

Table 1 List of studied stations including the core G3, geographic coordinates, sampling depth, and sampling year. GR refers to the Grado sector, while MA to the Marano sector. The asterisks mark the six sites at which temperature and salinity were measured throughout the water column by using a CTD probe

Station	Latitude N	Longitude E	Depth (m)	Sampling year
GR1*	45° 45' 24"	13° 21' 17"	2.3	2020
GR2	45° 45' 10"	13° 21' 14"	2.2	2021
GR3	45° 44' 47"	13° 21' 7"	2.7	2020
GR4	45° 44' 29"	13° 21' 00"	2.4	2022
GR5	45° 44' 10"	13° 20' 38"	0.7	2020
GR6*	45° 43' 51"	13° 20' 27"	3.0	2020
GR7	45° 43' 35"	13° 20' 31"	0.5	2022
GR8	45° 43' 10"	13° 20' 13"	1.0	2020
GR9	45° 43' 20"	13° 20' 37"	1.5	2022
GR10	45° 43' 37"	13° 18' 17"	3.2	2021
GR11*	45° 43' 14"	13° 18' 59"	2.8	2020
GR12	45° 42' 43"	13° 18' 47"	3.2	2020
GR13	45° 42' 24"	13° 18' 28"	3.0	2020
MA1*	45° 44' 3"	13° 5' 31"	4.2	2023
MA2	45° 44' 9"	13° 6' 6"	2.0	2023
MA3*	45° 43' 18"	13° 6' 34"	0.8	2023
MA4*	45° 42' 58"	13° 7' 32"	1.4	2023
core G3	45° 43' 59"	13° 20' 88"	1.0	2008

Direct Mercury Analyser (DMA-80, Milestone) according to US-EPA Method 7473 (US-EPA, 1998). The limit of detection (LOD) of the determination was approximately 0.005 ng of Hg. The accuracy of the method was evaluated through the analysis of a certified reference material (PACS-3, Marine Sediment Certified Reference Material, NRCC, Canada; $\text{Hg} = 2.98 \pm 0.36 \text{ mg/kg}$) in the same batches of the samples, obtaining acceptable recoveries (88–96%) and a precision, expressed as RSD, $< 3\%$.

The foraminiferal samples were left for at least 14 days in Rose Bengal solution, following the recommendation of Schönfeld et al. (2012), then wet-sieved over a 63 μm mesh. The sediment volume was detected subtracting the known preservative volume from the total sediment + preservative volume. The total fraction of sand was used for picking all live (Rose Bengal stained) benthic foraminifera. The subsamples 0–1 and 1–2 cm were treated separately for living foraminifera, to highlight the possible difference between the two levels. The “complete living assemblage”, considering the sediment levels 0–1 and 1–2 cm of each sample as an only assemblage (0–2 cm) was used to describe foraminiferal density and compare it with bottom water column parameters.

The core G3 located in front of the Natissa river’s mouth (Fig. 1) was studied to compare the present-day with paleoenvironment conditions of the past. Ten levels, one cm-thick, corresponding to the same core levels studied by Covelli et al. (2012), were chosen to include pre- and post-industrial activities due to the historical supply of THg from mining and industrial sources.

The short-lived radionuclide ^{210}Pb ($t_{1/2} = 22.3$ years) was used to estimate the sediment accumulation rate and the age of core G3 using the Constant Flux-Constant Sedimentation model (Robbins, 1978), based on excess ^{210}Pb activity-depth profiles below the mixed surface layer. The peak of the artificial radionuclide ^{137}Cs ($t_{1/2} = 30.2$ years), clearly identifiable in the sediments of northern Adriatic Sea due to the radioactive fallout from the Chernobyl disaster in April 1986, was used to validate the results (Covelli et al., 2012).

The foraminiferal taxonomy follows the Mediterranean studies of Jorissen (1987); Albani and Serandrei Barbero (1990); Sgarrella & Moncharmont-Zei (1993); Melis and Covelli (2013) and the estuarine foraminiferal guide of Jorissen et al. (2023). *Ammonia* is one of the genera most prominently represented in our study. Its identification is often difficult due to significant morphological diversity (ecophenotypic variations) and the presence of several species that, despite exhibiting similar morphological traits, differ genetically (cryptic species). The latest studies by Richirt et al. (2021) and Fouet et al. (2022) offer valuable recommendations for distinguishing the species, which are, however, classified at phylogenetic level (T). Considering

that these works generally concern areas outside the Mediterranean and based on the fact that a genetic review of this type has not yet been conducted in the Mediterranean, it was decided to follow the *Ammonia*’s taxonomy proposed by Schönfeld et al. (2021) who worked in a coastal sector of the central Adriatic Sea. Following these authors, we recognised *Ammonia tepida*, aware that this species, although acknowledged globally, has never been genetically mapped in the Mediterranean. Hayward et al. (2025) was used to recognize Elphidiidae and Cribroelphidiidae species. All the specific names are aligned with the World Register of Marine Species (WoRMS, 2025).

Four faunal parameters were calculated: (1) number of species (S), (2) foraminiferal density, as the number of specimens normalised to 50 ml (hereafter FD), (3) biased-corrected Shannon index (H'_{bc} , *sensu* Chao & Shen, 2003) and 4) $\text{Exp}(H'_{bc})$ index (Hill, 1973), which is the exponential function of the bias-corrected Shannon (H'_{bc}) used to define the true diversity; $\text{Exp}(H'_{bc})$ represents the number of species that, if uniformly distributed, would result in an equivalent H'_{bc} to that of the sample (see Bouchet et al., 2012, p. 68 for discussion). H'_{bc} and $\text{Exp}(H'_{bc})$ were calculated using the SpadeR package (Chao et al., 2015). The weighted-averaging (WA) optimum and tolerance were calculated for each living species to assess preference to the environmental parameters (S, T, pH, sand, TOC %) using the optimos.prime R package (Sathicq et al., 2020). The software estimates species optima and tolerance ranges by weighting occurrences, even when taxa are unevenly represented. These predicted optima help objectively define each species’ ecological requirements. The Foraminiferal Abnormality Index (FAI), defined as the percentage of abnormal specimens within the assemblage, was computed for every sample to evaluate anthropogenic and/or natural disturbances in the study area following Frontalini and Coccioni (2008); Coccioni et al. (2009) and Melis and Covelli (2013).

The Bray-Curtis similarity index (Bray & Curtis, 1957), calculated using the PAST4.17 software (Hammer et al., 2001), was used to compare the two investigated layers (0–1 and 1–2 cm) at each station based on the density (specimens/50 ml) of each species.

A cross-correlation was utilized to investigate the relationship between the absolute abundance of species in the 0–2 cm sediment layer, the sediment texture and the features of the bottom water column. The Spearman’s rank correlation was employed due to the majority of variables not passing the Shapiro–Wilk test for normality. This non-parametric method is more reliable than Pearson’s for non-linear data (see Francescangeli et al., 2020). A principal component analysis (PCA) was conducted on standardised abiotic data, including sand, silt, clay and TOC percentage, redox potential (Eh), THg content in sediments, and salinity,

temperature, dissolved oxygen (DO), and pH in the water column as primary variables. The biotic indices (FD, FAI %, number of species, and $\text{Exp}(H'bc)$), together with the relative abundance of benthic foraminiferal species found at a minimum of two stations, were incorporated as secondary variables. Since the latter are dependent variables on the abiotic parameters, they do not contribute to the distribution on the factor plan. PCA was conducted using the Addinsoft XLSTAT_2020 program.

A Q-mode cluster analysis was conducted to examine the similarity across the stations focusing on species with a relative abundance of no less than 3%, leading to the keeping of 19 species/groups. An additive logarithmic transformation $\log(1+x)$, where x represents the percentage of each species, was applied before the cluster analysis to reduce the interdependence among the species according to Frontalini et al. (2013). The Complete Linkage clustering algorithm utilising the Bray-Curtis distance correlation coefficient was used; the analysis was conducted with the PAST4.17 software (Hammer et al., 2001). Taxa present only once and stations having a total specimen count of ≤ 20 (stations GR3 and MA1) were excluded from both the PCA and cluster analysis, in order to reduce the background 'noise'.

Results

Environmental Data

Temperature and salinity profiles reveal thermo-haline stratification in both the Natissa and Stella Rivers (Fig. 2a, d). In each case, tidal dynamics produce a saltwedge, with slightly cooler freshwater flowing above warmer saltwater. This pattern is most evident in the Natissa River (station GR1, Fig. 2a), where a 0.6 m freshwater layer (4.7–6.9 PSU) overlies a 1.2 m saltwater layer (25.1–28.3 PSU). Temperatures follow the same trend, ranging from 18.3 to 18.9 °C at the surface to 23.8–24.3 °C at depth. The Stella River (station MA1, Fig. 2d) shows similar vertical variation but weaker water stratification. Surface salinity remains < 2 PSU down to ~ 1.1 m, then gradually increases to > 10 PSU below ~ 2.8 m, reaching 12.8 PSU near the bottom (4.2–4.4 m). Temperature varies little (14.3 °C near the surface to 15.1 °C at depth).

In both eastern and western sector of the lagoon, two vertical profiles were recorded, one in the inner part near the river mouths (stations GR6 – Fig. 2b and MA3 – Fig. 2e, respectively) and one in the outer part (stations GR11 – Fig. 2c, and MA4 – Fig. 2f, respectively). Profiles from the eastern lagoon show higher water temperatures and salinity throughout the water column (Figs. 2b and c) than those of the western sector (Figs. 2e and f). Temperature varied little

with depth, averaging 23.3 ± 0.4 °C (inner) and 25.1 ± 0.4 °C (outer) to the east, and 16.6 ± 0.6 °C (inner) and 16.8 ± 0.2 °C (outer) to the west. Salinity vertical profiles highlight the influence of freshwater inputs in the western lagoon. In this sector, surface salinity was relatively low (9.1–22.9 PSU at MA3, Figs. 2e and 14.6–32.1 PSU at MA4, Fig. 2f) and increased with depth, interestingly exceeding 30 PSU only near the sea at depths > 0.6 m (Fig. 2f). In the eastern lagoon, only the upper 0–0.6 m layer at station in front of Natissa River mouth (station GR6) showed slightly lower salinity (21.6–28.8 PSU, Fig. 2b), while station GR11 in the outer lagoon had high, nearly constant vertical salinity (34.6 ± 0.5 PSU, Fig. 2c), similar to seawater.

The physico-chemical parameters measured in the water samples are generally consistent with the vertical CTD profiles. Focusing on samples collected in bottom-water column, salinity varies from 3.0 to 35.0 PSU (Table S1). Except for stations GR5 and GR10, the lowest values are documented in front of the Stella River mouth and along the Natissa River.

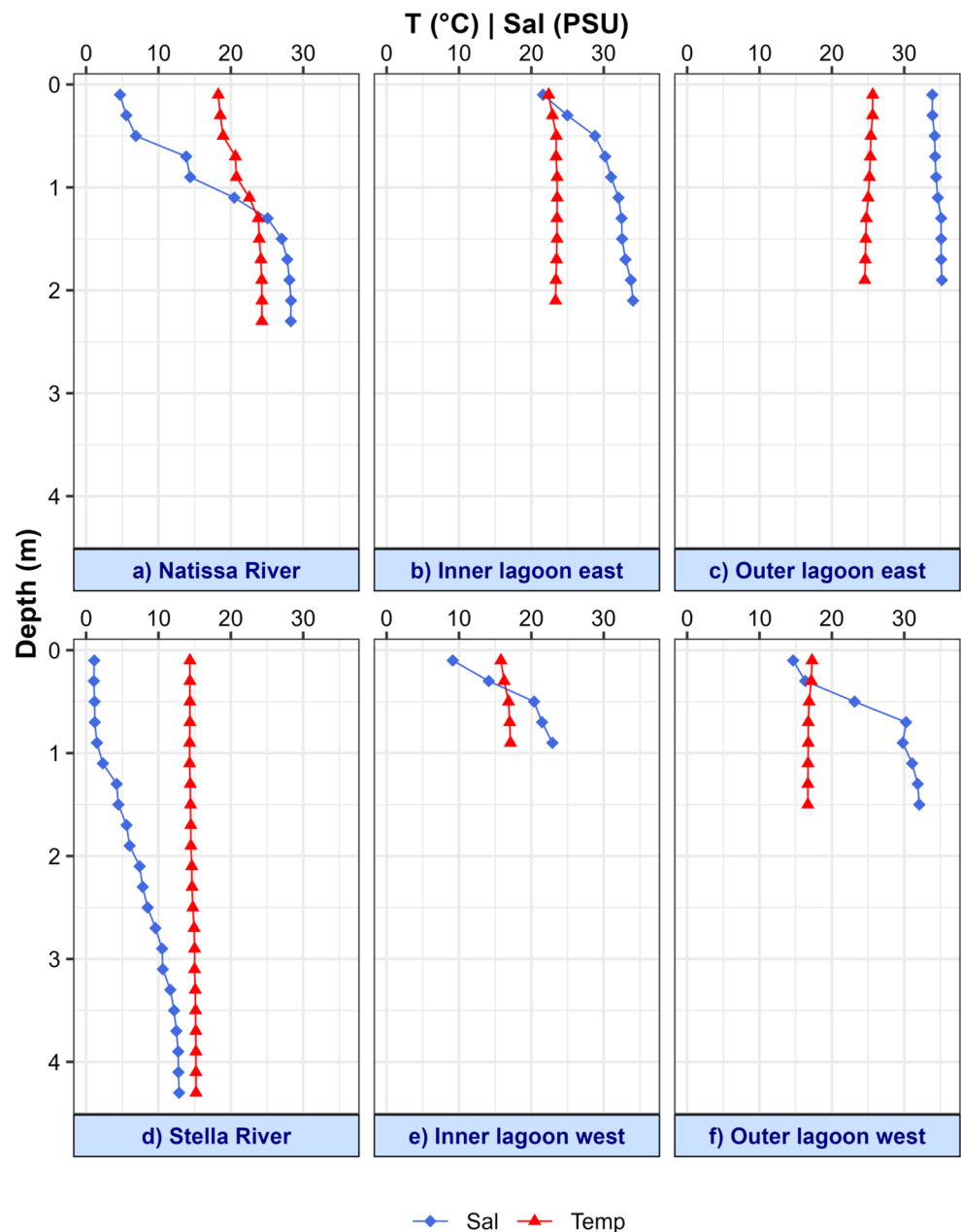
For the parameters not recorded by the CTD probe, pH values span from 7.5 to 8.6 (mean 8.1), with no significant differences between the two sectors (Table S1).

The concentration of dissolved oxygen (DO) ranges from 5.0 to 11.7 mg/L in bottom waters. Bottom waters along the Natissa River (stations GR1–4) exhibit reduced DO levels in comparison to central lagoon bottom waters, while the Marano sector appears to be more oxygenated overall (Table S1).

Sediment grain-size data indicate that sediments range from silty sand to clayey silt, the majority of them are sandy silt (Table S1). The sand content ranges from 12.0 to 58.6%, with a mean of 28.7% (Fig. 3a). The lowest percentages occur at stations along the course of the Natissa and Stella rivers, while the highest values generally correspond to the central Grado stations (GR6, GR8 and GR13) (Fig. 3a). The sandy fraction includes a substantial biogenic component, consisting mainly of gastropods, bivalves and serpulids. The silt content ranges from 37.3 to 73.5% (mean 61.5%), and the clay content ranges from 4.1 to 19.2% (mean value 9.9%) (Table S1). TOC values range from 1.12 to 4.38% (mean 2.56%); the highest concentrations are found in the Marano sector along the Stella River (Fig. 3b, Table S1).

THg concentration in the sediment samples ranges from 0.37 to 6.30 mg/kg (Fig. 3c), showing lower values in the Marano sector (0.37–1.79 mg/kg) than those in the Grado sector (2.18–6.30 mg/kg). In the eastern sector of the lagoon (Grado), THg concentrations increase from the inner Natissa River station (2.94 mg/kg) toward the outermost station of the Grado lagoon (6.30 mg/kg, Table S1), consistent with the general distribution of THg in sediments reported by Acquavita et al. (2012).

Fig. 2 Salinity and temperature profiles determined at selected stations in the Marano and Grado Lagoons: **(a)** GR1, Natissa River; **(b)** GR6, inner lagoon east (Grado sector); **(c)** GR11, outer lagoon east (Grado sector); **(d)** MA1, Stella River; **(e)** MA3, inner lagoon west (Marano sector); **(f)** station MA4, outer lagoon west (Marano sector)



Sediment Eh values from the sediments vary from -411 to -130 mV (Table S1), with no clear spatial trend emerging across the studied area.

Living Foraminifer's Data

The biocenosis comprises 30 species belonging to 20 genera, including 7 agglutinated, 16 hyaline and 7 porcelaneous taxa (Table S1). The most representative species are presented in Plates S1 and S2.

Ammonia tepida and *Haynesina germanica* are always present, as is *Aubignyna perlucida* with the exception of one station (G7). Other species, such as *Ammonia parkinsoniana*,

Bolivina dilatata, *B. striatula*, *Criboelphidium gunteri*, *Quinqueloculina jugosa* and *Q. seminulum*, are present in over 50% of the stations. The agglutinated species are present in a reduced number of stations, normally, the most abundant is *Textularia earlandi*. Other species, like *Ammonia veneta*, *Bulimina* spp., *Buliminella elegantissima*, species of *Quinqueloculina* and other agglutinated taxa, occur occasionally (Table S1). *Haynesina germanica*, along with *A. tepida*, *A. parkinsoniana* and *A. perlucida* dominate the assemblage. *H. germanica* dominates the stations collected along the Natissa River while, on the contrary, *A. parkinsoniana* achieves its highest frequency near the lagoon inlet.

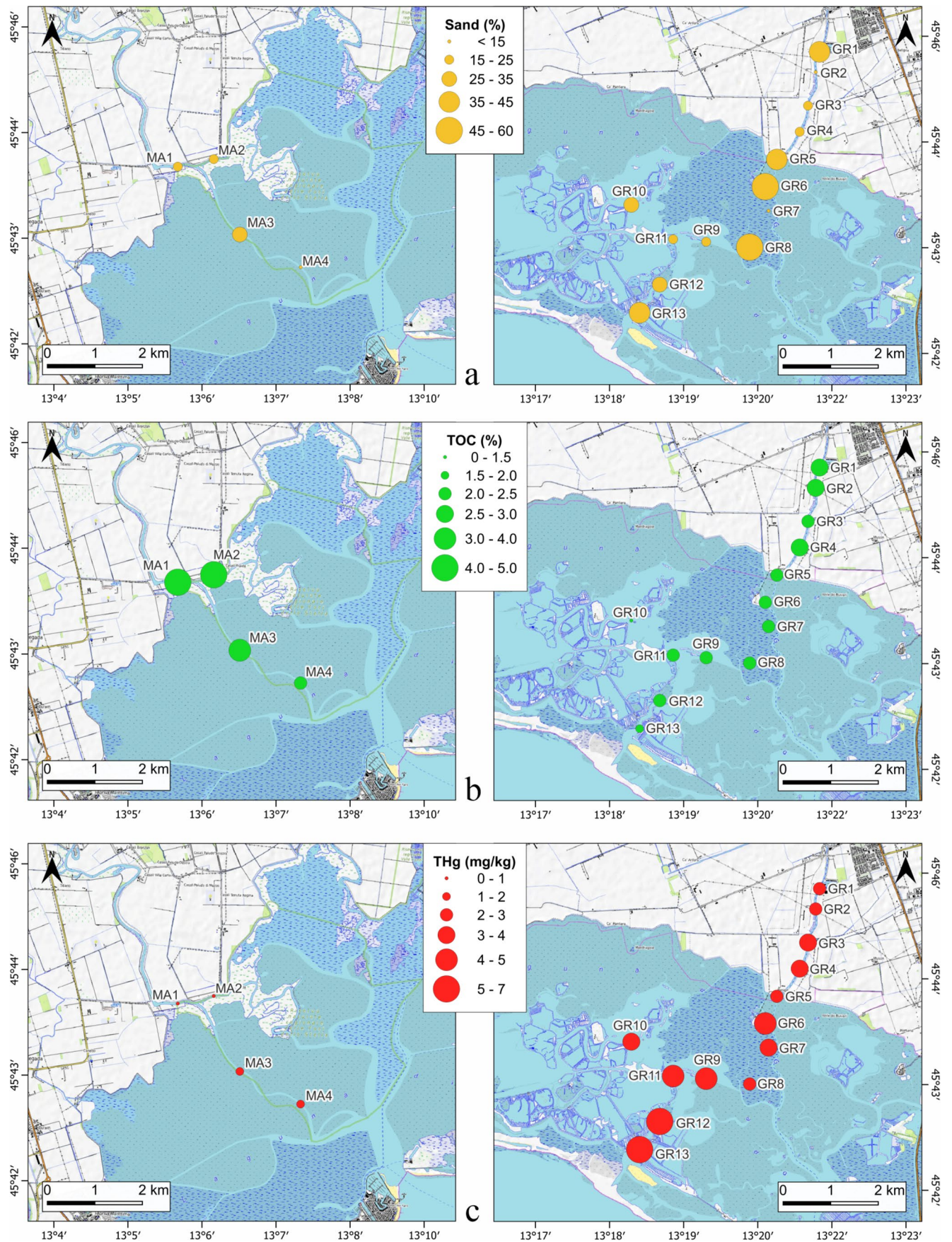


Fig. 3 Distribution maps of (a) sand content (%), (b) total organic carbon (TOC, %), and (c) total Hg (mg/kg) at the studied stations. In each panel, Grado sector is shown on the right and the Marano sector on the left

The comparison between the two analysed sediment layers of each station (0–1 and 1–2 cm) shows that the most living foraminifera occur in the 0–1 cm level, although foraminifera density often remains high even at the 1–2 cm (e.g., stations GR1, GR5, GR8, GR13, MA3 and MA4). The Bray-Curtis similarity index, used to compare the density of each species between the two layers at each station, indicated that 2 stations showed very low to low similarity between the 0–1 and 1–2 cm layers (B&C=0.2–0.4), 6 stations showed moderate similarity (B&C=0.4–0.6), and 9 stations showed high to very high similarity (B&C>0.6) (Table S2).

Epifaunal taxa like the porcelaneous generally, but not exclusively, concentrate in the uppermost layer. We therefore support using the 0–2 cm interval for this ecological study, as the commonly used 0–1 cm layer (e.g., Schönfeld et al., 2012), may not fully represent the living foraminiferal community (see discussion in Franzo et al., 2019). All subsequent discussions will thus refer to the 0–2 cm layer, considered more indicative of the competing live foraminiferal assemblage, in agreement with Bouchet et al. (2018) and Melis et al. (2019).

Species richness varies from 4 to 24, with the lowest values recorded in the inner lagoon and at the river mouths. The biocenosis density ranges from 10 to 353 specimens/50 cc (mean value 95 specimens/50 cc), and is generally lowest near the Natissa river mouth. The diversity (H'_{bc}) spans 1.2–2.6, increasing toward the central and outer sectors of the lagoon. The FAI index varies from 2.5 to 20.6%, with the highest values at the stations most affected by freshwater intrusion (Table S1).

Correlations with the Environmental Parameters

The cross-correlations between the absolute abundance of the species and the bottom-water parameters show that *A. parkinsoniana*, *Ammonoscalaria runiana*, *Bolivina striatula* and *Textularia earlandi* are positively correlated to pH, salinity and temperature (Table 2). *Bolivina dilatata*, *Bulimina* spp., *B. elegantissima*, and *Reophax nana* also show positive correlations with pH and salinity. The dissolved oxygen displays no significant correlation with any taxa.

In the sediment, *A. parkinsoniana*, *A. veneta*, *B. dilatata*, and *Cribrulphidium knudsenae* correlate positively with the sand content, whereas *Bulimina* spp., *B. elegantissima*, and *R. nana* are negatively correlated with clay. Species richness, as well as the abundance of *A. parkinsoniana*, *Bolivina* spp. and some species of *Quinqueloculina*,

exhibits negative correlation with TOC%. *Bolivina dilatata* has a positive correlation with sediment Eh content, but no other taxa do (Table 2).

Based on the WA optimum, *A. tepida*, *Q. milleti*, *Q. jugosa* and *C. gunteri* reach their optimum in the mesohaline conditions ($S < 20$ PSU), whereas the other species are distributed in polyhaline to euhaline sectors. Specifically, *B. elegantissima*, *Bolivina* spp., *T. earlandi*, *Q. carinatastriata*, *R. nana* and *A. runiana* exhibit notably reduced salinity tolerance (Table S3).

Temperature optimum ranges from 17.5 to 26.3 °C with reduced tolerance evidenced for *A. runiana*, *Q. boschiana* and *Toddinella incerta*. **pH** optima fall between 7.9 and 8.5, and all species exhibit a certain degree of tolerance, with *Pseudotriloculina rotunda*, *Q. schlumbergeri* and *H. germanica* being the most tolerant. **TOC** optima range between 1.5 and 3.2%, and most species fall below 2.5%. Higher TOC tolerance is observed in *C. gunteri*, *Q. milleti*, *H. germanica*, *Q. jugosa*, *A. tepida*, *A. veneta*, *A. perlucida*, and *Q. seminulum* (Table S3).

The PCA, used to assess the influence of environmental variables on the distribution of living foraminiferal, extracted two principal components explaining 69.1% of the total variance. F1 accounts for 46.9% of variance and is mainly driven by TOC (negatively) and, in contrast, THg, salinity, and temperature. F2 explains 22.3% of the variance and is associated with the sand content, Eh, and bottom-water DO (Fig. 4). Based on the distribution of environmental factors, F1 can be interpreted as reflecting organic matter enrichment and the degree of the lagoon confinement, whereas F2 represents sediments texture, which is associated with hydrodynamic conditions. When species are projected onto the PCA, *A. tepida*, *A. perlucida*, *H. germanica*, *C. gunteri*, and *Q. seminulum* plot on the negative side of F1, reflecting their affinity with higher TOC. In contrast, *A. parkinsoniana*, *Q. carinatastriata*, and the agglutinated taxa *T. earlandi* and *R. nana* plot on the positive side of F1, correlating with higher salinity and temperature.

The Q-mode cluster analyses carried out on 19 species across 15 stations identified three main groups, with two stations (GR7 and MA4) considered as outliers (Fig. 5). Cluster A comprises the stations located along the Natissa River and is characterised by the strong dominance of *H. germanica* (Table 3). **Cluster B** includes the stations located in the central lagoon and is represented by *H. germanica* with *A. perlucida* as well as *A. tepida* and *C. gunteri* as accessory species (Table 3). **Cluster C** includes the outer lagoon stations, dominated by *A. parkinsoniana*, with *A. tepida* as subordinate species (Table 3).

Table 2 Spearman's rank correlation between biotic variables (FAI%, Exp(H'bc) index, number of species, absolute abundance of the major species at the 0–2 cm level of GR and MA stations) and the sediment characteristics - sand, silt, clay, total organic carbon (TOC), THg, redox potential (Eh) - as well as bottom-water abiotic parameters (pH, dissolved oxygen, salinity and temperature). For species abbreviations, refer to (Table S1)

Variables	Sand	Silt	Clay	TOC	Hg	Eh sediment	pH	DO	S	T
FAI index	0.063	0.086	-0.212	0.340	-0.385	-0.320	-0.274	-0.088	-0.343	-0.108
H'bc	0.431	-0.363	-0.370	-0.358	0.413	0.227	0.347	-0.120	0.424	0.252
N° of species	0.176	-0.223	-0.113	-0.530	0.436	0.308	0.485	-0.295	0.477	0.450
Absolute abundance	0.270	-0.444	-0.178	-0.365	0.136	0.207	0.365	-0.162	0.225	0.402
Am_pa	0.486	-0.538	-0.434	-0.522	0.611	0.208	0.681	-0.269	0.607	0.689
Am_te	0.309	-0.361	-0.173	-0.233	0.109	0.041	0.212	-0.253	0.080	0.313
Am-ru	-0.155	0.066	0.053	-0.168	0.191	-0.432	0.547	-0.066	0.303	0.566
Am-ve	0.587	-0.570	-0.378	-0.362	0.001	0.197	0.155	0.043	-0.079	0.208
Au_pe	0.455	-0.520	-0.316	-0.291	-0.059	0.357	0.209	0.280	-0.086	0.047
Bo_di	0.639	-0.579	-0.579	-0.623	0.463	0.557	0.498	-0.187	0.515	0.457
Bo_st	0.262	-0.240	-0.298	-0.538	0.493	0.117	0.668	-0.181	0.545	0.631
Bu_el	0.404	-0.295	-0.513	-0.427	0.491	0.333	0.554	-0.203	0.653	0.412
Bu_spp	0.397	-0.285	-0.510	-0.409	0.470	0.318	0.556	-0.183	0.649	0.419
Cr_gu	0.119	-0.033	-0.131	0.263	-0.081	0.034	-0.382	-0.314	-0.063	-0.149
Cr_kn	0.577	-0.466	-0.592	0.015	0.036	0.137	0.145	0.111	0.148	0.177
Eg_sc	0.098	-0.157	0.050	-0.441	0.013	-0.035	0.369	0.164	0.011	0.310
Ha_ge	0.285	-0.428	-0.277	0.049	0.043	0.041	0.171	-0.310	0.189	0.344
Ps_ro	0.162	-0.248	0.024	-0.458	0.307	0.445	0.089	-0.349	0.387	0.098
Qu_bo	0.103	-0.152	-0.177	-0.505	0.002	-0.008	0.504	0.244	0.114	0.430
Qu_ca	0.385	-0.315	-0.455	-0.560	0.302	0.205	0.529	-0.072	0.474	0.516
Qu_ju	0.127	-0.445	0.121	-0.414	-0.044	0.327	0.162	-0.075	-0.084	0.057
Qu_mi	-0.069	-0.099	0.101	-0.157	0.144	0.080	0.165	-0.346	0.324	0.104
Qu_sc	0.474	-0.567	-0.223	-0.619	0.147	0.382	0.324	-0.123	0.079	0.241
Qu_se	-0.219	-0.066	0.459	0.014	-0.169	0.038	-0.248	-0.060	-0.222	-0.220
Re_na	0.398	-0.287	-0.511	-0.425	0.410	0.277	0.573	-0.128	0.626	0.468
Te_ea	0.169	-0.024	-0.359	-0.424	0.497	0.090	0.657	-0.036	0.693	0.529
To_in	-0.224	0.335	0.037	0.037	0.354	-0.149	0.336	0.037	0.410	0.149
Tr_bu	0.484	-0.484	-0.485	-0.447	0.186	0.186	0.485	-0.112	0.298	0.373

Fig. 4 Principal component analysis based on standardised abiotic parameters of water column and sediments (S= salinity; T=temperature; DO=dissolved oxygen; TOC= organic matter content; Eh=redox potential). Biotic data (FD=foraminiferal density, FAI %, number of species, and Exp(H'bc) index) together with the relative abundance of benthic foraminiferal species were incorporated as secondary variables. For species abbreviations, refer to (Table S1)

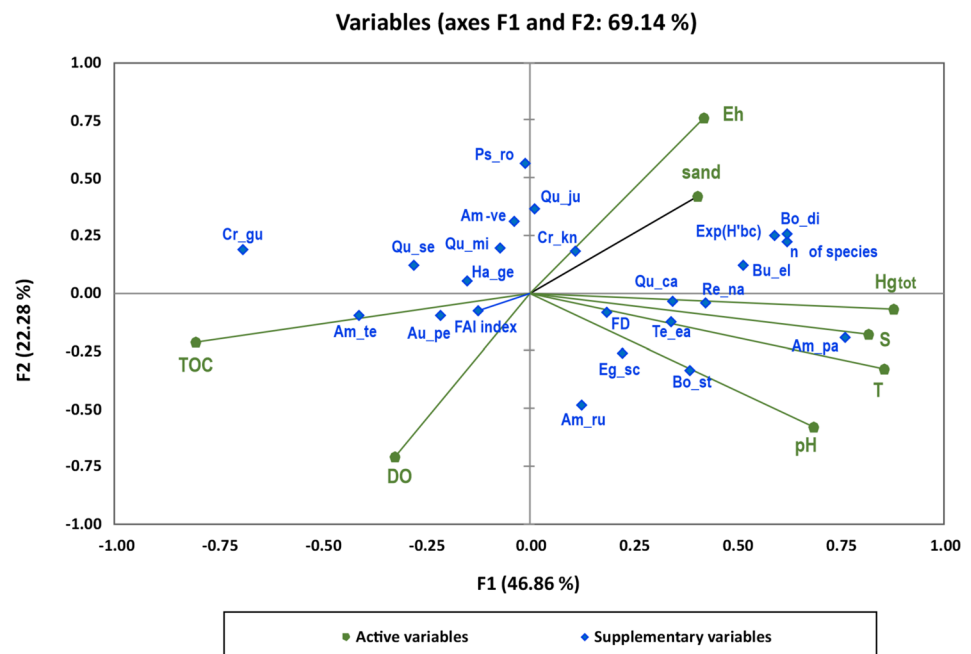


Fig. 5 Dendrogram of sampling stations classification from Q-mode cluster analysis (Complete Linkage algorithm and Bray-Curtis distance). The stations GR3 and MA1 were excluded from the analysis due to total specimen count of ≤ 20

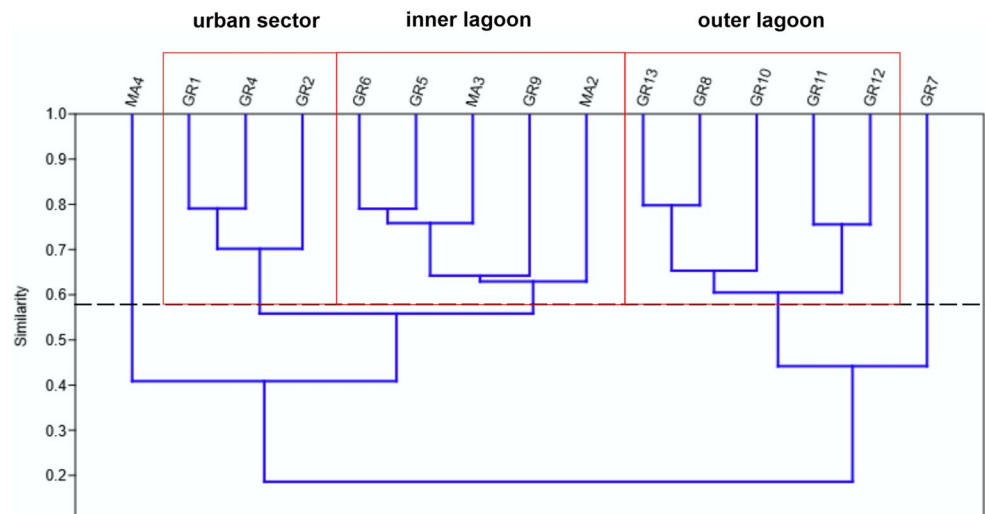


Table 3 Mean values and standard deviations of grain-size and geochemical sediment data, bottom-water abiotic parameters, foraminiferal relative abundance, FAI index, diversity index (H'_{bc}), foraminiferal density, and number of species calculated for each cluster identified by cluster analysis (n = number of cases). Two outlier stations are also reported

	Outlier	Cluster A ($n = 3$)		Cluster B ($n = 5$)		Cluster C ($n = 5$)		Outlier
	St. MA4	Mean	Dev.st.	Mean	Dev.st.	Mean	Dev.st.	St. GR7
Sand (%)	12.0	24.5	12.1	33.9	16.3	34.8	10.5	14.3
Silt (%)	68.8	62.9	6.6	58.2	13.6	57.2	10.0	73.5
Clay (%)	19.2	12.6	5.5	7.9	3.0	8.1	3.7	12.29
TOC %	2.15	2.7	0.1	3.0	1.0	1.9	0.5	2.3
Corg/Ntot	6.65	9.2	1.2	9.7	1.6	9.5	1.1	6.2
THg (mg g^{-1})	1.79	2.9	0.7	2.6	1.9	4.3	1.5	3.94
Eh sediment	-260	-325.7	75.5	-326.2	71.4	-237.8	66.1	-411
pH	8.1	7.9	0.4	8.1	0.2	8.3	0.2	8.4
O ₂ (mg/l)	9.4	5.3	0.3	8.6	2.1	6.6	1.2	8.6
S (PSU)	24.9	29.3	2.7	21.3	12.6	31.3	6.4	32.3
T (°C)	17.0	21.7	4.7	21.2	5.3	24.3	2.8	25.1
<i>Ammonia parkinsoniana</i>	0.0	5.0	2.5	9.3	7.7	21.8	5.0	29.4
<i>Ammonia tepida</i>	3.2	13.6	0.6	16.5	9.5	11.2	5.4	32.4
<i>Ammonia veneta</i>	0.0	0.0	0.0	1.7	2.3	1.7	1.4	0.0
<i>Ammoscalaria runiana</i>	0.0	2.4	4.1	0.0	0.0	0.5	0.8	14.7
<i>Aubignyna perlucida</i>	60.4	5.2	7.0	22.7	13.4	11.8	6.9	0.0
<i>Bolivina dilatata</i>	0.0	0.0	0.0	0.5	0.8	4.3	1.2	0.0
<i>Bolivina striatula</i>	0.0	0.1	0.1	0.1	0.2	1.9	0.9	5.9
<i>Buliminella elegantissima</i>	0.0	0.0	0.0	0.0	0.0	2.0	1.7	0.0
<i>Criboelphidium gunteri</i>	0.0	4.5	5.1	10.2	10.8	1.9	2.1	0.0
<i>Criboelphidium knudsenae</i>	0.0	0.0	0.0	6.0	9.4	1.5	3.2	0.0
<i>Eggerelloides scabrus</i>	0.0	0.0	0.0	0.0	0.0	2.0	4.0	2.9
<i>Haynesina germanica</i>	9.7	58.9	6.6	26.9	7.1	13.5	8.5	2.9
<i>Pseudotriloculina rotunda</i>	0.0	4.3	7.5	0.0	0.0	4.6	5.0	0.0
<i>Quinqueloculina carinatastriata</i>	0.0	0.0	0.0	0.0	0.0	0.9	1.3	0.0
<i>Quinqueloculina jugosa</i>	11.7	1.1	0.9	0.4	0.8	3.0	4.7	0.0
<i>Quinqueloculina milleti</i>	0.6	1.2	1.3	0.4	1.0	1.6	1.6	0.0
<i>Quinqueloculina seminulum</i>	14.3	2.5	0.8	1.0	1.8	1.5	1.6	0.0
<i>Reophax nana</i>	0.0	0.0	0.0	0.0	0.0	1.7	1.3	0.0
<i>Textularia earlandi</i>	0.0	0.0	0.0	0.0	0.0	6.7	9.0	5.9
FAI (%)	3.2	6.6	3.0	9.5	7.1	3.6	1.1	17.6
H'_{bc}	1.22	1.4	0.1	1.6	0.3	2.4	0.2	1.98
FD (spec./50cc)	126	130.6	138.1	70.2	56.0	140.6	122.5	23
N° species	6	8	2	7	3	19	4	9

Paleoenvironmental Data

The thanatocoenosis collected in core G3 comprises 23 species belonging to 16 genera (Table S4). In respect to living assemblages, more agglutinated species are present in the core. *Ammonia parkinsoniana*, *A. tepida*, *A. veneta*, *A. per lucida* and *H. germanica* are always present, as are *C. gunteri* with the exception of one level. A particular presence of *Pseudoeponides anderseni* and *Trochammia inflata* is recorded at a depth of 70 cm. H'(bc) ranges from 1.22 to 2.18, increasing from the bottom to the top and slightly decreasing in the uppermost recent levels. The FAI index varies between 3.3 and 11.8%, increasing in the upper 20 cm (Table S4). *Ammonia* spp. and *C. gunteri* are the species exhibiting the most pronounced shell deformation.

Discussion

Environmental Parameters of MGL

Physico-chemical parameters of water column such as temperature, salinity, and oxygenation strongly influence the structure of pelagic and benthic communities, especially in TEs such as coastal lagoons where they fluctuate widely (Lucena-Moya et al., 2012). According to the European WFD, their regular monitoring is therefore essential for assessing the ecological status of these systems.

For the MGL, recent studies have described temporal and spatial variability of water oxygenation, temperature, salinity, and nutrient concentrations (Pittaluga et al., 2022; Acquavita et al., 2024). Overall, water temperatures recorded in this study are consistent with those commonly found in late spring (May, June) and late summer (September) (Pittaluga et al., 2022). Slightly lower values in the western part of the lagoon reflect greater freshwater inputs from the numerous rivers entering this sector, which is less subject to the influence of the sea than the eastern lagoon (Ferrarin et al., 2010; Fontolan et al., 2012). This pattern is also confirmed by the lower salinity values measured in the western lagoon, particularly in surface waters.

Conversely, the eastern lagoon is most strongly influenced by marine waters, which show poly- to euhaline conditions even in the bottom water layer of the Natissa River, due to saltwedge intrusion. Previous studies in the rivers flowing in the MGL confirm a relevant landward propagation of the saltwedge up to around 12 km inland in the Aussa River (Covelli et al., 2009; Floreani et al., 2022). Such intrusion, controlled primarily by tidal range and river discharge, are known to influence nutrient redistribution and, consequently, biological production within these ecosystems (Watanabe et al., 2014).

Lower water temperatures and salinity in the western lagoon favour DO levels relatively high, as both conditions increase oxygen solubility (Benson & Krause, 1984). Overall, the water column was well oxygenated in both sectors of the lagoon: DO values were always above 5 mg/L, the threshold level below which sensitive organisms may have negative effects (Frodge et al., 1990). These observations are consistent with previous studies, confirming that in this open-lagoon system, water flow driven by riverine inputs and tidal exchange efficiently contributes to support water oxygenation. It must be considered that measurements were conducted during the daytime in spring, when the conditions are most favourable for photosynthetic oxygen production.

Conversely, considering that all the sampled sediments showed a thin oxidized layer (2–3 mm), the negative redox potential in the sub-surface sediment layer at all stations indicates anoxic conditions just a few millimetres below the sediment-water interface. Moreover, sediments were mostly fine-grained (from clayey silt to sandy silt), especially in the riverine and inner lagoon area farther from tidal inlets, consistent with Acquavita et al. (2012). The central lagoon stations GR6 and GR8 show a higher sand content (silty sand) than typically expected for this inner sector of the lagoon (Fig. 3a); however, a significant proportion of this sand is attributable to biogenic material. Such fine sediments limit oxygen penetration and favour organic matter accumulation through adsorption effects. As a result, microbial oxygen consumption is enhanced and quickly leads anoxic conditions in sub-surface layers (Giani et al., 2009; Ahmerkamp et al., 2017). This is supported by the weak but statistically significant relations between Eh values of both percentage of mud ($\rho = -0.52$, $p < 0.05$) and TOC ($\rho = -0.58$, $p < 0.05$).

On the other hand, no significant relationship was found between the TOC content and the fine fraction of sediments ($\rho = 0.252$). As noted by Acquavita et al. (2012), this likely reflect terrigenous organic matter supplies from rivers, particularly relevant in the case of the Stella River. The local enrichment in organic matter is further confirmed by the highest TOC values occurring in the riverine samples, with slightly lower and irregularly decreasing concentrations within the lagoon as distance from river mouths increases. Previous studies indicate that the nature and distribution of organic matter in the MGL sediments result from a complex but continuous pattern of terrestrial and marine sources.

Regarding THg, sediment concentrations are about one order of magnitude higher than natural background levels reported for the Gulf of Trieste (0.13 ± 0.04 mg/kg; Covelli et al., 2006) and for the western MGL (0.02 mg/kg; Covelli et al., 2017), reflecting historical anthropogenic inputs. Mercury contamination in the MGL mainly originates from the Isonzo River, which transports cinnabar (α -HgS) derived from historic mining at Idrija, active until 1995.

During flood events combined with Bora winds, this material is driven south-westward and enters the lagoon through the eastern inlets (Covelli et al., 2007), producing a general east-to-west decrease in THg concentrations (Acquavita et al., 2012; Bettoso et al., 2023). The THg values observed in this study match this spatial pattern: the highest concentrations were found in the outer eastern sector near the Morgo inlet (stations GR12 and GR13, Fig. 3c), the area most affected by riverborne Hg inputs. As reported previously, THg does not correlate with a specific grain size, due to the presence of Hg even in coarser sediments in the form of micro-crystalline α -HgS transported by river plumes from the upstream mining area (Biester et al., 2000; Acquavita et al., 2012). Cinnabar commonly occurs in sediments influenced by Hg mining activities (Gray et al., 2000; Rimondi et al., 2014; Garcia-Ordiales et al., 2019), and is widespread across the MGL, dominating in the eastern and outer sectors, while the non-cinnabar fraction becomes relatively more abundant westward (Piani et al., 2005; Acquavita et al., 2012). Because cinnabar is poorly bioavailable and not easily methylated (Jonsson et al., 2012), its predominance reduces the biological impact of elevated THg levels. This is consistent with the low methylmercury percentages measured in MGL sediments, generally below 0.5% of THg (Acquavita et al., 2012).

Foraminiferal Assemblages and Relationships with the Modern Environment

The living foraminiferal assemblages identified in the MGL consist of typical euryhaline taxa commonly found in Mediterranean lagoons (Debenay & Guillou, 2002; Albani et al., 2007; Carboni et al., 2009; Coccioni et al., 2009; Serandrei Barbero et al., 2008; Buosi et al., 2010; Frontalini et al., 2010, 2013, 2014; Melis & Covelli, 2013; Benito et al., 2016; Franzo et al., 2019). *Ammonia tepida*, *A. parkinsoniana*, *H. germanica*, *A. perlucida* and *C. gunteri* are the most representative species in the modern habitats undergoing investigation. Most taxa are infaunal, inhabiting the top 2 cm of sediments, while epifaunal taxa such as miliolids are usually more abundant near the lagoon inlets.

Although biocenosis density (FD) is lower than the typical spring values in the Gulf of Trieste (see to Melis et al., 2019), the presence of foraminifera in the lagoon indicates that environmental conditions are suitable for their development. The FD value is lower in areas with low or fluctuating salinity, such as the inner river mouths, and increases towards the outer lagoon where seawater exchange is greater (Table S1). The same gradient is observed for the H^{bc} diversity index, which rises from inner to outer sectors, reflecting increasingly favourable conditions. A comparable spatial pattern was previously documented in the

thanatocoenosis, with minimum diversity along the Aussa River (Melis & Covelli, 2013). This work, however, refers to different stations and it was based on the thanatocoenosis present in the first centimetres of sediment, corresponding to approximately 10 years of deposition; therefore, the comparison is only indicative of their recent historical behaviour.

The foraminiferal tests show a certain percentage of abnormalities (FAI), with higher values in the inner lagoon and consistently below 5% in the outer area (Table S1). All FAI values exceed the 1% threshold, which is considered indicative of stress in otherwise healthy population, as suggested by Geslin et al. (2000). The deformed living assemblage is mainly represented by *A. tepida*, *A. perlucida*, *C. gunteri*, *C. knudsenae*, and *H. germanica*, confirming their sensitivity to environmental and anthropogenic stress in TEs (Carboni et al., 2009; Coccioni et al., 2009; Buosi et al., 2010; Melis & Covelli, 2013).

Test deformation can represent one of the responses of foraminifera to pollution, especially in relation to high concentration of heavy metals (Yanko et al., 1998; Coccioni et al., 2009; Caruso et al., 2011; Bergamin et al., 2019; Liu et al., 2025). Heavy metal pollution can induce significant cytological changes, thicken the inner organic lining, alter cell membrane permeability, influence the enzymatic activity and functional capacity of lysosomes (e.g., Bresler & Yanko, 1995; Yanko et al., 1998; Frontalini et al., 2016, 2018; Boehnert et al., 2020). Severe heavy metal pollution may alter the foraminifer energy budget and its reproductive cycle, as well as also damage the cytoskeleton, promoting the deformation of the tests (Yanko et al., 1998).

However, deformations of foraminiferal tests are also widely recognised as indicators of natural environmental stressors, including variations in temperature, salinity, and redox and oxygenation conditions, which influence physiological processes during calcification and growth (e.g., Stouff et al., 1999; Geslin et al., 2000; Tavera Martínez et al., 2023). Although temperature can affect foraminiferal growth and calcification, its role in inducing test deformities is mainly indirect, acting through its influence on oxygen availability and redox conditions, which are key drivers of environmental stress. Under reducing or low-oxygen conditions, benthic foraminifera experience physiological stress that can interfere with biomineralization processes, leading to wall irregularities and test deformation (e.g., Debenay et al., 2009). Although the correlation matrix revealed no clear relationships with environmental parameters or sediment composition, the PCA indicates that FAI tends to increase in TOC-rich environments and it is negatively associated with salinity (Fig. 4). The influence of salinity on test deformation remains debatable; however, our results are consistent with several studies indicating that rapid salinity fluctuations may promote the development of deformations (Yanko

et al., 1998; Stouff et al., 1999; Geslin et al., 2000; Saraswat et al., 2015).

Elevated organic matter concentrations are found in the inner sectors of the lagoon and the western area of Marano (Fig. 3b), where Falace et al. (2009) identified mesotrophic/eutrophic conditions, accompanied by the lowest values of the Ecological Evaluation Index (EEI) values derived from macrophyte coverages (*Cymodocea nodosa* and *Zostera marina*). A similar pattern was observed in the foraminiferal thanatocoenosis by Melis and Covelli (2013), with more pronounced FAI values at stations located in the western sector (Marano). It remains to be determined whether the TOC accumulation observed here is natural or anthropogenic.

PCA analysis revealed that the main factor influencing foraminiferal distribution is organic matter accumulation (represented by TOC), reflecting the environmental trophic state, whereas salinity and THg content indicate less confined environments with high THg accumulation. Sediment texture and bottom-water DO also influence foraminiferal dispersion (Fig. 4). Projecting secondary variables onto the PCA plane shows that *A. parkinsoniana*, *Q. carinatastriata*, and the agglutinated *T. earlandi* and *R. nana*, correlate

positively with salinity, reflecting their marine affinity, while *A. tepida*, *A. perlucida*, *H. germanica*, *C. gunteri*, and *Q. seminulum* correlate positively with the TOC gradient (Fig. 4).

Ammonia tepida, *H. germanica*, *A. perlucida* and *C. gunteri* tolerate wide salinity variations and occur from mesohaline to euhaline sectors (Fig. 6). In contrast, *A. parkinsoniana* shows limited tolerance, preferring polyhaline conditions, consistent with its distribution in thanatocoenosis (Melis & Covelli, 2013). In the outer lagoon sector, near the Morgo tidal inlet, these taxa coexist with a greater number of species, most of which are less tolerant to temperature and salinity or mainly occur under euhaline conditions (Fig. 6). These species, including *Quinqueloculina bosciana* and *Q. carinatastriata*, show a clear marine affinity (see, for instance, Jorissen, 1987; Sabbatini et al., 2010; Melis et al., 2019 for the Adriatic Sea), whereas *Q. jugosa* and *Q. milleti* are more typical of mesohaline conditions, consistent with Frontalini et al., 2010, Melis and Covelli (2013), as *Q. costata* - and Fouet et al. (2022).

Q-mode cluster analysis of the sampling sites revealed three distinct groups (Fig. 5), each defined by a characteristic assemblage of taxa (Table 3) indicative of different environmental conditions. Cluster analysis grouped stations that, despite being sampled in different years, belong to similar sectors, indicating comparable environmental and faunal conditions across the three recognized biotopes (Table 3). Greater variability in environmental parameters over the sampling years was observed primarily in salinity, TOC, and Eh values in the sediments of Cluster B, which is associated with the inner lagoon (Table S1). This likely highlights the sector characterized by stronger exchanges between strictly lagoonal conditions and those under greater marine influence.

The identified clusters are as follows:

Haynesina germanica Assemblage, Accessory Species: *A. tepida* (Cluster A; stations GR1, GR2 and GR4 - urban biotope)

This assemblage is dominated by *H. germanica* ($58.9 \pm 6.6\%$) with a consistent but subordinate occurrence of *A. tepida* ($13.6 \pm 0.6\%$). It corresponds to minimum percentage of sand, strongly reducing conditions, high TOC, and low pH and DO, together with polyhaline/euhaline bottom waters (Table 3) and lowest foraminiferal diversity. The environment is subtidal, the water column is stratified, with evident salt wedge intrusion (Fig. 2a). This assemblage, corresponding to the urban biotope, occurs along the Natissa River, a sector connecting the port of Aquileia to the lagoon and exposed to intense motorboat traffic, a factor that may enhance local environmental stress. *Haynesina germanica*

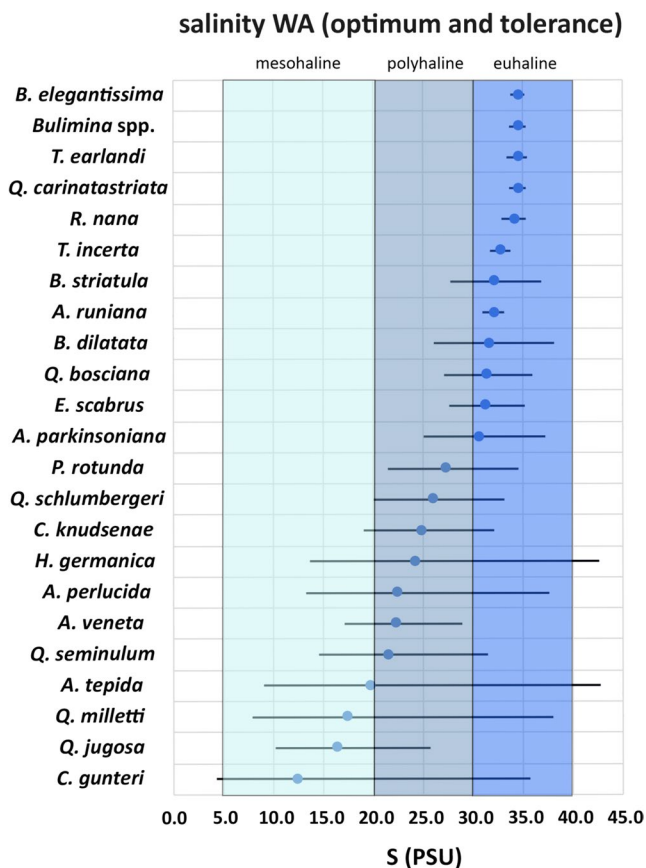


Fig. 6 Caterpillar plot showing the optimal salinity (blue dots) and tolerance ranges (bars) for benthic foraminiferal species from Marano and Grado Lagoon (MGL), alongside the categories of the lagoon's salinity (see Bettoso et al., 2023)

is widely recognised for its tolerance to heavy metals and hydrocarbons contamination (Armynot du Châtelet et al., 2004; Romano et al., 2008; Coccioni et al., 2009; Buosi et al., 2010; Francescangeli et al., 2020), but it is also characteristic of Mediterranean natural TEs that are semi-confined from the sea and rich in organic matter (Carboni et al., 2009; Frontalini et al., 2013; Benito et al., 2016; Bouchet et al., 2021; Fouet et al., 2022). Its presence along the Natissa River aligns with patterns observed in the subtidal settings of the Venice Lagoon (Marginal Urban/Urban Mixing Biotope, Albani et al., 2007), and in the Mixing sub-biotope of Lake Varano (Frontalini et al., 2013), where sediments are muddy, organic-rich and subjected to elevated salinity. Moreover, its thanatocoenosis distribution, as noted by Melis and Covelli (2013), further supports its affinity for eutrophic and less saline sectors of the western MGL, where high concentrations of nutrients are delivered by the freshwater outfalls (Falace et al., 2009).

Although occurring at low frequency, *A. tepida*, conforms to its well-documented distribution in TEs worldwide (see Hayward et al., 2021). Species from *A. tepida* morphogroup can reach >80% relative abundance in sheltered, unvegetated, mid-low tidal, and shallow subtidal settings (typically <3 m deep), which are typically slightly hyposaline (20–35 PSU) and muddy, on a global scale (e.g., Debenay & Guillou, 2002; Hayward et al., 2021). This species is also known for its tolerance to elevated trace element concentrations, including Hg, in Mediterranean lagoons and coastal systems (Carboni et al., 2009; Coccioni et al., 2009; Frontalini et al., 2009; Frontalini & Coccioni, 2011; Melis et al., 2019; Dimiza et al., 2022). In the present study, its abundance never becomes particularly high, in contrast to the thanatocoenosis described by Melis and Covelli (2013), where its dominance was related with thermo-haline stratification of the fluvial sector, muddy sediments, high TOC, and long-term Hg contamination linked to the former activities of a chlor-alkali plant (CAP) used for cellulose production from cane (*Arundo donax*), which was active in the 1940–1992 period.

***Haynesina germanica* and *Aubignyna perlucida* Assemblage, Accessory Species: *A. tepida* and *C. Gunteri* (Cluster B; stations GR5, GR6, GR9, MA2 and MA3 - Inner Lagoon Biotope)**

This assemblage is marked by a decline in *H. germanica* (26.9 ± 7.1) and a concomitant increase of *A. perlucida* (22.7 ± 13.4), while *A. tepida* becomes slightly more abundant ($16.5 \pm 9.5\%$). *C. gunteri* shows variable but notable contributions ($10.2 \pm 10.8\%$). This cluster corresponds to the **inner lagoon area**, characterised by highest TOC values, high variable bottom salinity (mesohaline to euhaline

conditions), strongly reducing substrates, but higher pH and DO compared to Cluster A. The FAI index reaches its maximum here (Table 3). The distribution of *A. perlucida* is consistent with observations from the lagoon of Venice, where this species is common, often exhibiting test abnormalities (Coccioni et al., 2009). In the same lagoon, this taxon, reported as *Valvulineria perlucida*, occurs mainly in the Inner and Outer Lagoon Biotopes, which are areas more strongly modified by human activities (Serandrei Barbero et al., 2008). Conversely, in Lake Varano this taxon typifies areas subjected to enhanced marine influence (Frontalini et al., 2013), in agreement with its thanatocoenosis distribution, predominantly observed in the outer MGL, under medium-low hydrodynamics, and often associated with *A. parkinsoniana* (Melis & Covelli, 2013).

Aubignyna perlucida is closely associated with *C. gunteri*, a taxon often referred to as *E. oceanense*, a synonym that is challenging to differentiate (see the debate in Hayward et al., 2025). *Criboelphidium gunteri* is documented in the intertidal sectors of TEs with fluctuating salinity (recorded as *Elphidium granosum* in the Venice Lagoon, Serandrei Barbero et al., 2008; as *Elphidium gunteri* in Melis & Covelli, 2013), exhibiting a propensity for shell abnormalities (Coccioni et al., 2009). It also occurs in the more accessible areas of Mediterranean estuaries (Fouet et al., 2022), and in Lake Varano, it is characteristic of environments with elevated TOC and anthropogenic inputs from urban and agricultural sources (Frontalini et al., 2013).

***Ammonia parkinsoniana* Assemblage, Accessory Species: *H. germanica*, *A. perlucida* and *A. tepida* (Cluster C; stations GR8, GR10, GR11, GR12 and GR13 - Outer Lagoon Biotope)**

In this assemblage, *A. parkinsoniana* reaches its highest presence ($21.8 \pm 5.0\%$), corresponding to the **outer lagoon area**, where bottom salinity shows limited variability (predominantly euhaline), highest sand content, lowest TOC, less negative Eh values, and elevated pH. This cluster also exhibits the highest foraminiferal richness and diversity. *Ammonia parkinsoniana* is significantly associated with both porcelaneous and agglutinated foraminifera, which are more abundant here than in the other assemblages. This pattern aligns with the known distribution of porcelaneous taxa in the Venice lagoon, where they preferentially occur near lagoon inlets (Serandrei Barbero et al., 2008) and in outer estuarine environments (Fouet et al., 2022). Notably, *Q. carinatastriata*, *Q. schlumbergeri*, *Reophax nana* and *Textularia earlandi* occur exclusively in this assemblage, indicating a clear preference for the less confined, more marine-influenced sector of the MGL.

The distribution of *A. parkinsoniana* adheres to their findings in TEs affected by marine inputs (Carboni et al.,

2009; Frontalini et al., 2013) and with its thanatocoenosis pattern reported by Melis and Covelli (2013), where this taxon coincides with the less confined, more mesotrophic and more salinity-stable sector of the studied lagoon (Ferrarin et al., 2010). *Ammonia parkinsoniana* is also known to be comparatively more sensitive to heavy-metal content in the sediments (Frontalini & Coccioni, 2008; Martins et al., 2015).

Relationships with the Organic Matter

As previously noted, the interaction between benthic foraminifera and organic matter (expressed as TOC) is considered to play a key role in evaluating the ecological quality (EcoQS) in coastal and TEs. Both the quantity and quality of organic matter strongly influences foraminiferal distribution (e.g., Sabbatini et al., 2012; Bouchet et al., 2021; Fouet et al., 2022). Labile, marine-derived sedimentary organic matter is vital to coastal and lagoonal ecosystems. The easily degradable organic molecules such as amino acids, carbohydrates, proteins, and lipids coming from phytoplankton and other marine primary producers, provide high-quality feed for benthic foraminifera, which use it as an efficient energy source for growth, reproduction, and metabolism

(Fontanier et al., 2008). At a larger ecosystem level, the quality and amount of this labile material govern patterns of benthic production, trophic interactions, and biogeochemical processes (Pusceddu et al., 2007).

Alve et al. (2016) and Jorissen et al. (2018) were the first in introducing the concept of ecological categories based on foraminiferal responses to TOC concentration. Five ecological groups (EGs), from **EGI** ('Sensitive species', low TOC tolerance) to **EGV** ('First-order opportunists', higher TOC tolerance), have been defined to reflect foraminiferal sensitivity and tolerance to TOC concentration (Alve et al., 2016; Jorissen et al., 2018). Jorissen et al. (2018) provide a list of species assignments to the EGs for Mediterranean coastal marine environments, while Bouchet et al. (2021) extended this framework to Mediterranean TEs. The comparison between these two macroenvironments reveals inconsistencies in the classification of some species across two or three EGs, likely reflecting taxonomic uncertainties, species plasticity, and methodology differences among numerous studies.

To further explore the foraminiferal responses to TOC, identified in this study as a key variable by PCA (Fig. 4), its relationships with the most abundant species was examined. Following Bouchet et al. (2021) and using the WA optima for each taxon in relation to TOC (Fig. 7; Table S3), species from MGL were assigned to EGs as follows: the range 0–2% of TOC content was used to assign the species to **EGI**, the range 2–2.5% to **EGII**, the range 2.5–3.4% to **EGIII**, and the range 3.4–4.1 to **EGIV**. The WA optima for TOC in the recovered species range from 1.5% to 3.2%, categorizing them into ecological groups **EGI** to **EGIII** (Fig. 7). Considering the most representative species present in at least 50% of the sampling stations, *A. parkinsoniana* is classified as 'Indifferent species' group **EGII**, rather than **EGI** as previously indicated by Bouchet et al. (2021); *Q. milletti* and *Q. seminulum* are placed in 'Third-order-opportunist' group **EGIII** instead of **EGI**. *Ammonia tepida*, *C. knudsenae*, *H. germanica*, and *Q. jugosa* maintain their affinity for **EGIII**, in agreement with Bouchet et al. (2021), while *C. gunteri* and *A. perlucida* show a preference for **EGIII** rather than the formerly assigned **EGV**. These results highlight that species can display variable responses even in similar environments, underscoring the need for further investigation of their relationships with organic matter, consistent with Bouchet et al. (2021).

Considering that the MGL is an environment that has been significantly impacted by human activities for several decades, the quality indices were calculated using the foraminiferal biocenosis. Numerous indices based on foraminiferal associations have been defined to assess the Ecological Quality Status of the environment, referred to as EcoQS. Important synthesis works have addressed this topic from

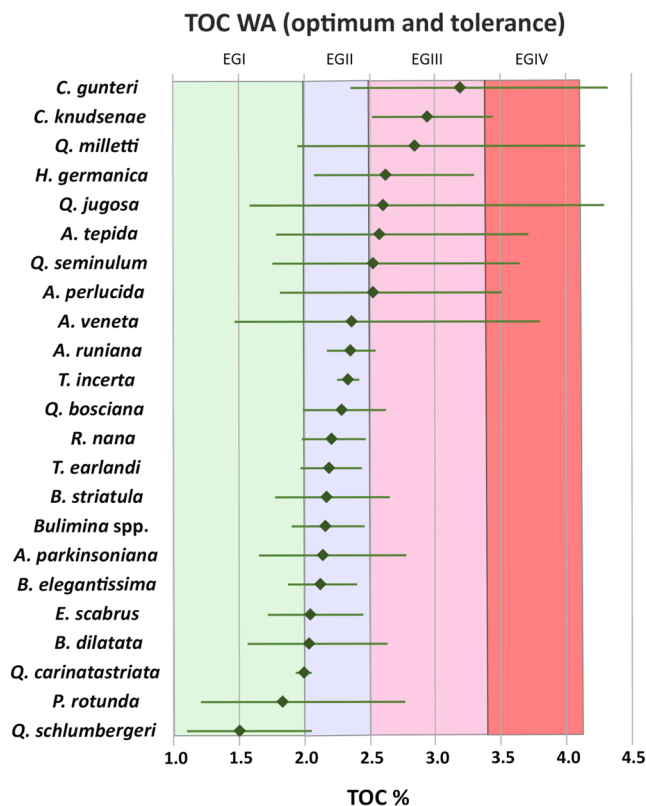


Fig. 7 Caterpillar plot showing the optimal percentage of TOC content (green diamonds) and tolerance range (bars) for benthic foraminiferal species obtained from MGL. The ranges of the ecological groups (EGs) are reported above

various aspects for both coastal environments (Parent et al., 2021) and TEs (O'Brien et al., 2021). Among these indices, the Foram-AMBI, introduced by Alve et al. (2016), is based on the categorization of species into 5 ecological classes (EGs), which represent the degree of sensitivity of foraminifera to organic matter content. This assignment can have a series of problems, as previously mentioned. Another interesting index is the “benthic foraminiferal-based diversity index” Exp(H'bc) (Hill, 1973), which was initially applied with foraminifera by Bouchet et al. (2012) to evaluate the EcoQS of the Norwegian coast. Subsequently, it has been successfully applied to various TEs and has demonstrated numerous good relationships with different types of contaminants, including organic matter content (see discussion in O'Brien et al., 2021). Aware of the fact that the representativeness of these indices is not particularly reliable when the sampling does not have replicates, we still wanted to evaluate the EcoQS of the investigated area, both for the biocenosis and for the historical series studied (core G3), in order to make a comparison between current periods and pre-industrial phases.

To evaluate the EcoQS based on the trend of the Exp(H'bc) index, the criteria set by Bouchet et al. (2018 and, 2021) were used, which foresee different intervals compared to the coastal environment, as TEs are naturally subject to stress factors compared to the latter. Following these guidelines, an Exp(H'bc) value < 3 indicates **bad** EcoQS, values 3–7 **poor** EcoQS, values 7–11 **moderate** EcoQS, values 11–15 **good** EcoQS, and values > 15 indicate **excellent** EcoQS. In the study area, Exp(H'bc) varies from 3.4 to 13.8, with a mean value of 6.7, indicating conditions that range from **poor** to **good** EcoQS (Fig. 8). The **poor** values relate to the inner sector, specifically the urban and inner biotopes, primarily associated with areas affected by inner freshwater sources (Fig. 8). Conversely, the outer

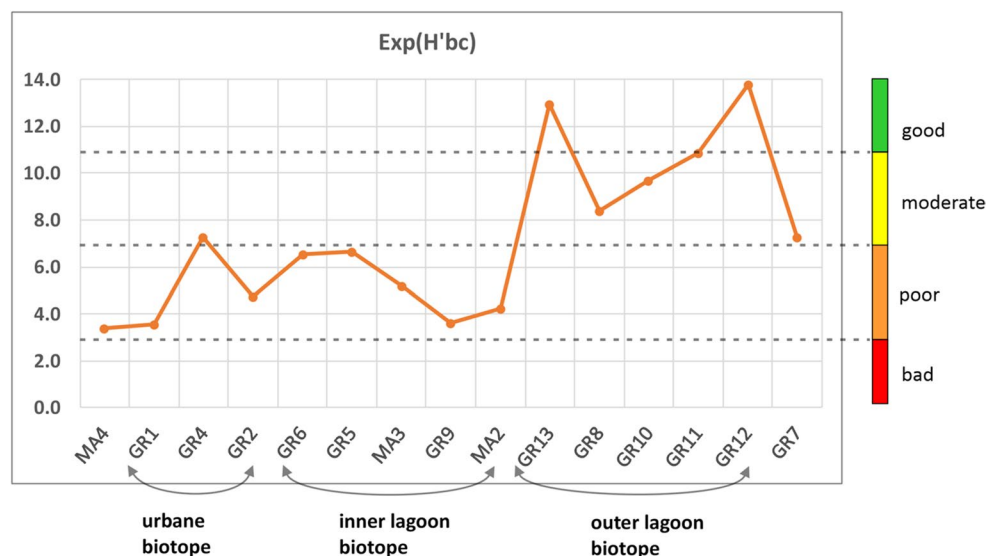
lagoon sectors have an improving EcoQS, as evidenced by **moderate** to **good** quality conditions. The PCA indicates that Exp(H'bc) is mostly positively correlated with T and S, while exhibiting a negative correlation with TOC content (Fig. 4). The diminished EcoQS conditions observed in the inner lagoon can mostly be ascribed to natural stress resulting from significant variations in physico-chemical parameters (including salinity and temperature), however anthropogenic influences cannot be excluded, considering that this part of the lagoon receives contributions from numerous inflowing rivers, that may represent an important pathway for contaminant transport to the lagoon via fluvial suspended matter and industrial discharges (e.g., Piani et al., 2005; Covelli et al., 2009).

Historical Data

To explore the potential impact of disturbances related to the recent industrial activities, we examined the core G3, located near the Natissa River mouth (Fig. 1). The analysis of foraminiferal thanatocoenoses in historical sedimentary sequences not only provides valuable paleoenvironmental insights, but also serves as a tool for assessing environmental conditions prior to modern human influence (O'Brien et al., 2021 and references herein). Calculating paleo-quality indices (Paleo-EcoQS) on fossil assemblages further supports the interpretation of present-day data by highlighting any shifts associated with recent anthropogenic pressures and by offering a reliable baseline against which current conditions can be evaluated (e.g., de Jesus et al., 2020; Hess et al., 2020; Moreno et al., 2025).

Similar to the present-day situation, the dead assemblage in core G3 is dominated by *A. parkinsoniana* and *A. tepida*, with subordinate abundances of *A. perlucida*, *C. gunteri*, and *H. germanica* (Table S4).

Fig. 8 Distribution of Exp(H'bc) values calculated for the studied stations, with the corresponding EcoQS categories on the right, following Bouchet et al. (2018, 2021). Stations are ordered according to the clustering results and biotope definitions (see Fig. 5)



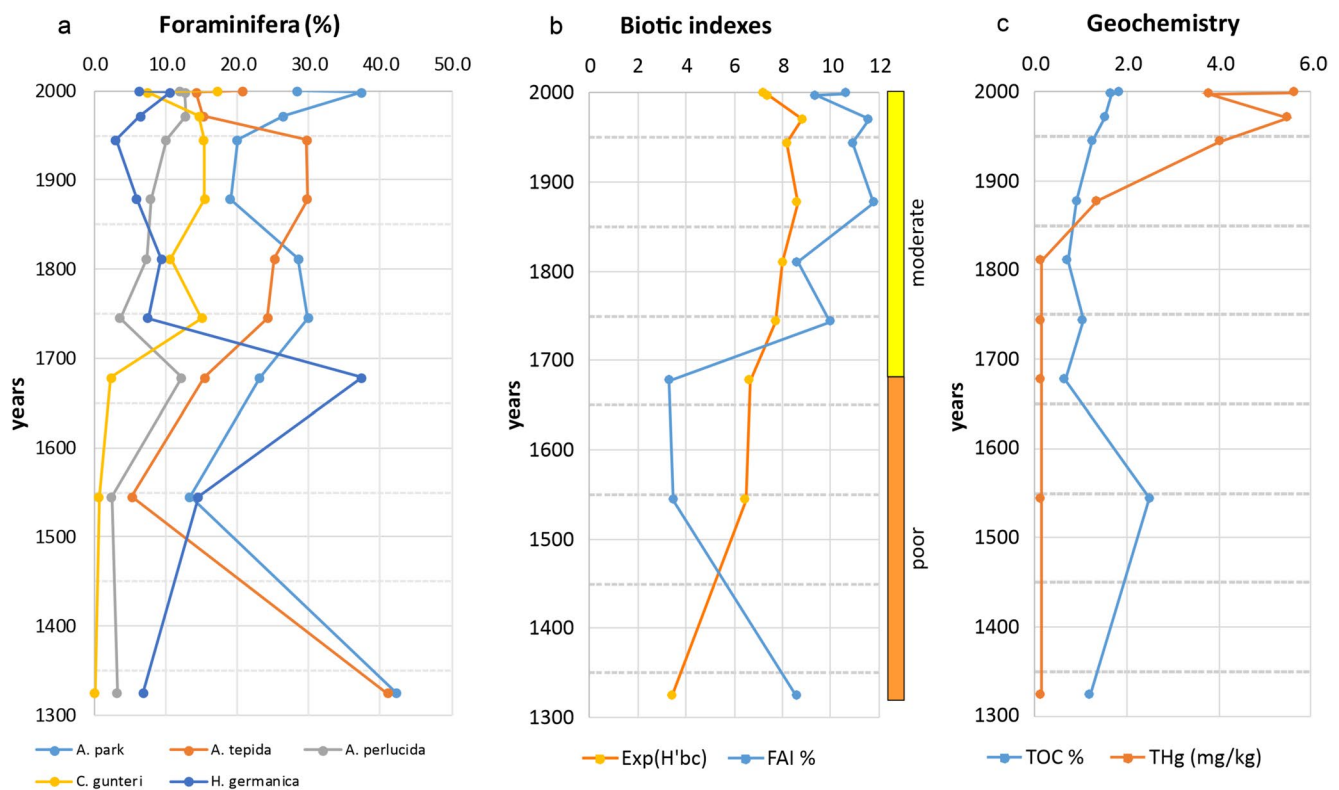


Fig. 9 (a) Distribution of the main foraminifera in core G3 in corresponding time; (b) distribution of $\text{Exp}(\text{H}'\text{bc})$ index and FAI (Foraminiferal Abnormality Index), with the corresponding EcoQS categories on the right in corresponding time; (c) distribution of TOC (%) and

total Hg (in mg/kg) in corresponding time. The timescale was calculated on the basis of the sedimentation rates estimated for the site by the ^{210}Pb activity-depth profile (Covelli et al., 2012)

The sedimentation rate for core G3, obtained from the examination of short-lived radionuclides, specifically the excess of ^{210}Pb and ^{137}Cs , is recorded at 0.13 cm/y (Covelli et al., 2012). This allows for investigation over a time span from the 14th century to the 2000s (Fig. 9). However, considering that the ^{210}Pb method allows the determination of sedimentation rates for the last 100–150 years, and that older ages in the core are extrapolated assuming a constant sedimentation rate, these should be treated with caution.

The MGL has served as a natural environment for rural exploitation for many centuries following the Middle Ages. However, over the last two centuries, human activities have prevented the lagoon from evolving naturally, limiting it into a controlled environment (Gatto & Marocco, 1992; Fontolan et al., 2012). The primary activities historically carried out in the area were fishing and aquaculture, until the establishment of the first fish-processing and shipbuilding enterprises in the mid-19th century (Cosolo et al., 2015). Only after the Second World War did small and medium-sized enterprises begin to develop significantly. Among these, the industrial hub of Torviscosa is particularly noteworthy, as it produces cellulose and artificial textile fibres. This production has been associated with the activities of the chlor-alkali plant, which used Hg-cells technology until

2008 (Covelli et al., 2012). In addition, the intensification of agricultural activity in the areas surrounding the lagoon over recent decades has resulted in a significant increase in nutrient loads, particularly nitrate (NO_3^-). This has led to eutrophication issues, especially in the western sector of the MGL (Acquavita et al., 2024 and references therein).

Mercury is one of the most significant contaminants in the MGL, consequently, the lagoon has been extensively monitored over the years, including historical reconstruction based on sediment core sample analyses (Covelli et al., 2012, 2017). Contaminated sediments in lagoon typically reach an average thickness of about 50 cm, with Hg concentrations up to 14 mg/kg in the eastern sector. The vertical distribution of THg in the core G3 distinctly marks the transition from pre-industrial to industrial activities. Considering that the natural background level of THg adopted here for the MGL was 0.13–0.04 mg/kg (Covelli et al., 2006, 2017), this transition is identifiable at approximately 20 cm depth, which corresponds to the period shortly after the late 19th century, when large-scale mining and ore-processing activities intensified at Idrija (Slovenia) (Covelli et al., 2012, 2017) (Fig. 9c). The rise in THg concentration in this area of MGL is mostly due to the deposition of fine sediment particles (mainly silt) rich in $\alpha\text{-HgS}$ (cinnabar), which

are conveyed into the lagoon by the Isonzo River (Covelli et al., 2007; Turritto et al., 2018).

When comparing the distribution of the most prevalent foraminifera, it is evident that *A. parkinsoniana* and *A. tepida* exhibit analogous distributions up to the early 19th century (30 cm depth in the core) (Fig. 9a), indicating inner-lagoon paleoenvironments. Around the late 19th century (20 cm depth in the core), in correspondence with the rising THg levels, *A. parkinsoniana* decreases whereas *A. tepida* with *C. gunteri* increase to then decrease in the more recent sediments (Fig. 9a, c). Although *A. tepida* and *C. gunteri* are considered species tolerant to the presence of heavy metals (e.g., Coccioni et al., 2009; Frontalini & Coccioni, 2011, Melis et al., 2019; Dimiza et al., 2022), their distribution in core G3 does not significantly coincide with the trend of THg. The prevalence of *A. parkinsoniana* by the mid-20th century (Fig. 9a), suggests conditions with greater marine influence than those observed today in this sector (see Table 3). The FAI% shows an increasing trend by the mid-18th century, clearly preceding the onset of the THg increase (Fig. 9b, c), which suggests that foraminiferal deformations were predominantly driven by factors other than the accumulation of this element.

Mercury, together with lead and zinc, are among the most toxic metals for the health of living organisms and significantly affects the physiological responses of foraminifera. Exposure to this element can induce cytological changes such as thickening of the inner organic lining, mitochondrial degeneration, degradation vacuole, and residual body proliferation (e.g., Frontalini et al., 2016, 2018; Tavera Martinez et al., 2023). However, Hg is a calcophilic element with a low affinity for carbonates minerals (White, 2013) and it is unlikely to interfere with the crystallisation processes of tests that lead to morphological anomalies, unlike other elements (e.g., Bergamin et al., 2019; Liu et al., 2025). Moreover, the elevated proportion of Hg in our sediments exists predominantly as α -HgS, rendering it less accessible for organismal uptake, which may explain the minimal impact of THg on foraminifera. Therefore, it cannot be recognized as the driving force for the occurrence of these foraminifera.

The concurrent increase in TOC may have further contributed to the observed increase in deformation frequency by the mid-18th century. The TOC value reaches highest levels around the mid-16th century, where there is a decrease in species richness and a dominance of *Helenina anderseni* and *Trochammina inflata* (Table S4), likely indicating a more isolated setting, probably associated with a marshland environment (Jorissen, 1987). A peak of *H. germanica* toward the end of the 17th century corresponds to the decrease in TOC, in contrast to what is observed in current sediments where, on the contrary, this species seems to have a good tolerance to the organic matter content (Fig. 7).

Subsequently, TOC tends to increase starting from the mid-18th century, in conjunction with the rise of FAI, but never exceeding a concentration of 2%. This increase could reflect multiple factors, including enhanced nutrient inputs from agricultural activities in the coastal hinterland; however, no direct evidence is available to confirm this hypothesis. The current distribution of foraminifera indicates that the trend of FAI is positively related to the trend of TOC and negatively with salinity (Fig. 4).

The downcore trend of Exp(H'bc), interpreted according to the criteria established by Bouchet et al. (2018, 2021), indicates **poor** Paleo-EcoQS conditions (ranging from 3.4 to 6.6) until the 17th century, luckily reflecting environments more isolated from the sea, with less water circulation. This is also evidenced by a low species richness. By the mid-18th century, a transition to moderate paleoecological conditions is observed (ranging from 7.2 to 8.8), which persist throughout the modern sediment record (Fig. 9b).

When compared with present-day conditions, these findings suggest that the moderate EcoQS observed in the inner Grado Lagoon is more likely attributable to natural environmental stress, as also documented in the historical foraminiferal record preceding the most intensive lagoon exploitation, in line with the 'estuarine quality paradox' (Elliott & Quintino, 2007). However, the intensification of industrial and agricultural activities in the lagoon during the 20th century may have further influenced the response of the foraminiferal assemblage, affecting the sensitive species *A. parkinsoniana* and promoting the increase of the more disturbance-tolerant taxa such as *A. tepida* and *C. gunteri* (e.g., Coccioni et al., 2009; Frontalini et al., 2010, 2013; Dimiza et al., 2022) (Fig. 9a).

Conclusions

The Marano and Grado Lagoon is a lentic, microtidal lagoon and forms part of the extensive system of transitional environments of the northern Adriatic Sea (Italy). It is a well-preserved wetland where conservation coexists with activities such as fishing, clam harvesting, shipping, and industry. However, the lagoon - particularly the eastern Grado sector - is known to be contaminated by mercury (Hg), which mainly originates from the transport of Hg-enriched material by the Isonzo River from the Idrija Hg mining district (Slovenia), active for more than 500 years until 1995.

For the first time, two sectors of the lagoon were investigated to examine the relationships between living foraminifera and the environmental conditions in which they occur. The lagoon was sampled during the late spring-summer season. Temperature and salinity data revealed thermo-haline

stratification (saltwedge) along the lower course of Natissa and Stella rivers, two of the major tributaries, whereas more saline and homogeneous conditions characterized the outer lagoon. The water column was well oxygenated in both sectors, with dissolved oxygen (DO) values consistently above 5 mg/L, indicating that the combination of riverine inputs and tidal exchange in this open-lagoon system efficiently sustain water oxygenation.

The analysis of the biocoenosis revealed living foraminifera in both investigated sectors (Marano and Grado). The most abundant and widespread species were *Ammonia tepida*, *A. parkinsoniana*, *Aubignyna perlucida*, *Cribrulphidium gunteri*, and *Haynesina germanica*, which are typical taxa of Mediterranean transitional environments. Foraminiferal assemblages showed varying degrees of morphological abnormalities, generally more pronounced in the inner lagoon. Based on organic matter content in the sediments, foraminiferal ecological groups ranging from EGI to EGIV were recognized. Elevated TOC content likely influenced foraminiferal distribution, allowing the identification of three main biotopes: an **urban biotope** dominated by *H. germanica*, an **inner lagoon biotope** characterized by *H. germanica* and *A. perlucida*, and an **outer lagoon biotope** dominated by *A. parkinsoniana*. The ecological quality of these biotopes increased from the urban sector toward the outer lagoon.

To investigate the effects of the most recent anthropogenic disturbances, the core G3 near the Natissa river mouth (Grado sector) was examined. Foraminiferal thanatocoenoses provided insights into environmental conditions through paleo-quality indices (Paleo-EcoQS), identifying shifts under recent human pressures related to industrial activities. Sedimentation rates, determined using radionuclides, indicate a transition to the most intensive phase of industrial activity at around 20 cm core depth, also associated with the intensification of mining-related inputs by the late 19th century. The distribution patterns of foraminifera are not significantly correlated with the increase in THg levels, which, despite the high concentrations, occurs in the sediments mainly as α -HgS, the least mobile form and the one that interacts least with the biotic component. An increase in foraminiferal deformations occurred prior to the onset of significant anthropogenic activity, suggesting that natural factors were the primary drivers, with current moderate EcoQS in this sector attributed to these natural stresses. This pattern reflects the ‘estuarine quality paradox,’ while 20th -century human activities may have affected the distribution of sensitive species by favouring those tolerant to disturbance.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-026-01723-4>.

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Author Contributions **Romana Melis:** Conceptualization, Methodology, Investigation, Data curation, Validation, Foraminiferal analysis, Writing - original draft, Supervision, Writing - review & editing. **Federico Floreani,** Methodology, Investigation, Geochemical analysis, Data curation, Validation, Writing - original draft, Writing - review & editing. **Kevin Terranova, Stefano Covelli:** Methodology, Analyses, Investigation, Data curation, Writing - review & editing.

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Data Availability Data will be available in Supplementary material.

Declarations

Ethical Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication All authors consent to publication.

Competing interests The authors declare that the work presented in the paper was not influenced by any known competing financial interests or relationships.

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References

- Acquavita, A., Bettoso, N., Blasutto, O., Pittaluga, F., & Orlandi, C. (2024). Seasonal and interannual variability of the trophic state in the Marano and Grado Lagoon (Adriatic Sea, Italy) during the 2011–2021 period. *Environments*, 11(7), Article 152. <https://doi.org/10.3390/environments11070152>
- Acquavita, A., Covelli, S., Emili, A., Berto, D., Faganeli, J., Giani, M., Horvat, M., Koron, N., & Rampazzo, F. (2012). Mercury in the sediments of the Marano and Grado Lagoon (northern Adriatic Sea): Sources, distribution and speciation. *Estuarine, Coastal and Shelf Science*, 113, 20–31. <https://doi.org/10.1016/j.ecss.2012.02.012>

- Ahmerkamp, S., Winter, C., Krämer, K., de Beer, D., Janssen, F., Friedrich, J., Kuypers, M. M. M., & Holtappels, M. (2017). Regulation of benthic oxygen fluxes in permeable sediments of the coastal ocean. *Limnology and Oceanography*, 62(5), 1935–1954. <https://doi.org/10.1002/lno.10544>
- Albani, A. D., & Serandrei Barbero, R. (1990). I foraminiferi della laguna e del golfo di Venezia. *Memorie di Scienze Geologiche*, 42, 271–341.
- Albani, A. D., Serandrei Barbero, R., & Donnici, S. (2007). Foraminifera as ecological indicators in the lagoon of Venice, Italy. *Ecological Indicators*, 7(2), 239–253. <https://doi.org/10.1016/j.ecolind.2006.01.003>
- Alve, E., Korsun, S., Schönfeld, J., Dijkstra, N., Golikova, E., Hess, S., Husum, K., & Panieri, G. (2016). ForAMBI: A sensitivity index based on benthic foraminiferal faunas from North-East Atlantic and Arctic fjords, continental shelves and slopes. *Marine Micropaleontology*, 122, 1–12. <https://doi.org/10.1016/j.marmicr.2015.11.001>
- Armynot du Châtelet, É., Bout-Roumazielles, V., Riboulleau, A., & Trentesaux, A. (2009). Sediment (grain size and clay mineralogy) and organic matter quality control on living benthic foraminifera. *Revue de Micropaléontologie*, 52(1), 75–84. <https://doi.org/10.1016/j.revmic.2008.10.002>
- Armynot du Châtelet, E., Debenay, J.-P., & Soulard, R. (2004). Foraminiferal proxies for pollution monitoring in moderately polluted harbors. *Environmental Pollution*, 127(1), 27–40. [https://doi.org/10.1016/S0269-7491\(03\)00256-2](https://doi.org/10.1016/S0269-7491(03)00256-2)
- Benito, X., Trobajo, R., Cearreta, A., & Ibáñez, C. (2016). Benthic foraminifera as indicators of habitat in a Mediterranean delta: Implications for ecological and palaeoenvironmental studies. *Estuarine, Coastal and Shelf Science*, 180, 97–113. <https://doi.org/10.1016/j.ecss.2016.06.001>
- Benson, B. B., & Krause, D. (1984). The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnology and Oceanography*, 29(3), 620–632. <https://doi.org/10.4319/lno.1984.29.3.0620>
- Bergamin, L., Di Bella, L., Ferraro, L., Frezza, V., Pierfranceschi, G., & Romano, E. (2019). Benthic foraminifera in a coastal marine area of the eastern Ligurian Sea (Italy): Response to environmental stress. *Ecological Indicators*, 96(1), 16–31. <https://doi.org/10.1016/j.ecolind.2018.08.050>
- Bettoso, N., Pittaluga, F., Predonzani, S., Zanello, A., & Acquavita, A. (2023). Mercury Levels in Sediment, Water and Selected Organisms Collected in a Coastal Contaminated Environment: The Marano and Grado Lagoon (Northern Adriatic Sea, Italy). *Applied Sciences*, 13(5), 3064. <https://doi.org/10.3390/app13053064>
- Biester, H., Gosar, M., & Covelli, S. (2000). Mercury speciation in sediments affected by dumped mining residues in the drainage area of the Idrija mercury mine, Slovenia. *Environmental Science & Technology*, 34(16), 3330–3336.
- Boehnert, S., Birkelund, A. R., Schmiedl, G., Kuhnert, H., Kuhn, G., Hass, H. C., & Hebbeln, D. (2020). Test deformation and chemistry of foraminifera as response to anthropogenic heavy metal input. *Marine Pollution Bulletin*, 155, 111112. <https://doi.org/10.1016/j.marpolbul.2020.111112>
- Bouchet, V. M. P., Alve, E., Rygg, B., & Telford, R. J. (2012). Benthic foraminifera provide a promising tool for ecological quality assessment of marine waters. *Ecological Indicators*, 23, 66–75. <https://doi.org/10.1016/j.ecolind.2012.03.011>
- Bouchet, V. M. P., Frontalini, F., Francescangeli, F., Sauriau, P. G., Geslin, E., Martins, M. V. A., Almogi-Labin, A., Avnaim-Katav, S., Di Bella, L., Cearreta, A., Coccioni, R., Costelloe, A., Dimiza, M. D., Ferraro, L., Haynert, K., Martínez-Colón, M., Melis, R., Schweizer, M., Triantaphyllou, M. V., Tsujimoto, A., Wilson, B., & Armynot du Chatelet, E. (2021). Indicative value of benthic foraminifera for biomonitoring: Assignment to ecological groups of sensitivity to total organic carbon of species from European intertidal areas and transitional waters. *Marine Pollution Bulletin*, 164, 112071. <https://doi.org/10.1016/j.marpolbul.2021.112071>
- Bouchet, V. M. P., Goberville, E., & Frontalini, F. (2018). Benthic foraminifera to assess Ecological Quality Statuses in Italian transitional waters. *Ecological Indicators*, 84, 130–139. <https://doi.org/10.1016/j.ecolind.2017.07.055>
- Bouchet, V. M. P., Seuront, L., Tsujimoto, A., Richirt, J., Frontalini, F., Tsuchiya, M., Matsuba, M., & Nomaki, H. (2023). Foraminifera and plastic pollution: Knowledge gaps and research opportunities. *Environmental Pollution*, 324, Article 121365. <https://doi.org/10.1016/j.envpol.2023.121365>
- Brambati, A. (1970). Provenienza, trasporto ed accumulo dei sedimenti recenti nelle Lagune di Marano e di Grado e nei litorali tra i fiumi Isonzo e Tagliamento. *Memorie della Società Geologica Italiana*, 9, 281–329.
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27(4), 325–349. <https://doi.org/10.2307/1942268>
- Bresler, V., & Yanko, V. (1995). Chemical ecology: A new approach to study living benthic epiphytic foraminifera. *Journal of Foraminiferal Research*, 25, 1–17.
- Buosi, C., Frontalini, F., Da Pelo, S., Cherchi, A., Coccioni, R., & Bucci, C. (2010). Foraminiferal proxies for environmental monitoring in the polluted lagoon of Santa Gilla (Cagliari, Italy). *Present Environment and Sustainable Development*, 4, 91–104.
- Carboni, M. G., Succi, M. C., Bergamin, L., Bella, L. D., Frezza, V., & Landini, B. (2009). Benthic foraminifera from two coastal lakes of southern Latium (Italy). preliminary evaluation of environmental quality. *Marine Pollution Bulletin*, 59(8), 268–280. <https://doi.org/10.1016/j.marpolbul.2009.08.010>
- Caruso, A., Cosentino, C., Tranchina, L., & Brai, M. (2011). Response of benthic foraminifera to heavy metal contamination in marine sediments (Sicilian coasts, Mediterranean Sea). *Chemistry and Ecology*, 27(1), 9–30.
- Chao, A., & Shen, T. J. (2003). Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample. *Environmental and Ecological Statistics*, 10(4), 429–443. <https://doi.org/10.1023/A:1026096204727>
- Chao, A., Ma, K. H., Hsieh, T. C., & Chiu, C. H. (2015). SpadeR: Species-richness prediction and diversity estimation in R. Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/
- Coccioni, R., Frontalini, F., Marsili, A., & Mana, D. (2009). Benthic foraminifera and trace element distribution: A case-study from the heavily polluted lagoon of Venice (Italy). *Marine Pollution Bulletin*, 59(8), 257–267. <https://doi.org/10.1016/j.marpolbul.2009.08.009>
- Cosolo, M., Sponza, S., & Fattori, U. (2015). La Laguna di Marano e Grado: un mosaico di biodiversità, un patrimonio da preservare. *Regione Autonoma Friuli Venezia Giulia*, 52 pp.
- Covelli, S. (2012). The MIRACLE Project: An integrated approach to understanding biogeochemical cycling of mercury and its relationship with lagoon clam farming. *Estuarine Coastal and Shelf Science*, 113, 1–6. <https://doi.org/10.1016/j.ecss.2012.08.011>
- Covelli, S., Acquavita, A., Piani, R., Predonzani, S., & De Vittor, C. (2009). Recent contamination of mercury in an estuarine environment (Marano lagoon, Northern Adriatic, Italy). *Estuarine, Coastal and Shelf Science*, 82(2), 273–284. <https://doi.org/10.1016/j.ecss.2009.01.021>
- Covelli, S., Fontolan, G., Faganeli, J., & Ogrinc, N. (2006). Anthropogenic markers in the Holocene stratigraphic sequence of the Gulf of Trieste (Northern Adriatic Sea). *Marine Geology*, 230(1–2), 29–51. <https://doi.org/10.1016/j.margeo.2006.03.013>

- Covelli, S., Langone, L., Acquavita, A., Piani, R., & Emili, A. (2012). Historical flux of mercury associated with mining and industrial sources in the Marano and Grado Lagoon (Northern Adriatic Sea). *Estuarine Coastal and Shelf Science*, 113, 7–19. <https://doi.org/10.1016/j.ecss.2011.12.038>
- Covelli, S., Petranich, E., Langone, L., Emili, A., & Acquavita, A. (2017). Historical sedimentary trends of mercury and other trace elements from two saltmarshes of the Marano and Grado lagoon (Northern Adriatic Sea). *Journal of Soils and Sediments*, 17(7), 1972–1985. <https://doi.org/10.1007/s11368-016-1618-8>
- Covelli, S., Piani, R., Acquavita, A., Predonzani, S., & Faganeli, J. (2007). Transport and dispersion of particulate Hg associated with a river plume in coastal Northern Adriatic environments. *Marine Pollution Bulletin*, 55(10), 436–450. <https://doi.org/10.1016/j.marpolbul.2007.09.006>
- de Jesus, M. S. S., Frontalini, F., Bouchet, V. M. P., Yamashita, C., Sartoretto, J. R., Figueira, R. C. L., & Sousa, S. H. M. (2020). Reconstruction of the palaeo-ecological quality status in an impacted estuary using benthic foraminifera: The Santos estuary (São Paulo State, SE Brazil). *Marine Environmental Research*, 162, Article 105121. <https://doi.org/10.1016/j.marenvres.2020.105121>
- Debenay, J.-P., & Guillou, J.-J. (2002). Ecological transitions indicated by foraminiferal assemblages in paralic environments. *Estuaries*, 25(6), 1107–1120. <https://doi.org/10.1007/BF02692208>
- Debenay, J.-P., Della Patrona, L., Herbland, A., & Goguenheim, H. (2009). The impact of easily oxidized material (EOM) on the meiofauna: Foraminifera abnormalities in shrimp ponds of New Caledonia; implications for environment and paleoenvironment survey. *Marine Pollution Bulletin*, 59, 323–335. <https://doi.org/10.1016/j.marpolbul.2009.08.012>
- Dimiza, M. D., Triantaphyllou, M. V., Koukousioura, O., Hallock, P., Simboura, N., Karageorgis, A. P., & Papathanasiou, E. (2016). The Foram stress index: A new tool for environmental assessment of soft-bottom environments using benthic foraminifera. A case study from the Saronikos Gulf, Greece, Eastern Mediterranean. *Ecological Indicators*, 60, 611–621. <https://doi.org/10.1016/j.ecolind.2015.07.030>
- Dimiza, M. D., Triantaphyllou, M. V., Portela, M., Koukousioura, O., & Karageorgis, A. P. (2022). Response of living benthic foraminifera to anthropogenic pollution and metal concentrations in Saronikos Gulf (Greece, Eastern Mediterranean). *Minerals*, 12(5), Article 591. <https://doi.org/10.3390/min12050591>
- Dorigo, L. (1965). La Laguna di Grado e le sue foci – Ricerche e rilievi idrografici, vol. 155, Magistrato delle Acque - Ufficio Idrografico (1965), 231 pp.
- Elliott, M., & Quintino, V. (2007). The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin*, 54(6), 640–645. <https://doi.org/10.1016/j.marpolbul.2007.02.003>
- Falace, A., Curiel, D., & Sfriso, A. (2009). Study of the macrophyte assemblages and application of phytobenthic indices to assess the ecological status of the Marano-Grado Lagoon (Italy). *Marine Ecology*, 30(4), 480–494. <https://doi.org/10.1111/j.1439-0485.2009.00300.x>
- Ferrarin, C., Umgiesser, G., Bajo, M., Bellafiore, D., De Pascalis, F., Ghezzi, M., Mattassi, G., & Scroccaro, I. (2010). Hydraulic zonation of the lagoons of Marano and Grado, Italy. A modelling approach. *Estuarine, Coastal and Shelf Science*, 87(4), 561–572. <https://doi.org/10.1016/j.ecss.2010.02.012>
- Floreani, F., Acquavita, A., Barago, N., Klun, K., Faganeli, J., & Covelli, S. (2022). Gaseous mercury exchange from water–air interface in differently impacted freshwater environments. *International Journal of Environmental Research and Public Health*, 19(13), Article 8149. <https://doi.org/10.3390/ijerph19138149>
- Fontanier, C., Jorissen, F. J., Lansard, B., Mouret, A., Buscail, R., Schmidt, S., Kerhervé, P., Buron, F., Zaragosi, S., Hunault, G., Ernoul, E., Artero, C., Anschutz, P., & Rabouille, C. (2008). Live foraminifera from the open slope between Grand Rhône and Petit Rhône Canyons (Gulf of Lions, NW Mediterranean). *Deep Sea Research Part I: Oceanographic Research Papers*, 55(11), 1532–1553. <https://doi.org/10.1016/j.dsr.2008.07.003>
- Fontolan, G., Pilon, S., Bezzi, A., Villalta, R., Lipizer, M., Triches, A., & D'Aiotti, A. (2012). Human impact and the historical transformation of saltmarshes in the Marano and Grado Lagoon, Northern Adriatic Sea. *Estuarine Coastal and Shelf Science*, 113, 41–56. <https://doi.org/10.1016/j.ecss.2012.02.007>
- Fouet, M. P. A., Singer, D., Coynel, A., Hélot, S., Howa, H., Lalande, J., Mouret, A., Schweizer, M., Tcherkez, G., & Jorissen, F. J. (2022). Foraminiferal distribution in two estuarine intertidal mudflats of the French Atlantic Coast: Testing the marine influence index. *Water*, 14(4), Article 645. <https://doi.org/10.3390/w14040645>
- Francescangeli, F., Quijada, M., Armynot du Châtelet, E., Frontalini, F., Trentesaux, A., Billon, G., & Bouchet, V. M. P. (2020). Multidisciplinary study to monitor consequences of pollution on intertidal benthic ecosystems (Hauts de France, English Channel, France): Comparison with natural areas. *Marine Environmental Research*, 160, Article 105034. <https://doi.org/10.1016/j.marenvres.2020.105034>
- Franzo, A., Asioli, A., Roscioli, C., Patrolocco, L., Bazzaro, M., Del Negro, P., & Cibic, T. (2019). Influence of natural and anthropogenic disturbances on foraminifera and free-living nematodes in four lagoons of the Po Delta system. *Estuarine, Coastal and Shelf Science*, 220, 99–110. <https://doi.org/10.1016/j.ecss.2019.02.039>
- Franzo, A., Caffau, M., Nasi, F., Marroccchino, E., Paletta, M. G., Bazzaro, M., & Cibic, T. (2023). Benthic foraminifera for the ecological status assessment of tourist marinas. *Ecological Indicators*, 147, Article 110006. <https://doi.org/10.1016/j.ecolind.2023.110006>
- Frodge, J. D., Thomas, G. L., & Pauley, G. B. (1990). Effects of canopy formation by floating and submergent aquatic macrophytes on the water quality of two shallow Pacific Northwest lakes. *Aquatic Botany*, 38(2), 231–248. [https://doi.org/10.1016/0304-3770\(90\)90008-9](https://doi.org/10.1016/0304-3770(90)90008-9)
- Frontalini, F., & Coccioni, R. (2008). Benthic foraminifera for heavy metal pollution monitoring: A case study from the central Adriatic Sea coast of Italy. *Estuarine, Coastal and Shelf Science*, 76, 404–417.
- Frontalini, F., & Coccioni, R. (2011). Benthic foraminifera as bioindicators of pollution: A review of Italian research over the last three decades. *Revue de Micropaléontologie*, 54(2), 115–127. <https://doi.org/10.1016/j.revmic.2011.03.001>
- Frontalini, F., Buosi, C., Da Pelo, S., Coccioni, R., Cherchi, A., & Bucci, C. (2009). Benthic foraminifera as bio-indicators of trace element pollution in the heavily contaminated Santa Gilla lagoon (Cagliari, Italy). *Marine Pollution Bulletin*, 58(6), 858–877. <https://doi.org/10.1016/j.marpolbul.2009.01.015>
- Frontalini, F., Coccioni, R., & Bucci, C. (2010). Benthic foraminiferal assemblages and trace element contents from the lagoons of Orbetello and Lesina. *Environmental Monitoring and Assessment*, 170(1–4), 245–260. <https://doi.org/10.1007/s10661-009-1229-6>
- Frontalini, F., Curzi, D., Cesarini, E., Canonico, B., Giordano, F. M., De Matteis, R., et al. (2016). Mercury-pollution induction of intracellular lipid accumulation and lysosomal compartment amplification in the benthic foraminifer *Ammonia parkinsoniana*. *PLoS One*, 11(9), Article e0162401. <https://doi.org/10.1371/journal.pone.0162401>
- Frontalini, F., Margaritelli, G., Francescangeli, F., Rettori, R., du Châtelet, E. A., & Coccioni, R. (2013). Benthic foraminiferal

- assemblages and biotopes in a coastal lake: The case study of Lake Varano (Southern Italy). *Acta Protozoologica*, 52(3), 147–160.
- Frontalini, F., Nardelli, M. P., Curzi, D., Martín-González, A., Sabatini, A., Negri, A., Losada, M. T., Gobbi, P., Coccioni, R., & Bernhard, J. M. (2018). Benthic foraminiferal ultrastructural alteration induced by heavy metals. *Marine Micropaleontology*, 138, 83–89. <https://doi.org/10.1016/j.marmicro.2017.10.009>
- Frontalini, F., Semprucci, F., du Châtelet, E. A., Francescangeli, F., Margaritelli, G., Rettori, R., Spagnoli, F., Balsamo, M., & Coccioni, R. (2014). Biodiversity trends of the meiofaunal and foraminiferal assemblages of Lake Varano (southern Italy). *Proceedings of the Biological Society of Washington*, 127(1), 7–22. <https://doi.org/10.2988/0006-324X-127.1.7>
- García-Ordiales, E., Higuera, P., Esbrí, J. M., Roqueñí, N., & Loredó, J. (2019). Seasonal and spatial distribution of mercury in stream sediments from Almadén mining district. *Geochemistry: Exploration, Environment, Analysis*, 19(2), 121–128. <https://doi.org/10.1144/geochem2018-029>
- Gatto, F., & Marocco, R. (1992). Caratteri morfologici ed antropici della Laguna di Grado (Alto Adriatico). *Gortania-Atti del Museo Friulano di Storia Naturale*, 14, 19–42.
- Geslin, E., Stouff, V., Debenay, J. P., & Lesourd, M. (2000). Environmental variation and foraminiferal test abnormalities. In R. E. Martin (Ed.), *Environmental micropaleontology* (Topics in Geobiology, 15, 191–215). Springer. https://doi.org/10.1007/978-1-4615-4167-7_10
- Giani, M., Berto, D., Rampazzo, F., Savelli, F., Alvisi, F., Giordano, P., Ravaioli, M., & Frascari, F. (2009). Origin of sedimentary organic matter in the north-western Adriatic Sea. *Estuarine, Coastal and Shelf Science*, 84(4), 573–583. <https://doi.org/10.1016/j.ecss.2009.07.031>
- Gray, J. E., Theodorakos, P. M., Bailey, E. A., & Turner, R. R. (2000). Distribution, speciation, and transport of mercury in stream-sediment, stream-water, and fish collected near abandoned mercury mines in southwestern Alaska, USA. *Science of The Total Environment*, 260(1), 21–33. [https://doi.org/10.1016/S0048-9697\(00\)00539-8](https://doi.org/10.1016/S0048-9697(00)00539-8)
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). Past: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica*, 4(1), 9pp.
- Hayward, B. W., Holzmann, M., Langer, M. R., Parker, J. H., & Tsuchiya, M. (2025). Molecular and morphological taxonomy and biogeography of living Cribroelphidiidae, Elphidiellidae, Elphidiidae, Haynesinidae and related taxa (Foraminifera, Rotalioida). *Micropaleontology*, 71, 433–803. <https://doi.org/10.47894/mpal.71.5.01>
- Hayward, B. W., Holzmann, M., Pawlowski, J., Parker, J. H., Kaushik, T., Toyofuku, M. S., & Tsuchiya, M. (2021). Molecular and morphological taxonomy of living *Ammonia* and related taxa (Foraminifera) and their biogeography. *Micropaleontology*, 67(2–3), 109–274. <https://doi.org/10.47894/mpal.67.3.01>
- Hedges, J. I., & Stern, J. H. (1984). Carbon and nitrogen determinations of carbonate-containing solids. *Limnology and Oceanography*, 29(3), 657–663. <https://doi.org/10.4319/lo.1984.29.3.0657>
- Hess, S., Alve, E., Andersen, T. J., & Joranger, T. (2020). Defining ecological reference conditions in naturally stressed environments – How difficult is it? *Marine Environmental Research*, 156, Article 104885. <https://doi.org/10.1016/j.marenvres.2020.104885>
- Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54(2), 427–432. <https://doi.org/10.2307/1934352>
- Horton, B. P., & Murray, J. W. (2007). The roles of elevation and salinity as primary controls on living foraminiferal distributions: Cowpen Marsh, Tees Estuary, UK. *Marine Micropaleontology*, 63(3), 169–186. <https://doi.org/10.1016/j.marmicro.2006.11.006>
- Jonsson, S., Skjellberg, U., Nilsson, M. B., Westlund, P. O., Shchukarev, A., Lundberg, E., & Björn, E. (2012). Mercury methylation rates for geochemically relevant HgII species in sediments. *Environmental Science & Technology*, 46(21), 11653–11659. <https://doi.org/10.1021/es3015327>
- Jorissen, F. J. (1987). The distribution of benthic foraminifera in the Adriatic Sea. *Marine Micropaleontology*, 12, 21–48. [https://doi.org/10.1016/0377-8398\(87\)90012-0](https://doi.org/10.1016/0377-8398(87)90012-0)
- Jorissen, F. J., Nardelli, M. P., Almogi-Labin, A., Barras, C., Bergamin, L., Bicchi, E., El Kateb, A., Ferraro, L., McGann, M., Morigi, C., Romano, E., Sabbatini, A., Schweizer, M., & Spezzaferri, S. (2018). Developing Foraminifera-AMBI for biomonitoring in the Mediterranean: Species assignments to ecological categories. *Marine Micropaleontology*, 140, 33–45. <https://doi.org/10.1016/j.marmicro.2017.12.006>
- Jorissen, F., Fouet, M., Armynot du Châtelet, É., Barras, C., Bouchet, V., Daviray, M., Francescangeli, F., Geslin, E., Le Moigne, D., Licari, L., Mojtahid, M., Nardelli, M. P., Pavard, J. C., Rolland, A., Schweizer, M., & Singer, D. (2023). Foraminifères estuariens de la façade atlantique française: Guide de détermination, *Zenodo*. <https://doi.org/10.5281/zenodo.14197875>
- Joshi, N., Arya, P. C., & Saulnier-Talbot, É. (2025). Benthic foraminifera as useful bioindicators of heavy metal and organic enrichment in northern temperate coastal zones: A comprehensive review. *Journal of Coastal Research*, 41(3), 516–535.
- Liu, Z., He, M., Han, P., Dong, S., & Chen, X. (2025). Bio-monitoring heavy metal pollution: Insights from benthic foraminiferal assemblages and shell morphology. *Frontiers in Marine Science*, 12, Article 1716252. <https://doi.org/10.3389/fmars.2025.1716252>
- Lucena-Moya, P., Gómez-Rodríguez, C., & Pardo, I. (2012). Spatio-temporal variability in water chemistry of Mediterranean coastal lagoons and its management implications. *Wetlands*, 32(6), 1033–1045. <https://doi.org/10.1007/s13157-012-0334-4>
- Martins, A. M. V., Zaaaboub, N., Aleya, L., Frontalini, F., Pereira, E., Miranda, P., Mane, M., Rocha, F., Laut, L., & El Bouret, M. (2015). Environmental quality assessment of Bizerte Lagoon (Tunisia) using living foraminifera assemblages and a multiproxy approach. *PLoS One*, 10(9), Article e0137250. <https://doi.org/10.1371/journal.pone.0137250>
- McLusky, D. S., & Elliott, M. (2007). Transitional waters: A new approach, semantics or just muddying the waters? *Estuarine, Coastal and Shelf Science*, 71(3), 359–363. <https://doi.org/10.1016/j.ecss.2006.08.025>
- Melis, R., & Covelli, S. (2013). Distribution and morphological abnormalities of recent foraminifera in the Marano and Grado Lagoon (North Adriatic Sea, Italy). *Mediterranean Marine Science*, 14(2), 432. <https://doi.org/10.12681/mms.351>
- Melis, R., Celio, M., Bouchet, V. M. P., Varagona, G., Bazzaro, M., Crosera, M., & Pugliese, N. (2019). Seasonal response of benthic foraminifera to anthropogenic pressure in two stations of the Gulf of Trieste (Northern Adriatic Sea, Italy): The marine protected area of Miramare versus the Servola water sewage outfall. *Mediterranean Marine Science*, 20(1), 120–141. <https://doi.org/10.12681/mms.16154>
- Moreno, J., Moreno, F., Fatela, F., Leorri, E., Leira, M., Masqué, P., & Freitas, M. C. (2025). Patterns of ecological quality in Portuguese transitional waters over the last five decades: A framework based on benthic foraminifera for the Sado Estuary. *Marine Pollution Bulletin*, 218, Article 118215. <https://doi.org/10.1016/j.marpolbul.2025.118215>
- O'Brien, P. A. J., Polovodova Asteman, I., & Bouchet, V. M. P. (2021). Benthic foraminiferal indices and environmental quality assessment of transitional waters: A review of current challenges and future research perspectives. *Water*, 13(14), Article 1898. <https://doi.org/10.3390/w13141898>

- Parent, B., Barras, C., Bicchi, E., Charrieau, L. M., Choquel, C., Bénéteau, É., Maillet, G. M., & Jorissen, F. J. (2021). Comparison of four foraminiferal biotic indices assessing the environmental quality of coastal Mediterranean soft bottoms. *Water*, 13(22), Article 3193. <https://doi.org/10.3390/w13223193>
- Piani, R., Covelli, S., & Biester, H. (2005). Mercury contamination in Marano Lagoon (Northern Adriatic Sea, Italy): Source identification by analyses of Hg phases. *Applied Geochemistry*, 20(8), 1546–1559. <https://doi.org/10.1016/j.apgeochem.2005.04.003>
- Pittaluga, F., Aleffi, I. F., Bettoso, N., Blasutto, O., Celio, M., Codarin, A., Cumani, F., Faresi, L., Guiatti, D., Orlandi, C., Zanello, A., & Acquavita, A. (2022). The SHAPE Project: An innovative approach to understanding seasonal and diel dissolved oxygen dynamics in the Marano and Grado Lagoon (Adriatic Sea) under the WFD/2000/60/CE. *Journal of Marine Science and Engineering*, 10(2), 208. <https://doi.org/10.3390/jmse10020208>
- Pusceddu, A., Gambi, C., Manini, E., & Danovaro, R. (2007). Trophic state, ecosystem efficiency and biodiversity of transitional aquatic ecosystems: Analysis of environmental quality based on different benthic indicators. *Chemistry and Ecology*, 23(6), 505–515. <https://doi.org/10.1080/02757540701760494>
- Richirt, J., Schweizer, M., Mouret, A., Quinchard, S., Saad, S. A., Bouchet, V. M. P., Wade, C. M., & Jorissen, F. J. (2021). Biogeographic distribution of three phylotypes (T1, T2 and T6) of *Ammonia* (foraminifera, Rhizaria) around Great Britain: New insights from combined molecular and morphological recognition. *Journal of Micropalaeontology*, 40(1), 61–74. <https://doi.org/10.5194/jm-40-61-2021>
- Rimondi, V., Bardelli, F., Benvenuti, M., Costagliola, P., Gray, J. E., & Lattanzi, P. (2014). Mercury speciation in the Mt. Amiata mining district (Italy): Interplay between urban activities and mercury contamination. *Chemical Geology*, 380, 110–118. <https://doi.org/10.1016/j.chemgeo.2014.04.023>
- Robbins, J. A. (1978). Geochemical and geophysical application of radioactive lead. In J. O. Nriagu (Ed.), *The Biogeochemistry of Lead in the Environment* (pp. 285–393). Elsevier.
- Romano, E., Bergamin, L., Ausili, A., Celia Magno, M., & Gabellini, M. (2016). Evolution of the anthropogenic impact in the Augusta Harbor (Eastern Sicily, Italy) in the last decades: Benthic foraminifera as indicators of environmental status. *Environmental Science and Pollution Research*, 23(11), 10514–10528. <https://doi.org/10.1007/s11356-015-5783-x>
- Romano, E., Bergamin, L., Finioia, M. G., Carboni, M. G., Ausili, A., & Gabellini, M. (2008). Industrial pollution at Bagnoli (Naples, Italy): Benthic foraminifera as a tool in integrated programs of environmental characterisation. *Marine Pollution Bulletin*, 56(3), 439–457. <https://doi.org/10.1016/j.marpolbul.2007.11.003>
- Sabbatini, A., Bonatto, S., Bianchelli, S., Pusceddu, A., Danovaro, R., & Negri, A. (2012). Foraminiferal assemblages and trophic state in coastal sediments of the Adriatic Sea. *Journal of Marine Systems*, 105–108, 163–174. <https://doi.org/10.1016/j.jmarsys.2012.07.009>
- Sabbatini, A., Bonatto, S., Gooday, A. J., Morigi, C., Pancotti, I., Pucci, F., & Negri, A. (2010). Modern benthic foraminifera at Northern shallow sites of Adriatic Sea and soft-walled, monothalamous taxa: A brief overview. *Micropaleontology*, 56(3/4), 359–376.
- Saraswat, R., Kouthankar, M., Kurtarkar, S. R., Nigam, R., Naqvi, S. W. A., & Linshy, V. N. (2015). Effect of salinity induced pH/alkalinity changes on benthic foraminifera: A laboratory culture experiment. *Estuarine Coastal and Shelf Science*, 153, 96–107. <https://doi.org/10.1016/j.ecss.2014.12.005>
- Sathicq, M. B., Nicolosi Gelis, M. M., & Cocherio, J. (2020). Calculating autoecological data (optima and tolerance range) for multiple species with the ‘optimos.prime’ R package. *Austral Ecology*, 45(6), 845–850. <https://doi.org/10.1111/aec.12868>
- Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., & Spezzaferri, S. (2012). The FOBIMO (FORaminiferal Bio-MONitoring) initiative—Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. *Marine Micropaleontology*, 94–95, 1–13. <https://doi.org/10.1016/j.marmicro.2012.06.001>
- Schönfeld, J., Beccari, V., Schmidt, S., & Spezzaferri, S. (2021). Biometry and taxonomy of Adriatic *Ammonia* species from Bellaria-Igea Marina (Italy). *Journal of Micropalaeontology*, 40(2), 195–223. <https://doi.org/10.5194/jm-40-195-2021>
- Serandrei-Barbero, R., Albani, A. D., & Donnici, S. (2008). Atlante dei Foraminiferi della Laguna di Venezia. *Istituto Veneto di Scienze, Lettere ed Arti, Venezia*, 130 pp., ISBN-10: 8895996046.
- Sgarrella, F., & Moncharmont Zei, M. (1993). Benthic foraminifera of the Gulf of Naples (Italy): Systematics and autoecology. *Bollettino Della Società Paleontologica Italiana*, 32(2), 145–264.
- Shepard, F. P. (1954). Nomenclature based on sand-silt-clay ratios. *Journal of Sedimentary Petrology*, 24, 151–158.
- Stouff, V., Geslin, E., Debenay, J.-P., & Lesourd, M. (1999). Origin of morphological abnormalities in *Ammonia* (foraminifera): Studies in laboratory and natural environments. *Journal of Foraminiferal Research*, 29(2), 152–170. <https://doi.org/10.2113/GSJFR.29.2.152>
- Tavera Martínez, L., Marchant, M., & Urbina, M. (2023). Are physiological responses in foraminifera reliable environmental stress bioindicators? A systematic review. *Environmental Research*, 216(2), Article 114515. <https://doi.org/10.1016/j.envres.2022.114515>
- Triches, A., Pillon, S., Bezzi, A., Lipizer, M., Gordini, E., Villalta, R., Menchini, G., Fontolan, G., & Ramella, R. (2011). *Carta batimetrica della Laguna di Marano e Grado*. Regione Autonoma Friuli Venezia Giulia – A cura di Autorità di Bacino Regionale del Friuli Venezia Giulia, Commissario Delegato per l'emergenza socio-economica ambientale determinatasi nella Laguna di Marano e Grado, Dipartimento di Geoscienze dell'Università di Trieste; OGS – Istituto Nazionale di Oceanografia e di Geofisica Sperimentale; Arti Grafiche Friulane, Imoco spa.
- Turritto, A., Acquavita, A., Bezzi, A., Covelli, S., Fontolan, G., Petranich, E., Piani, R., & Pillon, S. (2018). Suspended particulate mercury associated with tidal fluxes in a lagoon environment impacted by cinnabar mining activity (Northern Adriatic Sea). *Journal of Environmental Sciences*, 68, 100–113. <https://doi.org/10.1016/j.jes.2017.12.009>
- U.S. Environmental Protection Agency. (1998). *EPA method 7473 (SW-846): Mercury in solids and solutions by thermal decomposition, amalgamation, and atomic absorption spectrophotometry (Revision 0)*. U.S. Environmental Protection Agency.
- Watanabe, K., Kasai, A., Antonio, E. S., Suzuki, K., Ueno, M., & Yamashita, Y. (2014). Influence of salt-wedge intrusion on ecological processes at lower trophic levels in the Yura Estuary, Japan. *Estuarine, Coastal and Shelf Science*, 139, 67–77. <https://doi.org/10.1016/j.ecss.2013.12.018>
- Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology*, 30, 377–392.
- White, W. M., & Geochemistry (2013). Wiley-Blackwell Publication, 660 pp., ISBN-10: 0470656689; ISBN-13: 978-0470656686.
- WoRMS Editorial Board (2025). *World Register of Marine Species*. Retrieved December 20th, 2025, from <https://www.marinespecies.org>
- Yanko, V., Ahmad, M., & Kaminski, M. (1998). Morphological deformities of benthic foraminiferal tests in response to pollution by heavy metals: Implications for pollution monitoring. *Journal of Foraminiferal Research*, 28(3), 177–200.