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Late Holocene changes in the composition of foraminiferal, ostracod and molluscan communities in condensed sediments (northern Adriatic Sea)

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Abstract

Human-induced changes in sedimentation rates, pollution, and eutrophication significantly transformed the benthic communities in the northern Adriatic Sea during the late Holocene, particularly in recent centuries. Fossil assemblages from sediment cores record these changes but are often affected by stratigraphic condensation and mixing. Here, we show that molluscan, foraminiferal, and ostracod assemblages preserved in a condensed sediment core collected off the Po delta at 31 m water depth, still archive information about the composition of benthic communities prior to anthropogenic changes. All three groups exhibit a similar trend in total abundance (density): a gradual increase peaking in a 10 cm-thick shelly lag (≈ 2 – 6 kyr BP) with millennial time-averaging, followed by a significant decline in the uppermost 5 cm of highstand silts (representing the past 2 kyr BP) with centennial time-averaging. The molluscan assemblage in the shelly lag integrates across several baseline community states. The assemblage mainly comprises shallow-subtidal filter feeders and soft-bottom infauna, with the bivalve *Varicorbula gibba* and the gastropod *Turritellinella tricarinata* dominating and increasing in proportional abundance in the highstand silts. The ostracod and benthic foraminiferal assemblages in the shelly lag are dominated by opportunistic species such as *Cytheridea neapolitana*, *Ammonia beccarii*, and *Haynesina germanica*. In contrast, the foraminifera *Nonionella* sp. and the ostracod *Loxoconcha* sp. increase in proportional abundance in the highstand silts, characterised by an increase in filter-feeders among the molluscs, infaunalisation and a decrease in epiphytic species. Although an increase in net sediment accumulation primarily causes the decline in fossil density in the uppermost part of the core, upward changes in the relative abundance of species and functional groups reveal a difference between the baseline and impacted community states. Therefore, the time-averaged fossil assemblage in the shelly lag provides a valuable long-term record of an ecosystem in the region before human impact.

Keywords: Mollusca, Foraminifera, Ostracoda, fossil assemblages, palaeoecology, community responses, human impact

1. INTRODUCTION

1.1. Combining Conservation and Stratigraphic Palaeobiology

Conservation palaeobiology aims to expand the temporal perspective of conservation science by integrating ecology and palaeobiology to protect ecosystems and enhance biodiversity and to evaluate ecological responses to both human activities and natural environmental changes (JACKSON, 2001; WILLIS & BIRKS, 2006; JACKSON & HOBBS, 2009; DIETL & FLESSA, 2011). The differences between recent benthic communities and palaeoecological baselines observed in the Pleistocene and Holocene fossil records can be used to assess the magnitude and timing of human impacts on populations, communities and ecosystems (DIETL & FLESSA, 2011). The interdisciplinary nature of conservation palaeobiology provides a comprehensive approach to understand ecosystem changes by incorporating palaeobiological, archaeological, and historical data. Even the youngest fossil records can be affected by biases due to the variable completeness and resolution of fossil assemblages (e.g., SCARPONI et al., 2017; TOMAŠOVÝCH et al., 2023; NAWROT et al., 2024; ZECCHIN et al., 2024). These biases can impact our understanding of temporal population and community dynamics (AGER, 1973; PATZKOWSKY & HOLLAND, 2012). Stratigraphic palaeobiology is a subdiscipline of palaeobiology that examines spatial and temporal patterns of fossil distribution in a stratigraphic context. This approach explicitly recognises that both biological processes, such as speciation, extinction, and community assembly, as well as stratigraphic processes, including sedimentation, erosion, and condensation, impact the fossil record (DRESOW, 2023). Consequently, the integration of conservation palaeobiology with the toolkit used by stratigraphic palaeobiology can provide more rigorous reconstructions of the recent geological past and increase the reliability of the data on the long-term history of human impact on ecosystems.

Table 1. Selected stressors impacting the benthic ecosystem in the northern Adriatic.

Stressor	Causes (simplified)	Impact on the benthic ecosystem	References (selection)
Hypoxia and anoxia	Human-induced eutrophication in combination with ocean stratification	Mass mortalities; alteration of sediment biogeochemistry; alteration of faunal composition	STACHOWITSCH, 1984; JUSTIĆ, 1991; STACHOWITSCH, 2014
Mucilage aggregates	Diatom-blooms after human-induced eutrophication	Anoxia; mass mortalities	STACHOWITSCH et al., 1990; DEVESCOVI & IVEŠA, 2007; KRAUS & IVOŠEVIĆ DENARDIS, 2023
Chemical pollution	Human-induced influx of heavy metals, organic pollutants or other	Alteration of faunal composition; mass mortalities	Molluscs: GALLMETZER et al., 2017; SCHNEDL et al., 2018 Benthic foraminifera: FRONTALINI & COCCIONI, 2011; MELIS et al., 2019 Ostracods: BERGIN et al., 2006
Alien species	Shipping, aquaculture activities, or a natural range expansion	Competitive interactions with native species; alteration of the faunal composition; parasitism	ORLANDO-BONACA, 2010; OCCHIPINTI-AMBROGI et al., 2010; CROCETTA, 2011
Bottom trawling	Still used fishing technique	Alteration of faunal composition; decrease in faunal densities; habitat loss	KOLLMANN & STACHOWITSCH, 2008; PITCHER et al., 2022
Heat waves	Human-induced climate change	Alteration on faunal composition; mortality of temperature sensitive species; alien invasions, habitat loss	PAIRAUD et al., 2014; GÓMEZ-GRAS et al., 2022

1.2. Stressors in the northern Adriatic

The northern Adriatic Sea is a dynamic and diverse ecosystem that has experienced significant changes due to the combined effects of natural processes and human activities over the past millennia. This has led to considerable alterations in the composition of marine communities, making it one of the most disturbed continental shelves on Earth (LOTZE et al., 2011; GALLMETZER et al., 2019; HASELMAIR et al., 2021; SCARPONI et al., 2022) (see Table 1). It is essential to analyse fossil assemblages to understand the long-term effects on local ecosystems, as systematic ecological monitoring only began in the 20th century. Data from the Holocene fossil record show that the faunal composition in the northern Adriatic has changed significantly over the past millennia and centuries (e.g., TOMAŠOVÝCH et al., 2017, 2018; GALLMETZER et al., 2019; SCARPONI et al., 2022). While some species have drastically decreased in abundance, a few opportunistic species survived and proliferated (GALLMETZER et al., 2017; HASELMAIR et al., 2021). However, most studies that have examined Holocene changes in the composition of benthic assemblages within sediment cores have focused on single taxonomic groups, such as macrofauna (e.g., molluscs) (SCARPONI et al., 2017; GALLMETZER et al., 2017; MAUTNER et al., 2018) or microfauna (e.g., foraminifera or ostracods) (BARMAWIDJAJA et al., 1995; VIDOVIĆ et al., 2016; PICONE et al., 2008). For instance, benthic foraminifera in the sediments of the Po delta have recorded increased eutrophication and a decline in oxygen availability, which are linked to anthropogenic changes in the Po outflow (BARMAWIDJAJA et al., 1995). Comprehensive quantitative studies that assess the abundance and diversity of multiple phyla simultaneously remain rare (see, e.g., D'AMICO et al., 2013; ROSSI et al., 2021; AZZARONE et al., 2020). Furthermore, few multi-taxon studies connect biotic signals to sediment parameters such as grain-sizes or organic matter content (BARBIERI et al., 2019, 2021).

1.3. Objectives of the present study

Quaternary sequences provide a significant advantage for studying palaeoecological patterns within a sequence stratigraphic framework. The assemblages primarily consist of extant taxa with well-documented ecological, biogeographic, and phylogenetic relationships. This palaeoecological data can be compared with assemblage states observed in modern environments, offering insights into how human impacts affect the functioning of contemporary ecosystems.

In this study, we take a comprehensive approach to examine Holocene changes (over the past ≈ 10,000 years) in the composition of assemblages formed by three different phyla, all within the context of the sequence stratigraphic framework, at a site located in the central part of the northern Adriatic Sea. This method, which combines conservation and stratigraphic palaeobiology, has been successfully applied at other Holocene locations in the northern Adriatic Sea (e.g., WITTMER et al., 2014; GALLMETZER et al., 2019; BARBIERI et al., 2019). However, none of the previous studies directly compared responses of macro- and microfaunal assemblages to natural and human-induced environment changes.

BERENSMEIER et al. (2023) described the geochronology, geochemistry, and molluscan assemblages at this coring location. Despite intensive stratigraphic condensation and mixing of the fossil record at this site, the assemblages and sediments enriched in metals and organic carbon in the uppermost core increments reveal evidence of human impacts.

Furthermore, the core-chronological data from this study, based on molluscs, was used in a palaeoecological study of core data from the northern Adriatic by TOMAŠOVÝCH et al. (2024). They found that species diversity in fossil assemblages increases with the time averaging of samples, which is influenced by varying sediment accumulation.

The main objectives of the present study are to: (i) describe the faunal composition of molluscan, benthic foraminiferal, and ostracod fossil assemblages; (ii) analyse their diversity and species composition within the stratigraphic context; and (iii) assess whether the three types of assemblages respond differently to human impacts.

2. MATERIALS AND METHODS

2.1. Sampling locality and stratigraphic framework

In June 2017, the team of F. S. Poseidon-cruise no. 514 took the gravity core POS514-GC25-5 in the western part of the northern Adriatic Sea, ≈ 32 km to the East of the Po delta Pila

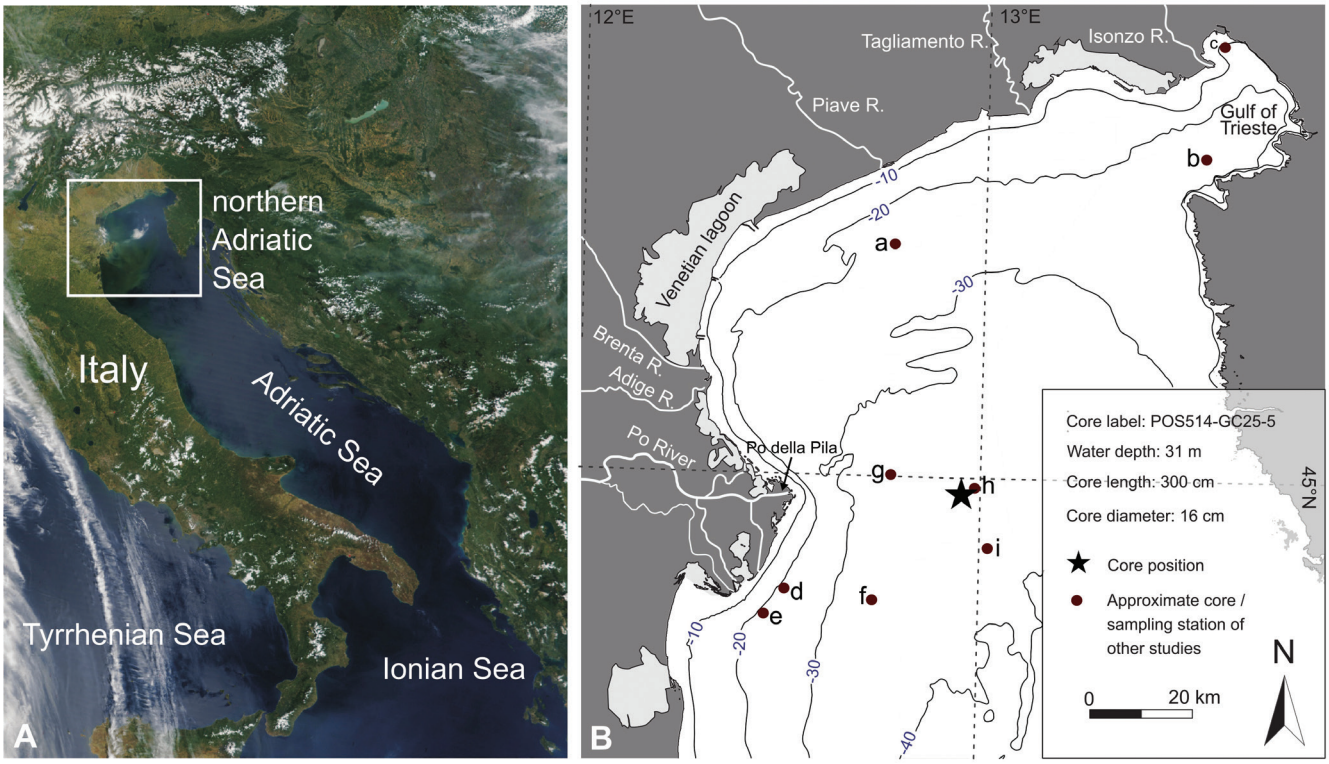

Figure 1. Location of the sampling station in the northern Adriatic Sea. **a** Satellite image of Italy and its surrounding sub-basins of the Mediterranean Sea. MODIS satellite image (Terra) of the northern Adriatic coast (EOIMAGES, 2024), collected on day 335, 2002, at 1030 Greenwich Mean Time (GMT); **b** Bathymetric map of the study area, including the core position, ca. 30 km off the Po della Pila mouth. Approximate core/sampling station from other studies: a – GALLMETZER et al., 2019, core Venice; b – GALLMETZER et al., 2019, NAWROT et al., 2022, cores Piran 1-2; c – TOMAŠOVÝCH et al., 2017, 2018, core Panzano; d – TOMAŠOVÝCH et al., 2017, core Po 3; e – TOMAŠOVÝCH et al., 2017, core Po 4; f – BARMAWIDJAJA et al., 1995, core 108; g – HRS-BRENKO, 2006, station SJ101; h – PICONE et al., 2008, core AAL87-19; i – PICONE et al., 2008, core AMA88-39.

mouth, at 31 m water depth (Fig. 1). This 3-m-long core, 16 cm in diameter, comprises Holocene sediments, of which the upper 75 cm represent the Holocene marine transgression. The sedimentology, stratigraphy, and geochemistry of the core and its sequence-stratigraphic framework and facies are described in BERENSMEIER et al. (2023) and follow the regional-scale Holocene facies architecture of the Po coastal plain and delta (e.g., AMOROSI et al., 2017; BRUNO et al., 2017; CAMPO et al., 2017). Based on faunal content and core chronology, the studied core section is divided into four facies from bottom to top: (i) shell-poor, bioturbated sandy silts (40 – 75 cm), (ii) silty sands (22.5 – 40 cm), and (iii) a shelly lag (10 – 22.5 cm), which together represent the transgressive systems tract, and (iv) shell-poor, bioturbated muddy silts belonging to the highstand systems tract (0 – 10 cm) (Fig. 2). The assignment of the facies to the depositional sequences was discussed in BERENSMEIER et al. (2023), who documented two major stratigraphic surfaces in the record: the maximum flooding surface and the wave ravinement surface (Fig. 2). These two surfaces define the general sequence stratigraphic architecture of the studied core, which is consistent with the regional architecture in the northwestern Adriatic (e.g., AMOROSI et al., 2017; SCARPONI et al., 2017). While the maximum flooding surface marks the transition from a transgression to regression (AMOROSI & COLALONGO, 2009), the wave ravinement surface forms in shallow-water settings during transgression (ZECCHIN et al., 2019, and references therein).

The core was sliced into 2.5-cm thick increments in the upper part (0 – 22.5-cm core depth) and into 5-cm-thick increments in the remaining part. Bulk sediment geochemistry was shown in BERENSMEIER et al. (2023). Increased nitrogen and heavy metal concentrations, such as mercury, are detected in core depths 0 – 10 cm, suggesting eutrophication and pollution impacting the study area in the last centuries. The upper 75 cm of the core were deposited under very low net sedimentation rates over the past ≈ 10,000 years, as indicated by the ages of bivalve shells (*Varicorbula gibba*, *Lentidium mediterraneum*) dated with radiocarbon-calibrated amino acid race-

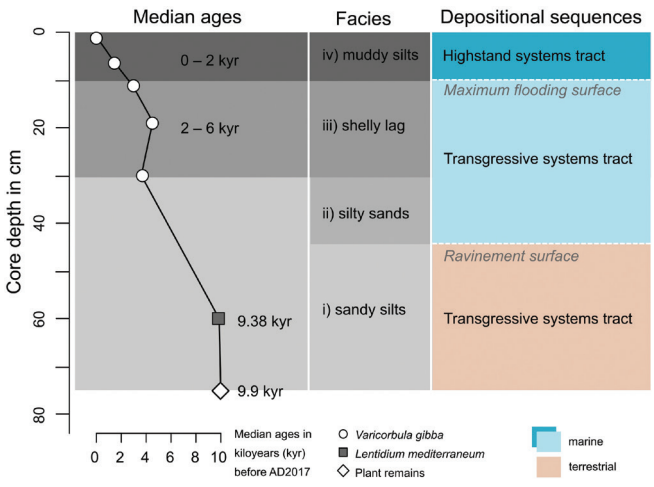

Figure 2. Stratigraphic framework and geochronological data of the core from BERENSMEIER et al. (2023). Median ages are based on age-dated shells of *Varicorbula gibba*, *Lentidium mediterraneum*, and plant remains, all ages in years before the year the core was collected (AD2017).

mization (AAR) methods and ^{210}Pb dating of the sediments (BERENSMEIER et al., 2023). The median postmortem ages (*Varicorbula gibba*, *Lentidium mediterraneum*, and coralline algae) increase down-core (BERENSMEIER et al., 2023). With the exception of centennial time-averaging in the uppermost increment (interquartile age range (IQR) of 300 years at 0 – 2.5 cm), the majority of the subsurface record at this site is affected by millennial time-averaging (3,400 years at 5 – 7.5 cm, 1,900 years at 10 – 12.5 cm and 3,000 years at 17.5 – 20 cm) and a sedimentation rate of ≈ 0.1 mm/yr (BERENSMEIER et al., 2023). The assemblages formed by all skeletal remains in the gravity core are termed here as fossil assemblages. The term *subfossil* is not used here despite shell ages younger than 10,000 years.

2.2. Palaeoecological analyses

The benthic foraminiferal and ostracod assemblage analysis was performed on subsamples taken from each increment. These subsamples had a volume of circa 30 cm^3 in the uppermost 22.5 cm and 60 cm^3 in the remaining part of the core. Each subsample was sieved through a 63 µm mesh size and standardised using a microsplitter. A minimum number of 300 benthic foraminiferal tests was counted in each sample of the upper 50 cm of the core. Below that depth, at least 250 tests per increment were counted due to low faunal density. Another subsample from each increment, representing the same volume of sediment used for foraminiferal analysis, was sieved for sieve size fractions 1 mm – 250 µm and 250 – 125 µm, in which all adult ostracod valves were identified and counted. All material >1 mm, including subsamples for benthic foraminifera and ostracods, was used to count molluscan remains. For each bivalve species, the higher number of single valves (either right or left) was added to the number of articulated specimens to get the minimum number of unique individuals in each increment. Gastropods were counted if at least 50% of the shell was preserved and the aperture was present. Only scaphopods with unbroken shell openings were counted. In polyplacophorans, abundance was assessed by adding the number of head valves (each representing one individual) to the number of other plates divided by eight, with decimal places rounded to integers (see Supplement 1 for a complete list of species and their abundances in each core increment).

The focus was on the marine species; freshwater or terrestrial taxa (mainly occurring at the base of the core) are rare and reworked and thus were omitted from analyses. The classification of benthic foraminifera at the species level is based on the criteria of LOEBLICH & TAPPAN (1987). The resulting species names were standardised according to the World Register of Marine Species (WoRMS, AHYONG et al., 2025). Due to poor preservation of the tests, the most common benthic foraminifera identified as *Haynesina germanica* and *Haynesina* sp. were summarised as *Haynesina* spp.

Small tests of *Ammonia* sp. that were not identified to the species level were pooled with other *Ammonia* species (*A. beccarii*, *A. inflata*, *A. tepida*) into *Ammonia* spp. Similarly, *Textularia agglutinans*, *T. bocki*, and *T. conica* were pooled into *Textularia* spp.

Table 2. Mean relative abundances of feeding guilds and habitat preferences of the molluscan assemblages in the depositional sequences: highstand silts, 0 – 10 cm and the shelly lag 10 – 22.5 cm. All values are given in %.

Feeding guilds of the molluscs	Shelly lag	Highstand silts
Filter feeder	69	73
Detritus feeder	13	14
Carnivore	11	6
Scavenger	4	3
Grazer	2	2
Chemosymbiont	1	2
Habitat preferences	**Shelly lag**	**Highstand silts**
Infauna	77	80
Epifauna, hard bottom	9	8
Epifauna, soft or hard bottom	8	6
Semi-infauna	2	1
Epifauna on vegetation	2	1
Epibiont/ectoparasite	1	3

Faunal densities of each taxon were calculated as the number of unique individuals divided by the volume of the entire or subsampled increment. Species diversity is reported as (i) the total number of species in each increment or subsample, (ii) the Shannon diversity index (effective number of species, exponential of the Shannon entropy H), and (iii) the Fisher's α index. The two calculated diversity indices, Shannon and Fisher's α, capture different aspects of diversity. The Shannon diversity index is a measure of entropy (uncertainty in species identity of a randomly selected individual) and considers the equal distribution of individuals across species, taking into account the abundance of each species (JOST, 2007). Fisher's α index is more focused on the absolute number of species and the abundance of rare species (SCHULTE et al., 2005). We calculate both indices to show how the diversity and heterogeneity of the three fossil assemblages (mollusc, benthic foraminifera and ostracod) changed in the stratigraphic context. To account for variability in fossil abundance, we used rarefaction to compare species richness and Shannon diversity between increments. Mean values of rarefied species richness and Shannon diversity expected at 50 specimens with corresponding 95% confidence intervals (based on the percentile method) were calculated based on 1,000 resampling iterations.

The multivariate analyses are based on proportional species and genera abundances. Non-metric multidimensional scaling (nMDS) based on Bray-Curtis distances and square-root transformed relative abundances was used to visualise changes in the assemblage structure along the core for each of the three fossil assemblages (molluscs, benthic foraminifera and ostracods) separately, (using only samples containing a minimum number of 50 individuals per increment) following KOWALEWSKI (2015). These ordinations visualise the changes in the assemblage structure and the differences between the subsurface increments, (undisturbed by human impacts) and the uppermost core increments affected by pollution and human impacts.

In addition to the nMDS, constrained hierarchical cluster analyses were carried out to evaluate whether groupings of in-

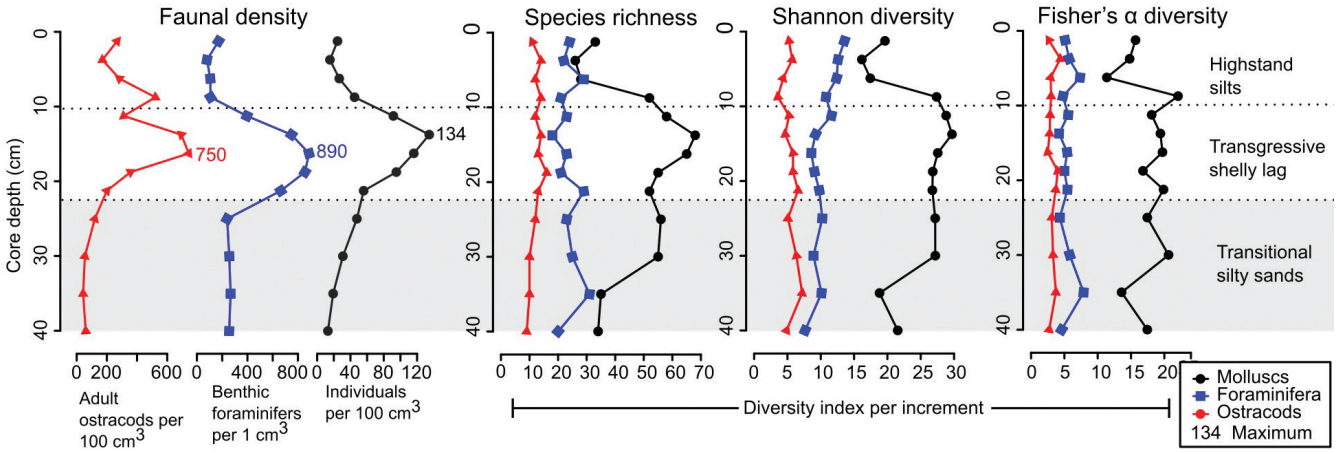

Figure 3. Faunal densities, species richness, Shannon and Fisher diversity of the ostracod, foraminiferal and molluscan assemblages. Maximum values of fossil density are indicated next to the graphs; faunal densities of all three taxa peak within the shell lag. A decrease in species richness and Shannon diversity in the highstand silts is only recorded in the molluscan assemblages.

crements with similar faunal composition correspond to distinct stratigraphic units. The cluster analysis considers the temporal sequence of samples (PATZKOWSKY & HOLLAND, 2012). For this purpose, the CONISS algorithm from the "chclust" function of the "rioja" package was applied to the Bray-Curtis distance matrix (JUGGINS, 2024).

Since the core comprises undisturbed and disturbed periods in the depositional history of the northern Adriatic, we have calculated biotic indices measuring the ecological quality of benthic habitats based on the fossil assemblages. The Marine Biotic Index (AMBI) of BORJA et al. (2000), based on the tolerance of macrobenthic taxa towards pollution, was applied to the molluscan assemblages to determine temporal changes in the Ecological Quality Status along the stratigraphic succession. Version 6.0 of AMBI software was used (AMBI, 2024). The Foram Stress Index (FSI, after DIMIZA et al., 2016) was calculated to evaluate whether foraminiferal assemblages record environmental stressors. The FSI is based on the relative abundances of sensitive and stress-tolerant (opportunistic) species according to their organic matter sensitivity (JORISSEN et al., 2018; DIMIZA et al., 2016). To classify the foraminiferal species according to their stress sensitivity or tolerance, the methods of JORISSEN et al. (2018) and ŽVAB ROŽIČ et al. (2022) and the reference therein were followed. The enhanced Benthic Foraminifera Oxygen Index (eBFOI) was calculated based on relative abundances of species typical of oxic, suboxic or dysoxic environments (KRANNER et al., 2022). All statistical analyses were performed in R 4.0.3 and RStudio version 2023.12.0.369 (R CORE TEAM, 2021; POSIT TEAM, 2023) using the "vegan" package (OKSANEN et al., 2025).

3. RESULTS

3.1. Species composition

Three benthic phyla dominate the core's fossil content in different grain size fractions: Mollusca dominate the >1 mm size fraction, Ostracoda the125 µm – 1 mm, and Foraminifera the 63 µm – 125 µm. These three groups share the same up-core pattern in densities: (i) low densities below the shelly lag (75 – 22.5 cm), (ii) a maximum density in the shelly lag (22.5 – 10 cm), and (iii) an abrupt decrease in the top 10 cm (Fig. 3).

The molluscan total assemblage comprises 3180 bivalve individuals (56 species), 1009 gastropods (43 species), 102 scaphopods (1 species), and 12 polyplacophorans (2 species). The most abundant species is the shallow-burrowing, suspension-feeding bivalve *Varicorbula gibba* that can also feed on resuspended detritus and benthic diatoms (YONGE, 1946; KIØRBOE & MØHLENBERG, 1981; HRS-BRENKO, 2006), and the semi-infaunal, filter-feeding gastropod *Turritellinella tricarinata* (Fig. 4). All scaphopods belong to the infaunal micro-carnivore *Antalis inaequicostata*. Polyplacophorans are represented by *Chiton olivaceus* and *Acanthochitona fascicularis*. The 15 most abundant molluscan species comprise about 70% of the molluscan assemblages. The molluscan density increases gradually from 40 cm up-core, from less than 3, to 134 molluscs per 100 cm^3 (Fig. 3). The shelly lag bears the highest densities of all mollusc species (Fig. 4). In the overlying highstand silts, the faunal densities decrease again. Formerly abundant species such as *Parvicardium scabrum*, *Ostrea* spp., or *Nucula* cf. *nucleus* decrease in relative abundance, whereas *T. tricarinata* increases to 16% (Fig. 4).

The foraminiferal total assemblage comprises 8937 individual tests (65 species and 23 genera in open nomenclature). The foraminiferal assemblages are dominated by Rotaliida (Table 3). The most abundant taxa are the rotaliids *Haynesina* spp. (forming 10 – 36% of the assemblages) and *Ammonia* spp. (11 – 26%), followed by the textulariid *Textularia* spp. (4 – 16%). The 15 most common benthic foraminifera form about 72% of the total assemblage (Fig. 5). Foraminiferal densities decrease significantly at 70 cm, and no benthic foraminifera were found below 77.5 cm. Within the shelly lag, the foraminiferal density peaks at ≈ 940 individuals per 1 cm^3 (Fig. 3). In the highstand silts, the foraminiferal densities decreased drastically, apart from representatives of *Nonionella* sp., which were more numerous in this interval (ca. 11% of the foraminiferal assemblages).

The ostracod total assemblage comprises 2528 individuals (12 species and 7 genus-level taxa). Most ostracods belong to marine species, except two non-marine species that attain less than 1% of the total assemblage: *Cyprideis torosa* (brackish) and *Candona* sp. (freshwater). An additional six taxa con-

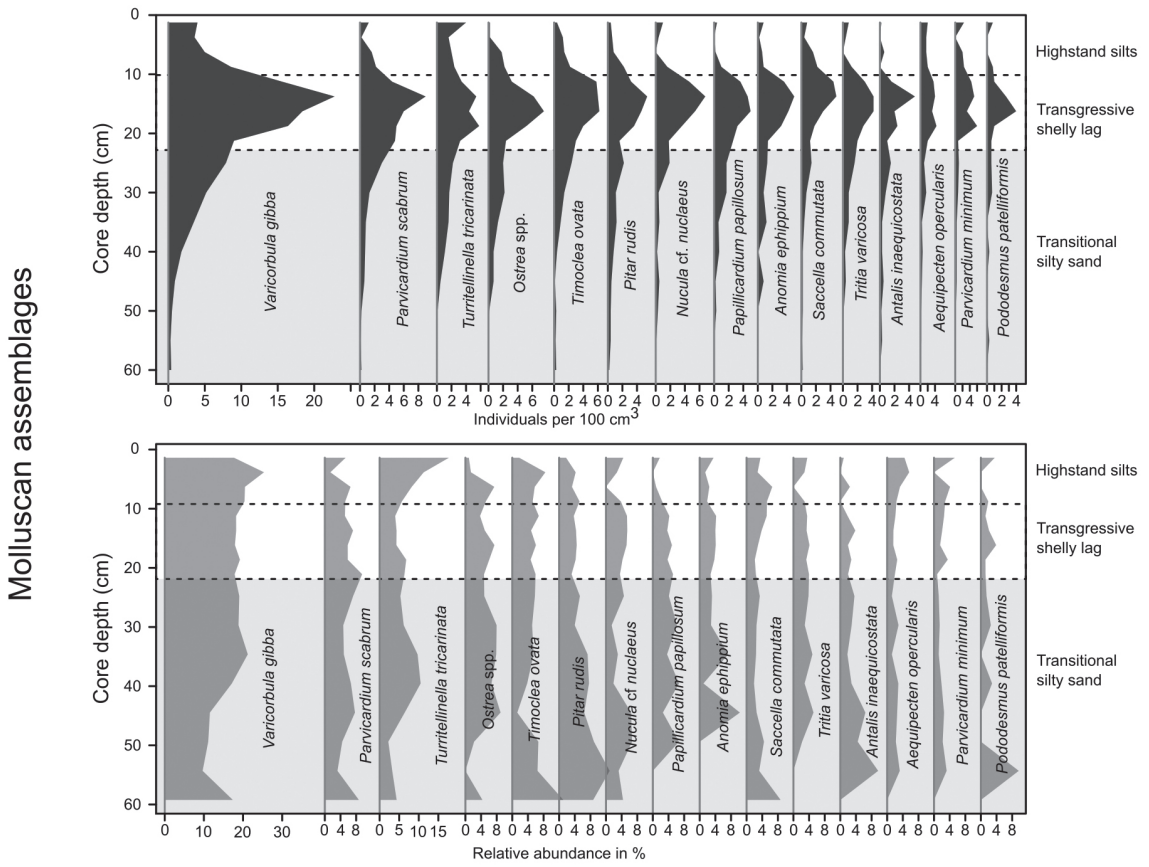

Figure 4. Faunal densities and relative abundances of the most abundant species of the molluscan assemblages.

stitute less than 1% of the total ostracod assemblage and are not displayed in Figure 6: *Aglayocypris* sp., *Aurila* spp. (*A. convexa* and *A. speyeri*), *Loxoconcha rhomboidea*, *Semicytherura cribriformis*, *Semicytherura* sp., *Xestoleberis communis*. The ostracod assemblages are strongly dominated by the marine species *Cytheridea neapolitana*, which forms up to 53% of the assemblages. Ostracod densities remain below 10 valves per increment below 40 cm core depth. They increase above 50 cm, reaching the highest density in the shelly lag, followed by a substantial decrease in density in the highstand silts (Fig. 3). The relative abundances show that *C. neapolitana* remains the dominant species throughout the whole core (Fig. 6). However, several taxa increase in relative abundance in the uppermost layers, including *Loxoconcha* sp., *Cystacythereis* sp. and *Callistocythere adriatica*.

Table 3. Mean relative abundances of benthic foraminiferal orders and habitat preferences in the depositional sequences: highstand silts, 0 – 10 cm and the shelly lag 10 – 22.5 cm. All values are given in %.

Orders	Shelly lag	Highstand silts
Rotaliina	80	80
Textulariina	13	13
Miliolina	6	7
Habitat preferences	**Shelly lag**	**Highstand silts**
Epifauna	8	6
Epiphytic	20	17
Infauna	3	12
Mixed preferences	69	65

3.2. Functional groups

Filter feeders dominate the molluscan assemblages, while other feeding guilds, such as detritus feeders and carnivores, are rare (Table 2; Fig. 7a). When comparing the mean relative abundances of feeding guilds between the shelly lag and highstand silts, filter feeders and detritus feeders increase in the latter. In contrast, higher trophic levels, such as carnivores and scavengers, decrease (Table 2; Fig. 7a). However, it is the infaunal and semi-infaunal species that truly dominate the molluscan assemblages with a relative abundance of ≈ 80%. In comparison, epifaunal molluscs constitute ≈ 20% of the molluscan assemblages (Table 2; Fig. 7b). In the Rotaliida-dominated total foraminiferal assemblage (Fig. 7c–d; Table 3), epifaunal/infaunal and epiphytic/infaunal species are the most common. Similarly, the functional composition of ostracod assemblages remains relatively constant throughout the core and consists mainly of stenohaline species. Brackish and freshwater species are singletons and can be regarded as reworked specimens. All observed ostracod species belong to the subclass Podocopa and are benthic mobile detritus-feeders.

3.3. Species diversity

The raw species richness, Shannon and Fisher diversity indices of the molluscan assemblages increase up-core (Fig. 3). The molluscan species richness reaches 68 species in the shelly lag. It decreases up-core to 26 species in the highstand silts. The Hill-transformed Shannon diversity of the molluscan assemblages peaks in the shelly lag at 29.7 and decreases to 16.1 in the highstand silts, and Fisher's index peaks with 22 at

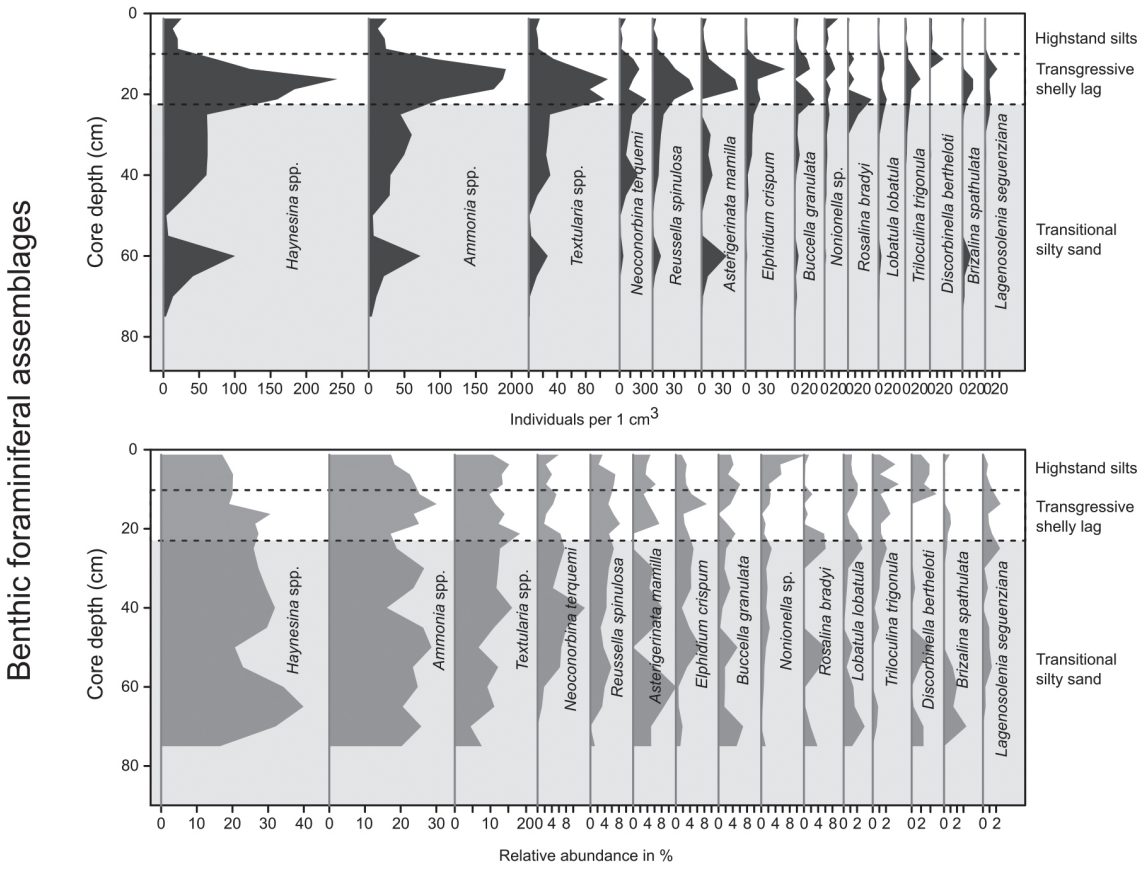

Figure 5. Faunal densities and relative abundances of the most abundant species of the benthic foraminiferal assemblages.

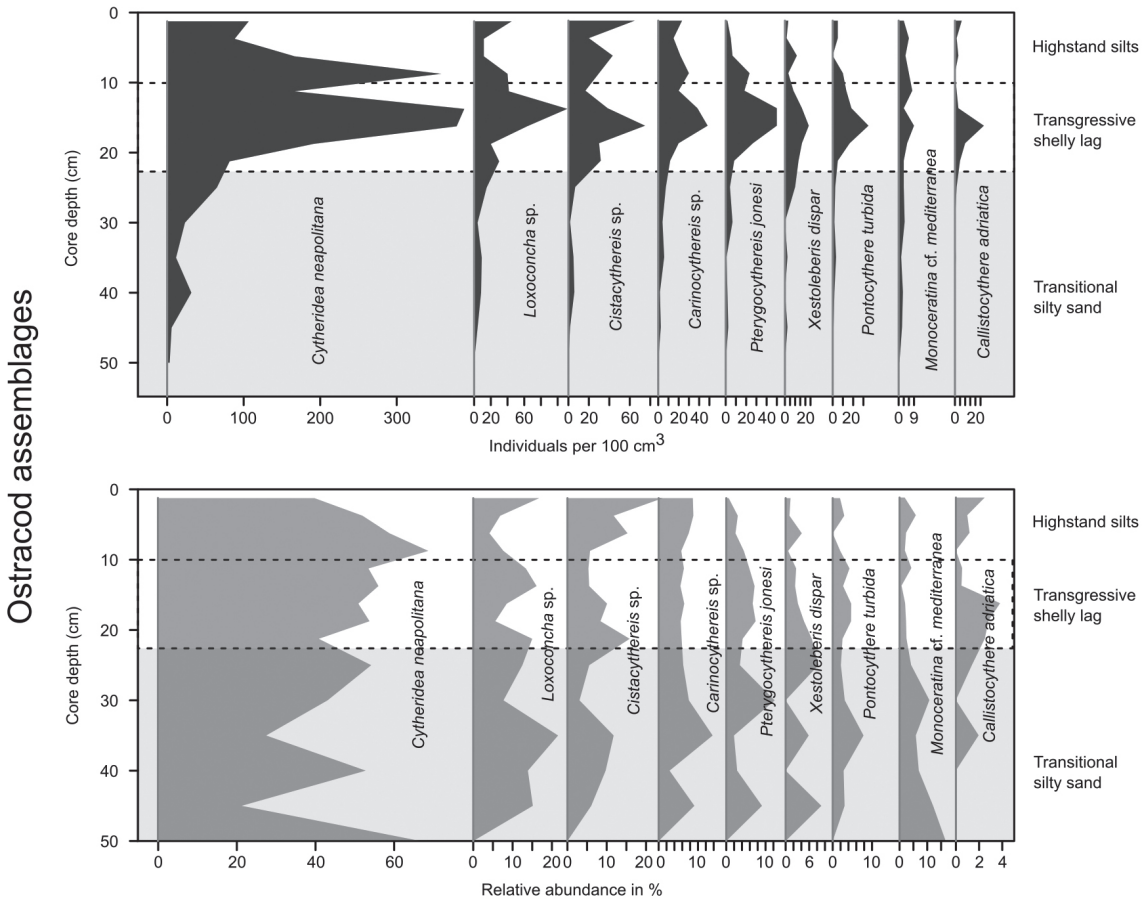

Figure 6. Faunal densities and relative abundances of the most abundant species of the ostracod assemblages.

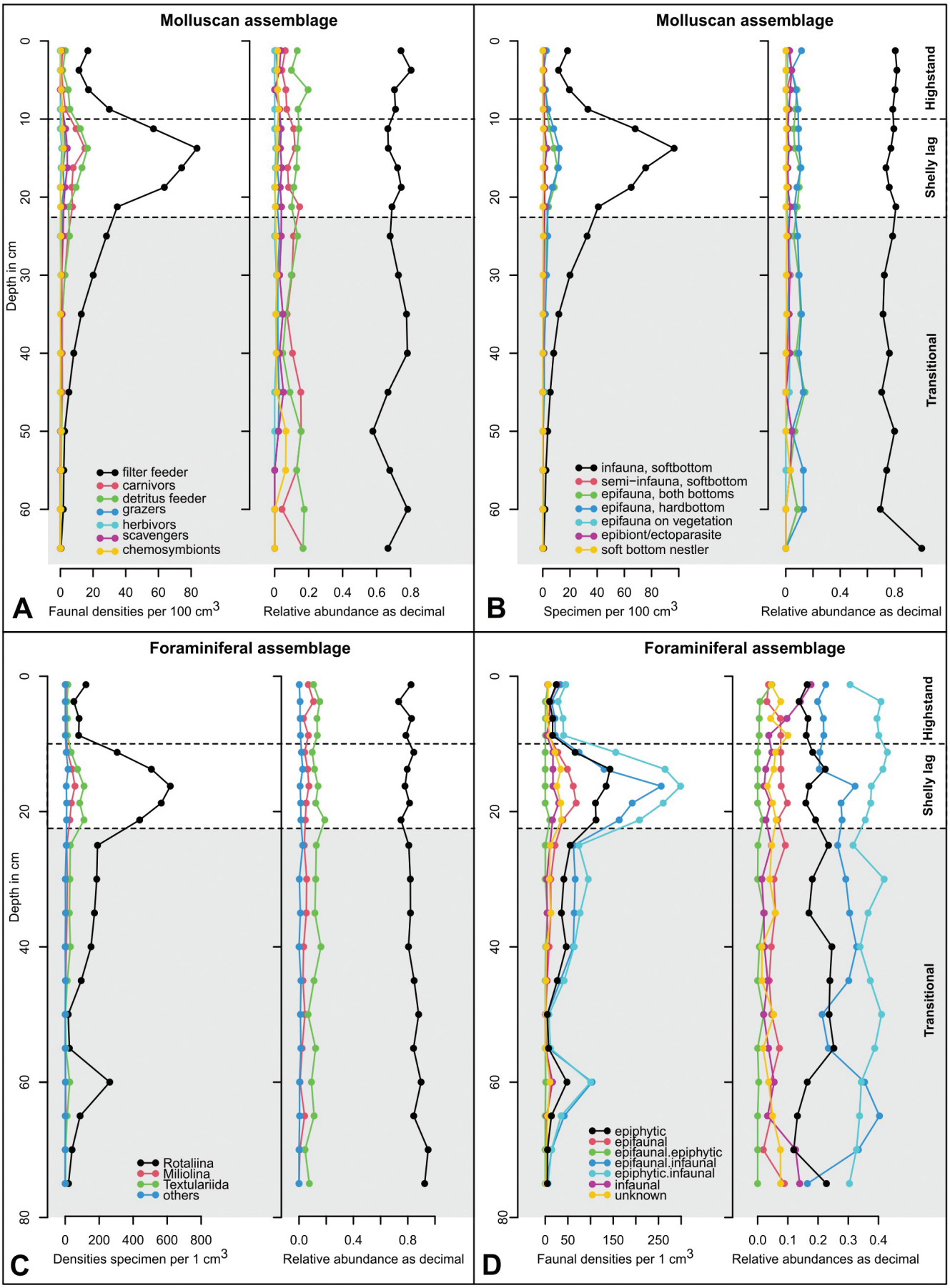

Figure 7. Feeding guilds **a** and habitat preferences **b** of the molluscan assemblages, and orders **c** and habitat preferences **d** of the benthic foraminiferal assemblages. Each increment has been analysed for its species composition and displayed here as faunal densities (absolute number of individuals/volume of the sample) and relative abundance (decimal).

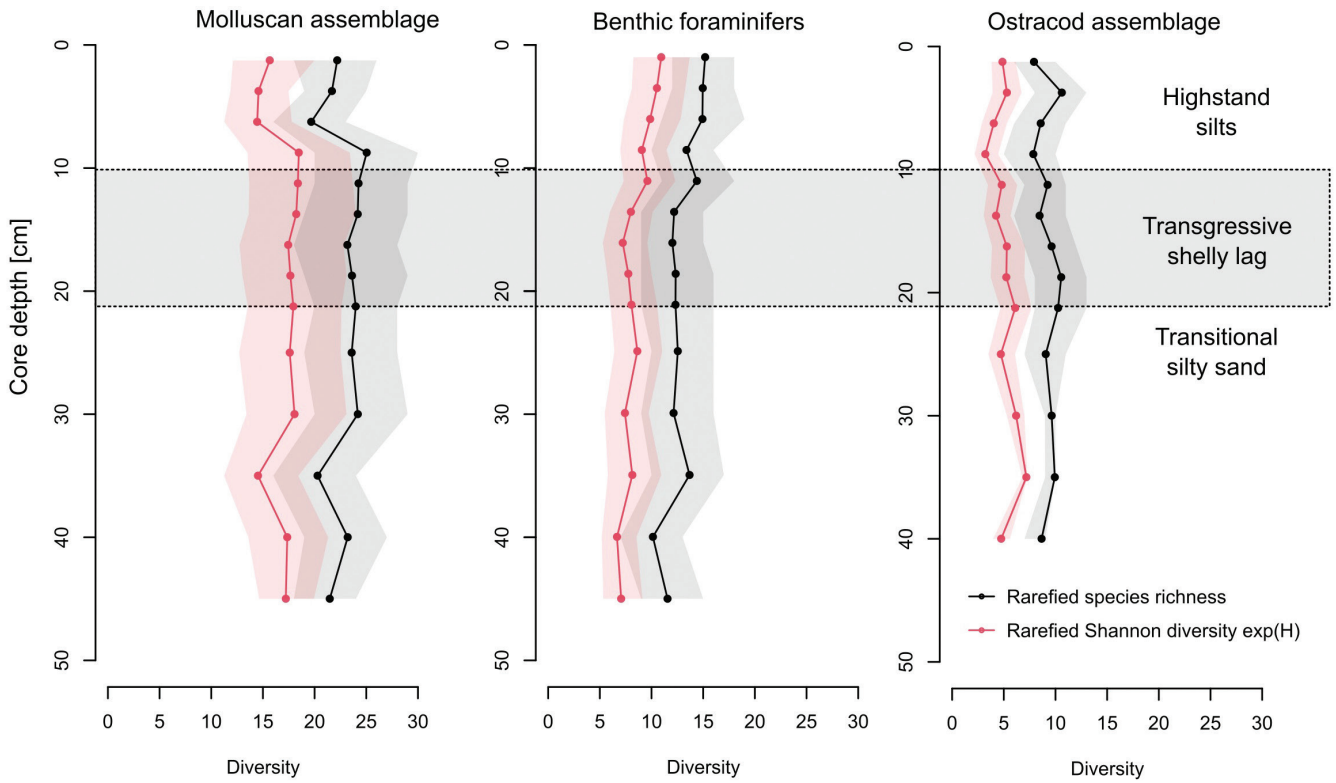

Figure 8. Trends in rarefied species richness and Shannon diversity along the core. Shading indicates 95% confidence intervals.

7.5 – 10 cm, and also decreases to 14.8 within the highstand silts. The maximum diversity of the total molluscan assemblage is recorded within the shelly lag or slightly above, followed by a remarkable drop in the highstand silts (Fig. 3).

Raw foraminiferal species richness ranges from 18 to 29 species in the shelly lag and from 21 to 29 in the highstand silts (Fig. 3). Shannon diversities of the foraminiferal assemblages increase from around 9 in the shelly lag to 13.5 in the highstand silts (Fig. 3). Fisher's index is slightly higher in the highstand silts (ranging from 4.8 and 7.4) than in the shelly lag (range from 4.2 to 5.6) (Fig. 3). Although the foraminiferal densities decrease in the uppermost 10 cm, their species richness and diversity do not decline significantly in the assemblages of the highstand silts.

Ostracod species richness ranges from 12 to 16 taxa in the shelly lag and from 11 to 14 taxa in the highstand silts (Fig. 3). Their Hill-transformed Shannon diversities range from 4.7 to 6.5 in the shelly lag, and decrease in the highstand silts to 3.5. The Fisher's α of the ostracod assemblages fluctuates from 2.5 to 4 in the shelly lag, and ranges from 2.7 to 4.4 in the highstand silts (Fig. 3). The species richness and diversity of the ostracod assemblages do not change significantly in the highstand silts despite the drop in density.

The rarefied molluscan diversity reveals a slight decrease in the highstand silts, but the diversity of benthic foraminiferal and ostracod assemblages shows no significant shifts within the record (Fig. 8).

3.4. Multivariate patterns in assemblage species composition

The NMDS ordination shows an up-core shift in the molluscan composition along the first NMDS axis, with a larger separation between assemblages at the base of the core on one hand and assemblages from the shelly lag and the highstand silts on the other (Fig. 9a). The constrained clustering indicates that the highstand silts (0 – 10 cm, last 2,000 yrs BP) differ in the molluscan composition relative to the extended shelly lag (10 – 40 cm), while the assemblages in transgressive sediments (2,000 – 7,800 yrs BP) are highly variable in composition (especially at 45 – 60 cm) and are less similar to those from the upper core increments (Fig. 9a). Similar to the molluscs, the NMDS ordination of the foraminiferal assemblage shows an up-core shift along the first NMDS axis and very high dispersion among assemblages occurring in the lowermost increments (50 – 75 cm, Fig. 9b). The NMDS ordination based on the ostracod assemblages reveals high similarity in the species composition among assemblages within the upper 30 cm of the core, with higher dispersion of assemblages at 30 – 40 cm (Fig. 9c). The Mantel test shows a positive Spearman correlation between molluscan and foraminiferal Bray-Curtis dissimilarities ($rho = 0.55$, $p < 0.001$), indicating that temporal changes in the composition of assemblages are shared by these two taxa, i.e., core increments with similar molluscan assemblages are also similar in terms of foraminiferal assemblages. In contrast, there is a low and insignificant correlation between molluscan and ostracod dissimilarities ($rho = 0.18$, $p = 0.24$).

3.5. Stress indices

The Marine Biotic Index (BORJA et al., 2000) for molluscs is 1.19 for the shelly lag (unpolluted/undisturbed status) and 1.44 for the highstand silts (slightly polluted status). The total foraminiferal assemblage comprises 44 sensitive, 15 stress-tolerant, and 10 species of unknown stress tolerance. The number of stress-tolerant and sensitive species remains relatively constant

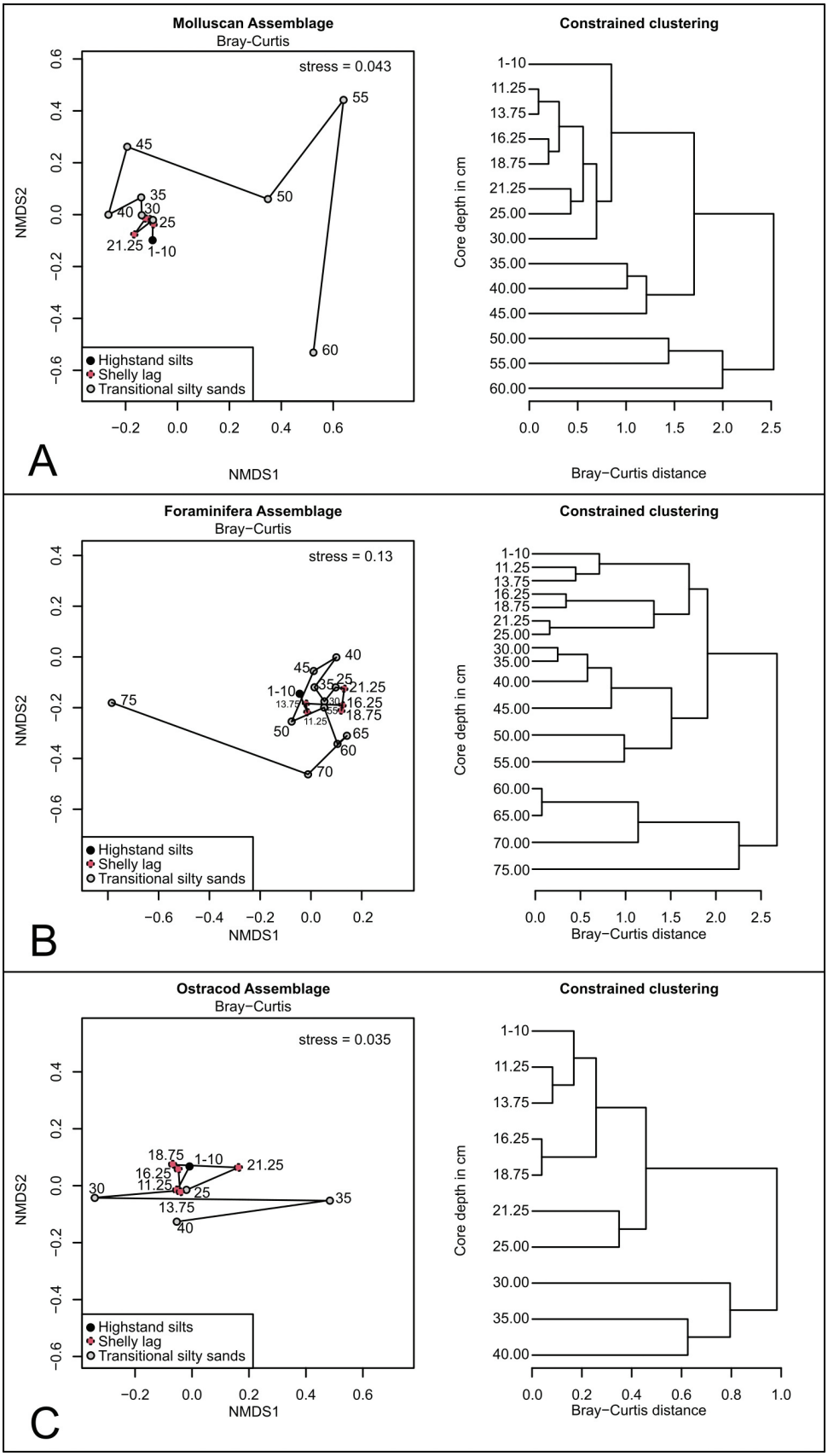

Figure 9. Non-metric multidimensional scaling ordination and constrained clustering of the three taxa. **a** Marine molluscs; **b** Benthic foraminifera; **c** Marine ostracoda. All numbers indicate the increment midpoints (core depth) in cm.

throughout the core. However, the relative abundances of *Nonionella* and *Bulimina* increase from the shelly lag to the highstand silts. The stress-tolerant species include the most abundant genera of the total foraminiferal assemblage, *Haynesina* spp. and *Ammonia* spp. The Foram Stress Index (FSI, DIMIZA et al., 2016) exceeds a mean value of 3.8 in the shelly lag and

3.9 in the highstand silts. Both values indicate a moderately polluted environment. The enhanced Benthic Foraminifera Oxygen Index (eBFOI, KRANNER et al., 2022) exceeds a mean value of 68.9 in the shelly lag and 67.7 in the highstand. Both values indicate a well-oxygenated environment.

4. DISCUSSION

4.1. A stratigraphic record affected by condensation, reworking and mixing

The gravity core preserves a palaeoecological marine archive of ≈ 10,000 yrs, characterised by centennial and millennial time averaging, affected by slow sedimentation (condensation), reworking, and vertical mixing of shells. *Varicorbula gibba* shell ages span 300 years in the uppermost core increment. In contrast, they range in age by several thousand years at the base of the highstand silt and in the shelly lag (mainly 2 – 6 kyr) (BERENSMEIER et al., 2023). Median ages of the shallow-subtidal bivalve *V. gibba* do not overlap between the highstand silt and the shelly lag (median age is 50 years at 0 – 2.5 cm, 1380 years at 5 – 7.5 cm, 2880 years at 10 – 12.5 cm, and 4480 years at 17.5 – 20 cm). Although the overlap in shell ages between the upper and the lower highstand silt increment is limited, age data demonstrate that the base of the highstand silts is already mixed with the shelly lag. Postmortem ages of the intertidal bivalve *L. mediterraneum* do not vary systematically within the upper 60 cm, with all shell ages ranging between 9380 and 10 510 cal years AD2017 (Fig. 2), indicating substantial post-depositional mixing of very old shells across the highstand silts and the shelly lag, induced either by bioturbation and/or by their transport from adjacent locations. However, this species is numerically rare and does not significantly alter the overall molluscan composition (BERENSMEIER et al., 2023).

To conclude, the shelly lag is characterised by millennial-scale time averaging. It thus integrates across molluscan, foraminiferal and ostracod communities that inhabited the seafloor prior to the anthropogenic impacts in the northern Adriatic Sea (from ≈ 2 kyr BP up to ≈ 6 kyr BP). Although the lowermost increments of the overlying silts are still mixed with the shelly lag, the shell-poor, organic and metal-rich silts at the top of the core are less time-averaged and less affected by mixing with the underlying strata. In contrast, as the shelly lag does not contain shells from recent centuries, its fossil assemblages with molluscs, benthic foraminifera, and ostracods can be representative of pre-impact conditions. However, the highstand silts probably represent the mixture of pre- and post-impact conditions, and even the uppermost increment, averaging across the past ≈ 300 years, can be expected to integrate across distinct phases of the eutrophication history.

Although the upward decline in macro- and microfaunal densities between the shelly lag and the highstand silts can reflect a substantial decline in benthic production, a positive correlation between molluscan fossil density and sample size-independent diversity is observed in this core (TOMAŠOVÝCH et al., 2024). This positive correlation indicates that the decline in fossil density reflects an increase in sedimentation rate over the past centuries and thus does not necessarily correspond to any temporal change in standing population densities of molluscs, benthic foraminifers or ostracods. Analyses of a total foraminiferal assemblage collected in a sediment core at a muddy site location in the Po Delta not far from our coring location also indicate that sedimentation rates increased during the 19th and 20th centuries (BARMAWIDJAJA et al., 1995).

4.2. The shelly lag as a compositional baseline

As interpreted above, relative abundances of molluscs, benthic foraminifera, and ostracods in the shelly lag represent a time-averaged compositional baseline for assemblages inhabiting sub-tidal, muddy habitats in the northern Adriatic Sea. The molluscan, foraminiferal and ostracod assemblages in the shelly lag are dominated by opportunistic taxa such as *V. gibba*, *Haynesina* spp. and *C. neapolitana,* that typically tolerate organic enrichment, pollution and some degree of oxygen depletion (Table 4). However, the relative abundances of *Haynesina* spp., and *C. neapolitana* decline in the overlying highstand silts. Moreover, shelly lag assemblages also include species that are relatively sensitive to pollution and organic enrichment, e.g. the molluscs *T. tricarinata*, *Timoclea ovata*, *Parvicardium scabrum*, and *Papillicardium papillosum* (e.g., NERLOVIĆ et al., 2011; TOMAŠOVÝCH et al., 2018) and benthic foraminifera *Neoconorbina terquemi*, *Asterigerinata mamilla* or *Elphidium crispum*. The shell lag assemblage reflects a moderately diverse molluscan community (or set of communities) dominated by filter feeders and infaunal species preferring soft bottoms. The diversity values are similar to the other Holocene assemblages exhibiting millennial time averaging at other sub-tidal locations affected by low sedimentation rates in the northern Adriatic Sea (GALLMETZER et al., 2019; TOMAŠOVÝCH et al., 2020, 2024; PICONE et al., 2008; BARBIERI et al., 2019). The microfaunal assemblage within the shelly lag is characterised by stenohaline ostracods and a highly diverse shallow-water benthic foraminiferal fauna.

Table 4. The dominant species of each total assemblage (molluscan, benthic foraminiferal, and ostracod) and their responses to environmental stressors.

Total assemblage	Dominant species	Response to organic pollution	Response to heavy metal pollution	Response to oxygen depletion	Used as index species	Ecogroup
Molluscs	*Varicorbula gibba*	Very tolerant (HRS-BRENKO, 2006)	Tolerant (GALLMETZER et al., 2017)	Tolerant (HRS-BRENKO, 2006)	MORAITIS et al., 2018; TOMAŠOVÝCH et al., 2017, 2018	Species that are tolerant to organic matter enrichment (Group III after BORJA et al., 2000)
Benthic foraminifera	*Haynesina* spp. (mostly *H. depressula* and *H. germanica*)	Tolerant (VIDOVIĆ et al., 2009; BERGIN et al., 2006; BARBIERI et al., 2019)	Tolerant (BERGIN et al., 2006; ŽVAB ROŽIČ et al., 2022)	Moderately tolerant (GLOCK, 2023)	MELIS et al., 2019; ŽVAB ROŽIČ et al., 2022	Species that are indifferent to or relatively favoured by organic enrichment (Group II and III after JORISSEN et al., 2018)
Ostracods	*Cytheridea neapolitana*	Tolerant (BARBIERI et al., 2019)	Ostracods are, in general, sensitive RUIZ et al., 2005; SALVI et al., 2015	Tolerant (BARBIERI et al., 2019)	BARBIERI et al., 2019	Opportunist

4.3. The human-impacted shell-poor silts

The relative abundances of infaunal molluscs and benthic foraminifera increased in the highstand silts. In contrast, all other groups, particularly the epifaunal molluscs and epiphytic foraminifera, decreased from the shelly lag towards the top of the highstand silts. The foraminiferal assemblages also exhibit a significant increase in the relative abundance of infaunal species (such as *Nonionella* sp., *Bulimina marginata*, and *Bulimina aculeata*) within the muddy highstand silts relative to their abundance in the shelly lag. These taxa are considered to be opportunists by JORISSEN et al. (2018) and DIMIZA et al. (2016). In contrast, the relative abundances of epiphytic species decreased (such as *Asterigerinata mamilla* and *Neoconorbina terquemi*). BARMAWIDJAJA et al. (1995) described a similar decrease in the relative abundance of epiphytic species close to the sampling area (see Fig. 1). Although *V. gibba* tolerates hypoxia (HRS-BRENKO, 2006) and organic matter enrichment (Group III of the Marine Biotic Index, BORJA et al., 2000), shells of this species in the shelly lag are typically smaller than in the overlying highstand silt (BERENSMEIER et al., 2023) where they also increase in proportional abundance, indicating stronger eutrophication during deposition of the uppermost core increments compared to the shelly lag.

Despite their low thickness and mixing at the base, the highstand silts are sedimentologically and geochemically distinct from the underlying shelly lag. The highstand silts correspond to an increase in fine-grained sediment accumulation over the last ≈ 2,000 years, driven by the transition from wave-dominated to the river-dominated, rapidly prograding Po deltaic system with prodelta lobes reaching water depths of 30 m (AMOROSI et al., 2019), further enhanced by a shift of the Po River northwards to its present-day position ca. 800 years ago (CORREGGIARI et al., 2005). This change in sedimentary dynamics ≈ 2 kyr BP was at least partly caused by increased soil erosion and sediment discharge due to the intensification of deforestation and agriculture during the Roman Empire (MASELLI & TRINCARDI, 2013). The shift in habitat preferences between the shelly lag and highstand matches the basin-wide trend of infaunalisation observed in live-dead studies (HASELMAIR et al., 2021) and other sediment cores (e.g., GALLMETZER et al., 2019), indicating a substantial change in soft-bottom environments in the northern Adriatic Sea. However, *T. tricarinata*, a species sensitive to pollution or seasonal oxygen depletion, even increases in relative abundance in the highstand silts. Monitoring studies focusing on living assemblages and stratigraphic records from non-condensed cores in the Po prodelta and Gulf of Trieste showed that *T. tricarinata* declined, whereas *V. gibba* increased in abundance (and also in shell size) during the 20th century (station SJ101 in HRS-BRENKO, 2006; TOMAŠOVÝCH et al., 2017, 2018; MANARINI et al., 2019). The increase in *Turitellinella*'s relative abundance can reflect conditions associated with earlier phases of eutrophication and Po prodelta progradation that were not yet associated with the negative consequences of seasonal oxygen depletion or pollution. Despite the stratigraphic condensation, the highstand silts preserve, to some extent, a community state that differs from the shelly lag assemblage based on the observed changes in community composition of all three taxonomic groups.

4.4. Discrepancy between molluscan and foraminiferal stress indices

The Marine Biotic Index based on the molluscan assemblages (BORJA et al., 2000) indicates the transition from an unpolluted environment recorded in the shelly lag to a slightly polluted environment recorded in the highstand stilts. Due to the insufficient percentage of foraminiferal species assigned to ecological categories based on sensitivity to organic carbon content (BORJA et al., 2000; BORJA & MUXIKA, 2005; ALVE et al., 2016), the Foram-AMBI index was not considered for discussion. Therefore, the ecological status was interpreted only by the FSI (DIMIZA et al., 2016). The values of the FSI (DIMIZA et al., 2016) indicate a slightly polluted environment in both the shelly lag and the highstand silts. Although the stress indices based on molluscan and foraminiferal assemblages differ to some degree, the associated changes in the relative abundances of species and functional groups in both taxa point to a partial degradation of the ecosystem status during the deposition of highstand silts relative to the deposition of the shelly lag. The discrepancy in molluscan and foraminiferal stress indices of the shelly lag could result from several factors, including (1) differing tolerances of macro- and microfauna to organic enrichment or pollution, with benthic foraminifera or ostracods considered more sensitive to pollution than molluscs (YANKO et al., 2003; RUIZ et al., 2005; SALVI et al., 2015), (2) differences in the degree of time averaging because mixing processes are known to be size-selective (however, time averaging of benthic foraminifers and molluscs was documented to be similar at other locations in the northern Adriatic Sea, NAWROT et al., 2022), and/or (3) uncertainties related to the lack of species-level discrimination. However, the Mantel test demonstrates the positive correlation between the composition of molluscan and foraminiferal assemblages, suggesting that the living communities of these two taxa responded similarly to environmental changes and that their death assemblages were not subjected to different condensation and mixing despite their differing sizes and organizational levels (single-celled versus multicellular organisms).

Both molluscan and foraminiferal datasets differ in the number of unassigned species, with 26% foraminiferal taxa and 14% molluscan taxa not determined to species level. The Marine Biotic Index (BORJA et al., 2000) and Foram Stress Index (DIMIZA et al., 2016) are expected to be calculated with less than 1% unassigned species in the molluscan assemblages, and up to 10% unassigned species in the foraminiferal assemblages. While the molluscan stress index is reliable in this regard, the foraminiferal stress index can be biased by the high proportion of individuals undetermined to species level. Even with this uncertainty, the overall shift in the AMBI index is congruent with the increasing relative abundances of pollution-resistant foraminifera, such as *Bulimina* or *Nonionella*, even when the FSI does not show any significant change. Moreover, temporal changes in the relative abundances of functional groups align with the results of other palaeoecological studies about benthic foraminifera in the northern Adriatic Sea (e.g., BARMAWIDJAJA et al., 1995; BARBIERI et al., 2019, 2021).

The molluscan and foraminiferal fossil assemblages still record these ecological trends, even though they are preserved within the thin, time-averaged stratigraphic succession.

5. CONCLUSION

The gravity core collected at ≈ 30 km east of the Po delta in 31 m water depth, in the northern Adriatic Sea, records the composition of the benthic communities that existed in the region prior to human impact (shelly lag, 2 – 6 thousand years ago BP). Although the highstand silts deposited over the past two millennia average across pre- and post-impact community states, they show benthic and geochemical signatures of human impact. To accurately interpret the palaeoecological data, it is essential to combine fossil and stratigraphic information. Even seemingly minor changes in sedimentation rates can significantly impact the temporal resolution of the fossil record. Although the sediment core examined here is characterised by condensation and mixing, which obscures ecological signals within the fossil assemblages, including molluscs, benthic foraminifera, and ostracods, the shelly lag deposited prior to the onset of human impacts remains largely segregated from the highstand silts that archive the most recent changes in the community composition. Changes in species abundances and functional groups reflect infaunalisation that coincides with environmental changes reconstructed from geochemical proxies. Despite the incomplete nature of the fossil record, the assemblages in the shelly lag thus offer insights into a baseline largely unaffected by human impacts. At the same time, the highstand silts, while still averaging out across the past centuries, show fingerprints of eutrophication and pollution, even when the magnitude of the impact is rather minor. These data provide a foundation for future studies on multi-taxon palaeoecological datasets in the northern Adriatic Sea and contribute long-term information that is valuable for marine conservation efforts.

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SUPPLEMENTARY MATERIAL

Electronic supplementary material is available online with the article at https://www.geologia-croatica.hr