

Benthic ostracoda and foraminifera from the North Adriatic Sea (Italy, Mediterranean Sea): A proxy for the depositional characterisation of river-influenced shelves



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ABSTRACT

We investigated the distribution of ostracoda and benthic foraminifera from the shallow (< 40 m water depth) river-influenced North Adriatic shelf. Combining faunal and environmental data from a sub-set of literature databases (Breman, 1975; Jorissen, 1988), we recognised the main environmental drivers for ostracoda (grain-size and bathymetry) and benthic foraminifera (organic matter concentration). Integrating these benthic groups, we identified five depositional settings dependent on the relative position from the main source of riverine material: the Po River. Near the Po Delta, where high fluxes of sediment occur, taxa tolerant to organic-rich muddy substrates and oxygen deficiency are abundant (*Palmoconcha turbida*, *Leptocythere ramosa*, *Ammonia tepida*, *Ammonia parkinsoniana*, *Nonionella turgida*). Downdrift of the delta, ostracoda discriminate between shallow sandy substrates (*Semicytherura incongruens*, *Xestoleberis* spp.) subject to longshore currents and deeper clayey environments (*S. incongruens*, *Palmoconcha turbida*), whereas benthic foraminifera are monotonous being represented by taxa tolerant to moderate organic matter concentrations (*A. parkinsoniana*, *A. tepida*, *Aubignyna perlucida*). The mud-loving *Cytheridea neapolitana* and *Bulimina denudata*, tolerating high organic matter fluxes, characterise the 20–40 m deep mud-belt subject to the major accumulation of riverine material. Updrift, sandy substrates with low organic matter are typified by *S. incongruens*, *Pontocythere turbida* and Milioloidea. Out of the fluvial influence (water depth > 20 m), diversified meiofaunal assemblages occur with ostracoda discriminating sediment-starved areas enriched in sand. Our results demonstrate that the combined use of ostracoda and benthic foraminifera represents a powerful tool for the depositional characterisation of river-influenced shelves and to achieve detailed palaeogeographical reconstructions from shallow marine successions.

1. Introduction

Benthic ostracoda and foraminifera represent useful ecological indicators of the depositional dynamics of continental shelves, due to their abundance and adaptations to different environmental conditions (Athersuch et al., 1989; Murray, 2006). However, multiple factors are responsible for the meiofaunal community turnover in shelf settings, which are complex ecosystems subject to the interaction of sedimentary, hydrodynamic and biological processes and their variation in time and space (e.g., Jorissen, 1987; Murray, 2006; Rodriguez-Lazaro and Ruiz-Muñoz, 2012). This is further emphasised on river-influenced shelves, as changes in spatial distribution patterns of the riverine inputs are known to strongly affect meiofaunal assemblages (e.g., Van der

Zwaan and Jorissen, 1991; Mojtahid et al., 2009; Goineau et al., 2015).

The interpretation of ostracod and benthic foraminiferal assemblages exclusively based on environmental affinities to extant taxa produces palaeoecological reconstructions that implicitly include several palaeoenvironmental parameters commonly estimated in a qualitative way. This is partially in contrast with the requirements of modern palaeoecology that aspires to quantify palaeoenvironmental changes through time, connecting biotic assemblages with a reduced set of significant abiotic (i.e., environmental) factors (Holland, 2005; Patzkowsky and Holland, 2012). When multiple fossil groups are applied as proxies, the necessity of finding independent connections between single faunal groups and controlling factors is vital for detailed palaeoenvironmental reconstructions (Amorosi et al., 2014; Barbieri

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and Vaiani, 2018). Several stratigraphic studies have taken advantage of the combined application of ostracoda and foraminifera as palaeoenvironmental proxies (Alberti et al., 2013; Fanget et al., 2016; Amorosi et al., 2017; Rossi et al., 2017; Moissette et al., 2018), but only few works have clearly linked the stratigraphic distribution of fossils to specific controlling factors (Morigi et al., 2005; Yasuhara et al., 2012; Amorosi et al., 2014; Azzarone et al., 2018; Rossi et al., 2018). Moreover, the integration of ostracoda and benthic foraminifera was rarely adopted on river-influenced shelves, even though these settings represent a common situation all over the world (Walsh and Nittrouer, 2009). If the contribution of single environmental parameters on their distribution is disentangled, it will be feasible to obtain more accurate interpretations of the fossil record.

In order to understand the ecological response of both ostracoda and benthic foraminifera, modern databases should be comparable in terms of study area, measured variables and sampling techniques. In the Mediterranean basin, several databases were created to examine the relationships among the distribution patterns of ostracoda or benthic foraminifera and a set of environmental parameters in marine areas (e.g., Donnici and Serandrei Barbero, 2002; Goineau et al., 2011, 2015; Frezza and Di Bella, 2015). However, the integrated meiofauna analysis for the ecological characterisation of modern marine environments is scarcely adopted (Pascual et al., 2008; Angue Minto'o et al., 2013), and most of these studies focus on the effects of anthropogenic activities in specific coastal areas (Frontalini et al., 2011; Salvi et al., 2015; Balassone et al., 2016).

The Adriatic Sea databases produced by Breman (1975) for ostracoda and Jorissen (1988) for benthic foraminifera share the same abiotic variables with a significant relevance for the analysed environmental setting (i.e., water depth, percentage of organic matter, sand and calcium carbonate), furnishing the opportunity to compare meiofauna dynamics. We use in our work part of these databases focusing on the North Adriatic inner shelf (i.e., < 40 m water depth), which is subject to the major influence of the Po River and several subordinate Alpine and Apennine rivers distributed along the eastern Italian coast (Frignani et al., 2005; Fig. 1).

Here, we describe the quantitative distribution, composition and species-environmental relations of modern ostracoda and benthic foraminifera on the North Adriatic river-influenced shelf, subject to the interaction among river sediment inputs, oceanographic processes, physiographic setting and their variation in time and space. Specifically, we define the main biofacies and discern the contribution of single environmental parameters on the distribution of ostracoda and benthic foraminifera groups, applying a set of multivariate statistical analyses that jointly consider faunal and abiotic variables. Moreover, we illustrate that ostracoda and benthic foraminifera are complementary (palaeo)biological indicators able to identify depositional environments under different degrees of river inputs, providing an improved characterisation of continental shelves, also in a stratigraphic perspective.

2. Study area

The Adriatic Sea is a narrow (ca. 200 × 800 km) epicontinental basin elongated in a northwest-southeast direction in the Mediterranean Sea (Fig. 1). It represents the foreland basin of the Apennine and Dinaric thrust belts, that resulted from the subduction of the Adriatic plate and the accretion of the Apennine chains in the Mesozoic (Doglioni, 1993). The western side of the Adriatic Sea is a Plio-Quaternary foredeep divided into two sectors by a structural high in proximity of Ancona (Ori et al., 1986; Ricci Lucchi, 1986).

The Adriatic Sea can be divided into three morphological domains: i) the northern Adriatic, characterised by a 300 km-long platform dipping towards the SE of about 0.02°, bordered by the shelf break at ca. 120 m water depth; ii) the central Adriatic, that reaches a depth of 260 m in the Meso-Adriatic Depression and is bordered by a narrower

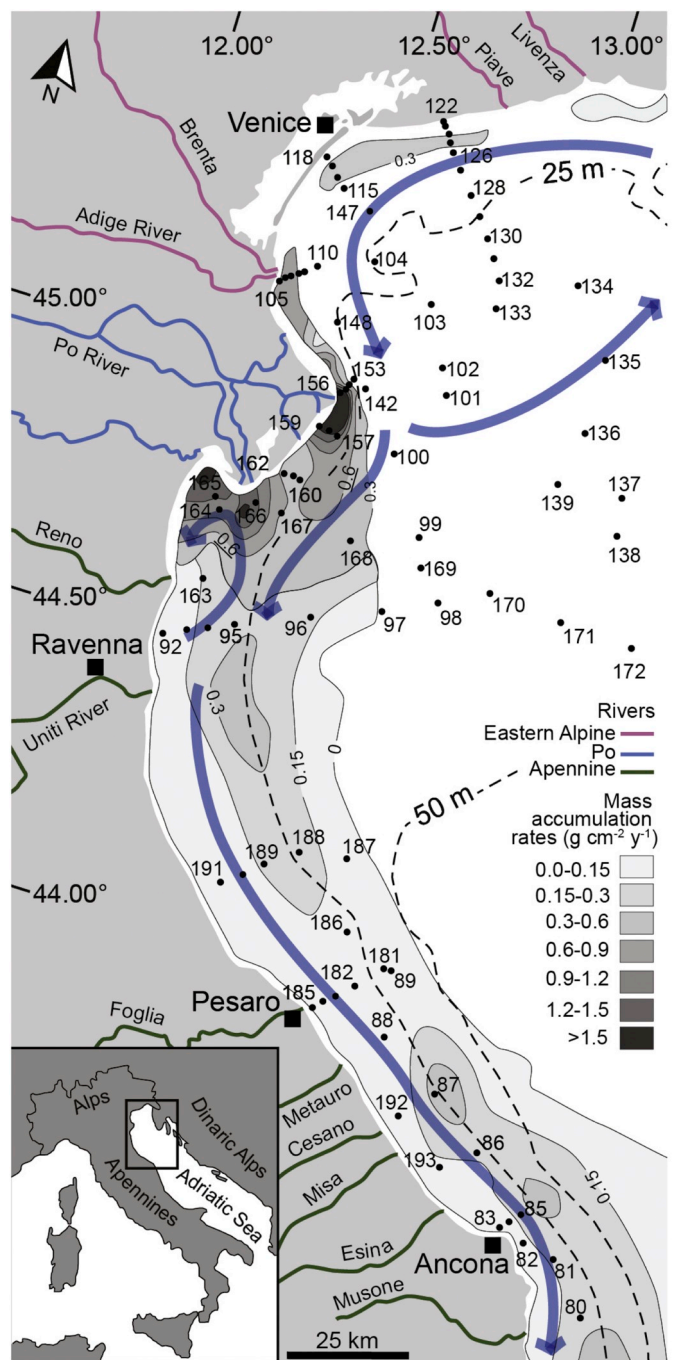


Fig. 1. Map of the northern Adriatic Sea and distribution of samples analysed within this work for ostracoda (Breman, 1975) and benthic foraminifera (Jorissen, 1988). Rivers are coloured according to their geographical grouping (after Cattaneo et al., 2003). Mass accumulation rates are derived from Frignani et al. (2005). Blue arrows indicate the simplified pattern of sediment flux, influenced by the surface circulation pattern of the Adriatic Sea (after Harris et al., 2008). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(ca. 50 km) and steeper (ca. 0.5°) shelf; iii) the southern Adriatic, the deepest portion with a maximum depth of 1200 m (Cattaneo et al., 2003; Storms et al., 2008).

The microtidal Adriatic Sea is strongly influenced by a cyclonic thermohaline circulation prone to seasonal variability, and driven by wind forcing and freshwater input from rivers. Three main water masses are present: i) a surficial temperature-mixed layer (0–30 m) characterised by less saline (ca. 38 psu) and cooler (ca. 12.5 °C in

winter) waters mainly derived by the Po River runoff (Western Adriatic Coastal Current, WACC); ii) a Levantine Intermediate Water layer (30–130 m) with salinity > 38.5 psu and temperature > 13.5 °C and iii) a deep (> 130 m), very cold (12 °C) and saline (38.5 psu) water (Russo and Artegiani, 1996; Cattaneo et al., 2003).

Sediment inputs are mostly provided by the rivers located along the northern and western sides of the Adriatic Sea (Fig. 1). The main sources are the Eastern Alpine rivers (providing 3.2 Tg·yr⁻¹ of sediments, mainly by the Adige River), the Po River (12.22 Tg·yr⁻¹, representing the major source of sediments of the whole Adriatic Sea) and the Apennine rivers down to Ancona (16.9 Tg·yr⁻¹). In this sector of the basin, the river input is higher than the sediment accumulation, i.e., the amount of sediment provided by rivers is higher than the amount of sediment deposited on the seafloor (Frignani et al., 2005). The surficial counter-clockwise WACC transports and deposits the excess of sediment in the central and southern Adriatic, where the sediment accumulation on the sea bottom overcomes the low fluvial supply (Frignani et al., 2005). The interaction between sea currents and riverine inputs also determines the distribution of sediments on belts parallel to the Adriatic coastline according to the grain size, with sands along the coast followed basinward by mud and offshore relict sands (Brambati et al., 1983).

Based on mass accumulation rates and sediment characteristics, three main areas can be distinguished on the North Adriatic inner shelf (Frignani et al., 2005; Fig. 1): i) North of the Adige River, where the low sediment accumulation promotes the formation of scattered mud patches exclusively in front of the river outlets; ii) from the Po outlets to Ravenna, where the maximum values of mass accumulation rates are recorded; iii) from Ravenna to Ancona, where the values of sedimentation rates are moderate. South of the Po Delta, high amounts of sediments are accumulated at 20–40 m water depth along the “Adriatic mud-belt” (Van der Zwaan and Jorissen, 1991). Here and in areas of maximum sediment deposition immediately south of the Po Delta, periodical/seasonal oxygen deficiency occurs at the sediment-water interface due to the intense accumulation and degradation of organic matter (Van der Zwaan and Jorissen, 1991; Alvisi et al., 2013). The organic material included in prodelta sediments is mainly represented by refractory organic matter of terrestrial origin, with a great contribution of soil-derived organic matter (Tesi et al., 2007). Labile organic matter derived from phytoplankton represents a minor portion of the organic material deposited on the shelf and it is rapidly degraded (Miserocchi et al., 2007; Tesi et al., 2013).

The highest values of mass accumulation rate (3.3 g·cm⁻²·y⁻¹) are recorded in front of the Po River outlets, where both continuous and episodic sedimentation phases occur (Frignani et al., 2005; Palinkas and Nittrouer, 2007; Fig. 1). The latter are related to major flood events with a sub-decadal return time (Cattaneo et al., 2003), which lead to the deposition of thick fine-grained layers becoming progressively thinner in a southward direction (Wheatcroft et al., 2006). Two main peaks in water and sediment discharge occur yearly, one during the late autumn related to the precipitation maximum and the other in the late spring triggered by snow melting (Cattaneo et al., 2003).

In the sectors of the North Adriatic shelf not affected by riverine sedimentation, sediment-starved conditions occur and the modern seafloor is represented by remains of alluvial plain deposits developed during the last glacial period and, to a lesser extent, by patches of transgressive back barrier-coastal deposits that represent the result of the backstepping migration of a wide barrier-lagoon-estuary system in response to the Holocene transgression (Trincardi et al., 1994; Storms et al., 2008; Ronchi et al., 2018).

3. Methodological approach

3.1. The Adriatic Sea database

The analysed data were derived from the modern ostracod and

benthic foraminiferal databases of the Adriatic Sea, published by Breman (1975) and Jorissen (1988). A total of 357 grab samples and piston-core tops were collected during the oceanographic cruise in 1962 from 7.5 to 1205 m of water depth in the whole Adriatic Sea to perform analyses on ostracoda and benthic foraminifera. Treatment and preparation of samples for meiofaunal analyses followed standard procedures described in detail in Breman (1975) and Jorissen (1988). The analyses were performed on the sediment fraction between 150 and 450 µm for ostracoda and 150–595 µm for benthic foraminifera. The fraction > 150 µm was selected by the authors in order to retain most of the adult individuals and keep the data comparable to other (palaeo-) ecological studies (Breman, 1975; Jorissen, 1987, 1988). Each sampling station was also characterised in terms of water depth (m), content of sand (%), calcium carbonate (%) and organic matter (%) by Van Straaten (1970).

Basic statistical analyses were previously performed on the original works (Breman, 1975; Jorissen, 1987, 1988). Specifically, Breman (1975) ran a Q-mode PCA on a reduced set (120) of ostracod samples from the whole Adriatic Sea, selected due to the limited storage space of the employed statistical program. Concerning benthic foraminifera, statistical analyses were performed on the entire dataset (285 samples), analysed with a Q-mode PCA and an R-mode cluster analysis on the 50 most abundant taxa (Jorissen, 1987; Appendix III of Jorissen, 1988). Moreover, a subset of 124 samples from biofacial units II and IV was analysed with an R-mode cluster analysis on the 40 most abundant taxa (Appendix IV, Jorissen, 1988). Here, we apply a suite of most recent statistical methods to ostracoda and benthic foraminifera from a North Adriatic subset of stations ($n = 87$) at maximum 40 m water depth, distributed from the northern coasts down to the Conero promontory near Ancona (Fig. 1), in order to characterise in detail the portion of the shelf directly influenced by river inputs.

Ostracod taxa were reported by the author at species level as standardised relative frequencies on the total assemblage and the total number of identified valves was included (Breman, 1975). We removed transported or reworked freshwater and brackish water taxa (such as *Candona* spp., *Ilyocypris* spp., *Limnocythere* spp., *Cyprideis torosa*, *Lepocythere lagunae* and *Loxococoncha elliptica*; complete list included in Supplementary Material 1 Table 1) from the original data and we recalculated the relative frequencies. Afterwards, only seventy-one samples including at least 20 valves were retained for the construction of the ostracod matrix; this number is considered a suitable threshold value to discern small samples (valves < 20) not suitable for quantitative studies in marine settings (Cronin et al., 1999; Bassetti et al., 2010). Finally, we grouped selected species up to genera level according to their taxonomy and ecological characteristics to reduce the dispersion of the data (list of taxa in Supplementary Material 1) (Table 1).

The benthic foraminiferal matrix is composed of 78 samples including > 250 counted tests of unstained individuals (i.e., total assemblages), excluding the contribution of finely agglutinated taxa such as *Eggerella scabra* and *Reophax* spp. due to their susceptibility to fragmentation after burial (Jorissen, 1988). Some taxa were gathered into groups in the complete dataset reported in Appendix III and were differentiated in the subset of samples reported in Appendix IV of Jorissen (1988), which includes only 2/3 of the samples considered in our analyses. To further improve the characterisation of the foraminiferal assemblages, we separately analysed the samples of Appendix IV included in our portion of the database and the results were reported in Supplementary Material 2. In the main body of the text, we report the analyses on the samples of Appendix III of Jorissen (1988) to keep the ostracod and benthic foraminiferal datasets comparable. The relative abundances of foraminiferal taxa were expressed in the original datasets as compositional data in percentage form.

3.2. Multivariate statistical analyses

The most common ostracod and benthic foraminiferal taxa with a relative abundance > 5% in at least one sample were included in the matrices for multivariate statistical analyses, following reference works on Mediterranean river-influenced shelves (Frezza and Di Bella, 2015; Goineau et al., 2015). We calculated the square root of the relative proportions of the data (Hellinger transformation) and then applied the Euclidean distance to compute the Hellinger distance, a measure recommended for clustering and ordination of quantitative species data, which gives less statistical weight to rare taxa (Legendre and Gallagher, 2001). We standardised to zero mean and unit variance (z-standardization) the abiotic variables in order to compare environmental parameters with different orders of magnitude (e.g., absolute values of water depth and concentration-like data of sediment composition).

Finally, we separately performed the following statistical analyses on both ostracod (71 samples and 27 taxa) and benthic foraminiferal (78 samples and 22 taxa) matrices:

1. Multivariate Regression Trees (MRT) were performed to determine biofacies focusing on the relationship between sites with similar meiofaunal content and environmental conditions (De'ath, 2002). MRT is a constrained clustering technique that defines quantitative values of environmental variables to discriminate groups with a similar faunal composition (De'ath, 2002). This operation is performed on the whole dataset (including biotic and abiotic variables) to obtain the first partition and then it is successively repeated for every defined group until each sample forms a single group. The resulting tree must be "pruned", i.e., its dimension must be reduced until it retains the most informative partitions, expressed as the best predictive performance of the tree. Usually, it is the smallest solution within one standard error of the lowest value of cross-validated relative error (CVRE). The final tree is formed by a series of splits (nodes) with a related value of one explanatory variable, and terminal nodes (leaves) represent groups of sites (clusters) resulting from the chosen partition. In order to assess if MRT groups significantly differ in terms of environmental variables, a Kruskal-Wallis test was applied (Supplementary Material 1 Table 3). If the *p*-value was significant (< 0.05), a post-hoc test was performed to identify significantly different groups by means of a pairwise Wilcoxon test for multiple sample, with a Bonferroni correction to reduce the probability of making Type-I errors (Supplementary Material 1 Tables 4, 5).
2. A Similarity Percentage analysis (SIMPER) based on the Euclidean distance was applied to the groups derived from MRT to quantify biotic and abiotic variables responsible for the grouping of samples, and to assess which species mostly contribute to the similarity between samples of the same group (Tables 1–4; Clarke, 1993).
3. A Metric Multidimensional Scaling (MDS; Gower, 1966) was performed on each matrix to further test the relationships between assemblages and environmental parameters and to determine the main factor(s) driving meiofaunal turnover across the study area. The MDS was computed exclusively using faunistic data, in order to assess if the MRT clusters could still be discriminated from the faunal composition of samples. This ordination technique allows to obtain a Euclidean representation of points projected onto a space of reduced dimensionality, preserving their distance relationships. Since both MRT and MDS use the same metric distance, this type of ordination is recommended to order groups of points defined by the MRT in a low-dimensional space (De'ath, 2002). The connection between samples and environmental variables was visualised fitting the latter as vectors and contour plots on the MDS graphs.
4. The ostracod and benthic foraminiferal databases were correlated by means of a Spearman's correlation matrix, in order to assess the relationship among ostracod, benthic foraminiferal taxa and environmental variables (*p*-values and *R*-values provided in

Supplementary Material 1 Table 6). Only the stations shared by both databases were included (69 samples).

MRT, SIMPER and MDS were also performed on the subset of samples with differentiated species from Appendix IV of Jorissen (1988; Supplementary Material 2).

All the analyses were carried out with the R software (R Core Team, 2018), except for the calculation of SIMPER, performed using the software PAST (PAleontological STatistic – version 3.10 by Hammer et al., 2001). The following R packages were used: base (base statistics, Kruskal-Wallis and Wilcoxon tests, MDS), mvpart and MVPARTwrap (MRT), vegan (fitting environmental vectors and contours on MDS), ade4 (for the function *is.euclid*), ggplot2 and ggthemes (MDS plots), Hmisc and corrplot (computation and graphical representation of correlation matrices).

Moreover, we produced spatial distribution maps of the environmental variables included in the Adriatic Sea database using the software Surfer (Golden Software, version 11.0) and the kriging interpolation as gridding method, since it provides the best resolution for irregularly spaced data. Some stations not included in the analysed subset of samples were added to obtain a complete map of the area. The blank boundary in correspondence to the Adriatic coasts was defined, digitising the coastline and adding it as a breakline for the grids.

4. Results: North Adriatic meiofaunal biofacies

The combination of MRT, SIMPER and Kruskal-Wallis test reveals a distinctive set of meiofaunal biofacies (sensu Jackson, 1997) distributed across the inner portion (< 40 m water depth) of the North Adriatic shelf. In total, we identify seven ostracod biofacies and five benthic foraminiferal biofacies.

4.1. Ostracod biofacies

The MRT performed on the ostracod matrix gathered the analysed samples into 7 groups/clusters (Fig. 2), which correspond to specific environmental conditions (Figs. 3, 4a–c) characterised by a distinctive faunal assemblage (Tables 1, 2).

The first node separates samples on the basis of the sand content in the sediment, with a threshold value of 15.6%. Depth determines the second subdivisions on each side of the tree. Samples with < 15.6% of sand on the left side at < 20.5 m are further separated by the CaCO₃ limit placed at 24.7%, which defines the first two leaves of the tree (cluster 1 and cluster 2), whereas samples at ≥ 20.5 m water depth are grouped into the third leaf (cluster 3). On the right side of the diagram, samples with ≥ 15.6% of sand content placed at < 29 m water depth are divided between samples at < 18 m water depth (cluster 4) and samples comprised between 18 and 29 m water depth (cluster 5). On the other hand, samples located at ≥ 29 m water depth are split into cluster 6 and cluster 7, based on the concentration of sand (≥ 51% and < 51%, respectively).

4.1.1. Biofacies O1 (cluster 1)

Biofacies O1 comprises stations located south of the Po Delta down to Ravenna (Fig. 4a–c). These samples are placed at shallow water depths (8–17 m), show a low concentration of sand (0.5–15.2%) and calcium carbonate (20.1–23.5%), and the highest values of organic matter concentration (3.9% on average; Figs. 3, 4a–c). The most abundant species of this biofacies are *Palmoconcha turbida*, *Leptocythere ramosa* and other *Leptocythere* species that include *L. laevis*, *L. tenera*, *L. rara* and *Leptocythere* sp. A (average abundances of 28.8%, 8.6% and 23.7%, respectively). All these taxa show a significant (*p*-value < 0.05, Supplementary Material 1 Table 6) negative correlation with sand and depth and have the highest positive correlation with organic matter of the entire dataset (Fig. 5).

Table 1
Similarity percentage (SIMPER) analysis performed on faunal composition of ostracod assemblages defined by the MRT (Fig. 2).

Taxon	Av. dissim.	Contrib. %	Cumulative %	Biofacies O1	Biofacies O2	Biofacies O3	Biofacies O4	Biofacies O5	Biofacies O6	Biofacies O7
<i>Semicytherura incongruens</i>	562.3	26.1	26.1	2.8	26.6	12.5	36.7	31.8	18.7	10.3
<i>Pontocythere turbida</i>	403.7	18.7	44.8	1.3	6.8	0.5	17.9	19.5	34.6	12.4
<i>Palmoconcha turbida</i>	354.6	16.4	61.2	28.8	23.0	13.8	11.0	0.8	0.0	1.0
<i>Cytheridea neapolitana</i>	287.3	13.3	74.5	0.3	2.1	24.7	0.5	0.8	5.3	22.3
<i>Leptocythere</i> spp.	159.8	7.4	81.9	23.8	4.8	4.9	2.2	0.3	0.4	0.6
<i>Loxoconcha tumida</i>	56.7	2.6	84.6	0.0	6.2	2.7	4.6	11.7	4.7	4.9
<i>Leptocythere ramosa</i>	46.6	2.2	86.7	8.6	2.3	7.5	3.2	0.0	0.1	0.4
<i>Carinocythereis whitei</i>	45.8	2.1	88.8	8.0	6.1	8.9	3.6	0.7	4.1	9.4
<i>Hiltermannicythere turbida</i>	38.0	1.8	90.6	6.0	5.3	8.7	3.4	2.2	7.9	9.5
<i>Cytheretta</i> spp.	37.6	1.7	92.3	1.5	3.2	0.2	4.0	7.7	1.4	0.7
<i>Aurila</i> spp.	28.5	1.3	93.7	0.0	0.4	0.1	0.1	6.1	3.9	2.3
<i>Semicytherura</i> spp.	28.1	1.3	95.0	4.1	0.7	0.7	2.2	6.1	5.9	5.1
<i>Xestoleberis dispar</i>	18.1	0.8	95.8	4.3	1.3	0.0	1.8	0.6	0.7	0.4
<i>Loxoconcha</i> ex gr. <i>rhomboidea</i>	16.1	0.7	96.5	0.0	2.2	0.0	1.4	1.1	0.5	0.2
<i>Callistocythere</i> spp.	12.7	0.6	97.1	1.8	0.5	1.1	1.2	2.2	3.1	5.9
<i>Sagmatocythere versicolor</i>	10.8	0.5	97.6	0.5	1.1	4.2	0.0	0.5	0.9	1.3
<i>Leptocythere bacescoi</i>	9.3	0.4	98.1	3.1	3.5	1.6	1.2	0.5	1.1	2.7
<i>Pterigocythereis</i> spp.	8.8	0.4	98.5	0.0	0.1	2.4	0.0	2.2	2.2	4.1
<i>Loxoconcha rubritincta</i>	6.0	0.3	98.8	2.2	0.2	0.0	0.9	0.0	0.0	0.0
<i>Xestoleberis fuscomaculata</i>	5.3	0.2	99.0	0.0	0.6	0.3	1.6	0.5	0.4	0.5
<i>Costa edwardsii</i>	5.2	0.2	99.2	0.0	0.0	1.6	0.0	0.1	0.3	3.2
<i>Cytheropteron</i> spp.	3.9	0.2	99.4	0.2	0.1	1.7	0.0	0.1	0.5	2.4
<i>Bosquetina</i> spp.	3.2	0.1	99.6	0.0	0.0	0.5	0.0	0.0	0.5	2.5
<i>Pontocypris</i> spp.	2.7	0.1	99.7	0.2	1.4	0.5	0.1	0.2	0.1	0.3
<i>Paracytheridea</i> spp.	2.7	0.1	99.8	0.0	0.0	0.0	0.1	2.2	1.4	0.1
<i>Loxoconcha neapolitana</i>	2.7	0.1	99.9	0.0	0.1	0.0	0.1	2.2	0.0	0.3
<i>Neocytherideis fasciata</i>	1.3	0.1	100.0	0.0	0.5	0.1	1.0	0.0	0.0	0.0

4.1.2. Biofacies O2 (cluster 2)

This biofacies groups samples mainly positioned in front of the Adige River mouth and along the Adriatic coast south of Ravenna between ca. 13 and 20 m water depth (Figs. 3, 4a–c). Two scattered samples are also present near the Po Delta and along the northern Adriatic coast (Fig. 4). Stations of biofacies O2 have a low sand content (0.7–11.2%) and moderate CaCO₃ values (25.9–57.4%; Fig. 3). This biofacies includes relatively high frequencies of *Semicytherura incongruens* and *Palmoconcha turbida* (average values of 26.6% and 23%, respectively). *Loxoconcha tumida* and *Loxoconcha* ex gr. *rhomboidea* reach their maximum average abundance, even though with relatively low frequencies (6.2% and 2.2%, respectively), within this biofacies. These taxa, as well as *S. incongruens*, show a positive correlation with sand and CaCO₃ percentages and are negatively correlated to organic matter (Fig. 5).

4.1.3. Biofacies O3 (cluster 3)

Biofacies O3 includes samples distributed along the Adriatic coast south of the Po Delta between 21 and 35 m of water depth (Figs. 3, 4a–c). A very low sand content (0.5–7%) and relatively high organic matter concentration (0.7–1.8%, average value of 1.35%) characterise this biofacies (Fig. 3). *Cytheridea neapolitana* is the most abundant species, with an average abundance of 24.7%. It shows a positive correlation with depth and organic matter, and a negative correlation with sand (Fig. 5). Relatively high frequencies of *Palmoconcha turbida* and *S. incongruens* (average abundances of 13.8% and 12.5%, respectively) are recorded, together with *Carinocythereis whitei*, *L. ramosa* and *Sagmatocythere versicolor* (average values of 8.9%, 7.5% and 4.2%, respectively). These species are negatively correlated to sand, and *C. whitei* and *L. ramosa* show a significant positive correlation with organic matter (Fig. 5).

Table 2

Similarity percentage (SIMPER) analysis performed on abiotic parameters related to ostracod assemblages defined by the MRT (Fig. 2).

Variable	Av. dissim.	Contrib. %	Cumulative %	Biofacies O1	Biofacies O2	Biofacies O3	Biofacies O4	Biofacies O5	Biofacies O6	Biofacies O7
Sand (%)	2356.0	79.7	79.7	6.3	4.9	2.2	51.9	75.8	66.4	32.7
CaCO ₃ (%)	394.2	13.3	93.0	21.8	32.1	28.1	50.4	49.6	30.6	32.5
Depth (m)	200.4	6.8	99.8	11.7	17.0	27.5	12.3	24.2	35.0	34.4
Organic matter (%)	66.53	0.2	100.0	3.9	1.1	1.4	0.5	0.5	0.7	0.7

4.1.4. Biofacies O4 (cluster 4)

This biofacies includes samples characterised by sandy sediments (15.9–90.4% of sand content) distributed along the Adriatic coasts at shallow depths (8–17 m water depth), specifically in the northern sector and from Pesaro to Ancona (Figs. 3, 4a–c). The most common species is *S. incongruens* (average value of 36.7%), followed by *Pontocythere turbida* (17.9% on average). Both are positively correlated to sand and negatively correlated to organic matter (Fig. 5). Even though with relatively low values, *Xestoleberis dispar* and *Xestoleberis fuscomaculata* show their highest average concentrations within this biofacies (1.75% and 1.63%, respectively).

4.1.5. Biofacies O5 (cluster 5)

Biofacies O5 includes samples restricted to the shelf north of the Po Delta, with high sand content (19.4–97.4%) at 18–29 m water depth (Figs. 3, 4a–c). *Semicytherura incongruens* and *Pontocythere turbida* are the most abundant species (average values of 31.8% and 19.5%, respectively). The ostracod fauna also includes taxa positively correlated to sand (Fig. 5), such as *Aurila* spp. (mainly *A. speyeri* and *A. convexa*), *Cytheretta* spp. (*C. adriatica* and *C. judaea*), *Loxoconcha tumida*, *Paracytheridea* spp., *Sagmatocythere neapolitana* and *Semicytherura* spp.

4.1.6. Biofacies O6 (cluster 6)

Samples of biofacies O6 are located at 30–40 m water depth on the North Adriatic shelf (Fig. 4a–c), in correspondence with bottoms enriched in sand (53.5–74.8% of sand). *Pontocythere turbida* is the species recorded with the highest frequencies (average value of 34.6%), followed by *S. incongruens* (18.7% on average). Both species show a positive correlation with sand and a negative correlation with organic matter (Fig. 5). Subordinate taxa are *Aurila* spp. and *Semicytherura* spp.

4.1.7. Biofacies O7 (cluster 7)

This biofacies is located in front of the Po Delta, at water depths

Table 3

Similarity percentage (SIMPER) analysis performed on faunal composition of benthic foraminiferal assemblages defined by the MRT (Fig. 2).

Taxon	Av. dissim.	Contrib. %	Cumulative %	Biofacies F1	Biofacies F2	Biofacies F3	Biofacies F4	Biofacies F5
<i>Ammonia parkinsoniana</i> - <i>A. tepida</i>	1220.0	61.2	61.2	57.2	36.8	14.7	12.6	7.4
<i>Bulimina</i> ex gr. <i>marginata</i>	114.4	5.7	67.0	2.3	1.3	0.1	21.1	1.6
<i>Nonionella turgida</i>	103.3	5.2	72.1	8.3	4.6	0.4	5.9	0.6
<i>Textularia agglutinans</i>	88.5	4.4	76.6	5.4	6.1	6.4	12.7	9.0
<i>Buccella granulata</i>	70.5	3.5	80.1	0.1	1.6	4.8	1.9	11.0
<i>Aubignyna perlucida</i>	58.5	2.9	83.1	2.4	9.2	3.9	5.0	0.2
<i>Criboelphidium</i> ex gr. <i>granosum</i>	54.0	2.7	85.8	0.9	9.7	11.0	6.4	9.0
<i>Criboelphidium</i> ex gr. <i>poeyanum</i>	43.9	2.2	88.0	2.8	9.2	9.5	7.8	4.4
<i>Asterigerinata mamilla</i>	36.1	1.8	89.8	0.0	0.0	0.6	0.6	7.2
<i>Ammonia</i> ex gr. <i>beccarii</i>	33.4	1.7	91.4	3.4	4.7	4.4	3.0	8.4
<i>Reussella spinulosa</i>	30.4	1.5	93.0	0.1	0.3	0.8	2.2	5.9
<i>Quinqueloculina seminula</i>	23.8	1.2	94.2	3.5	2.3	7.7	4.1	1.3
<i>Cibicides lobatulus</i>	22.8	1.1	95.3	0.2	0.1	0.1	1.1	5.8
<i>Quinqueloculina</i> spp.	16.7	0.8	96.1	0.1	0.2	3.2	1.0	3.4
<i>Adelosina</i> spp.	16.0	0.8	97.0	1.8	1.3	6.9	0.5	1.4
<i>Neoconorbina terquemi</i>	13.9	0.7	97.7	0.0	0.0	0.5	0.5	3.4
<i>Triloculina trigonula</i>	13.1	0.7	98.3	2.2	1.6	5.9	0.5	1.8
<i>Elphidium advenum</i>	13.0	0.7	99.0	2.5	2.7	2.7	2.0	3.1
<i>Elphidium crispum</i> gr.	11.7	0.6	99.5	0.3	3.7	3.3	3.2	3.8
<i>Rosalina bradyi</i>	5.3	0.3	99.8	0.1	0.0	1.7	0.7	1.9
<i>Valvulineria bradyana</i>	2.4	0.1	99.9	0.0	0.0	0.0	2.1	0.0
<i>Cassidulina laevigata</i> gr.	1.5	0.1	100.0	1.0	0.1	0.0	0.0	0.0

between 30 and 40 m (Figs. 4a–c) on moderately sandy substrates (17.6–49.2%; Fig. 3). Biofacies O7 shows relatively high frequencies of a variety of taxa. *Cytheridea neapolitana* is the most abundant species (average frequency: 22.7%), associated with lower percentages of other taxa with a significant positive correlation with water depth (Fig. 5), such as *Callistocythere* spp. (mostly *C. adriatica* and *C. intricadoidea*), *C. whitei*, *Hiltermannicythere turbida*, *Pterygocythereis* spp. (mostly *P. jonesii*) and *Semicytherura* spp. (mostly *S. ruggierii* associated with other species with low frequencies). *Bosquetina carinella*, *Costa edwardsii* and *Cytheropteron* spp. (mostly represented by *C. rotundatum*) reach their highest frequencies within biofacies O7, while they are almost absent in the other biofacies.

4.2. Benthic foraminiferal biofacies

The MRT performed on the benthic foraminiferal matrix grouped the analysed samples into 5 clusters (Fig. 6), which correspond to peculiar environmental conditions (Figs. 4d–f, 7) where distinctive associations of taxa occur (Tables 3, 4). With respect to the biofacial units previously identified in the Adriatic Sea by Jorissen (1987), clusters 1–3 are gathered within biofacial unit II, while cluster 4 roughly coincides with biofacial unit IV and cluster 5 corresponds to biofacial unit III.

In the MRT (Fig. 6), the discriminant environmental parameter for the first node is water depth, with the limit placed at 22.5 m. The shallower samples on the left side of the tree are subdivided by the CaCO₃ content: samples with < 48% of CaCO₃ are further split on the basis of the percentage of organic matter (cluster 1 with ≥ 1.45%, cluster 2 with < 1.45%), whereas samples including ≥ 48% of CaCO₃ are gathered into cluster 3. On the right side of the tree (samples at water depths ≥ 22.5 m), the last two leaves are discriminated by the organic matter concentration (≥ 1.2% in cluster 4 and < 1.2% in cluster 5).

Table 4

Similarity percentage (SIMPER) analysis performed on abiotic parameters related to benthic foraminiferal assemblages defined by the MRT (Fig. 2).

Variable	Av. dissim.	Contrib. %	Cumulative %	Biofacies F1	Biofacies F2	Biofacies F3	Biofacies F4	Biofacies F5
Sand (%)	2317.0	78.5	78.5	4.2	13.5	49.7	2.9	59.7
CaCO ₃ (%)	416.0	14.1	92.6	26.5	29.5	62.0	28.6	36.8
Depth (m)	210.3	7.1	99.8	14.3	16.0	14.5	30.7	31.6
Organic matter (%)	6.7	0.2	100.0	3.3	0.8	0.6	1.5	0.6

The MRT performed on the shallowest sub-dataset provided very similar results (Supplementary Material 2). The distinction of some species allowed to obtain more detailed information about the taxonomic composition of the shallowest assemblages.

4.2.1. Biofacies F1 (cluster 1)

This biofacies is characterised by shallow water depth (9–22 m), low sand (0.7–14.4%) and CaCO₃ content (20.1–42.3%) and high organic matter concentration (1.6–14.4%; Fig. 7). Samples of biofacies F1 are situated in proximity to the Adige and Po outlets and south of the Po Delta near Ravenna (Fig. 4d–f). The dominant taxa are *Ammonia tepida* and *A. parkinsoniana* (average frequency of 57.2%), with a prevalence of the former species (Suppl. Mat. 2), associated with subordinate *Nonionella turgida* (8.3% on average). These taxa show a significant positive correlation with organic matter and a negative correlation with sand and CaCO₃ (Fig. 5).

4.2.2. Biofacies F2 (cluster 2)

Biofacies F2 is distributed from the Po Delta to Ancona along the Adriatic coast between 8 and 22 m water depth (Figs. 4d–f, 7). Samples of this clusters have a moderate organic matter concentration (0.1–1.3%), relatively low CaCO₃ (20.7–48%) and variable sand content (0.2–73.3%). *Ammonia parkinsoniana* and *A. tepida* are the most common taxa (average frequency of 36.8%), but *A. parkinsoniana* is more abundant (Suppl. Mat. 2). This biofacies is characterised by the maximum average frequency of *Aubignyna perlucida* (9.2%), which shows a negative correlation with depth and sand (Fig. 5). Additional secondary taxa are *Criboelphidium* ex gr. *granosum* and *Criboelphidium* ex gr. *poeyanum* (on average 9.7% and 9.3%, respectively, with prevailing *Criboelphidium lidoense* and *Criboelphidium decipiens*). The former does not show any significant correlation with environmental parameters, whereas the latter is negatively correlated to sand and

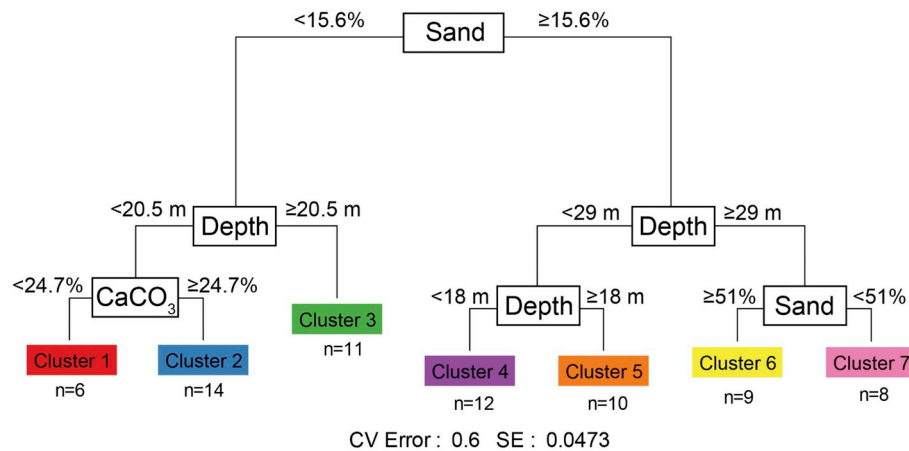


Fig. 2. Multivariate Regression Tree (MRT) obtained from the ostracod matrix and four explanatory variables (concentrations of sand, organic matter, CaCO₃ and water depth in m). Discriminant variables and threshold values are reported at each node of the tree. Cross validation error and Standard error are also indicated.

water depth.

4.2.3. Biofacies F3 (cluster 3)

This biofacies is located north of the Po Delta at shallow water depth (8–22 m, Fig. 4d–f). Biofacies F3 shows the highest values of CaCO₃ of the entire database (48.9–73%), along with high sand (7.6–80.8%) and moderate organic matter concentrations (0.3–1.4%; Fig. 7). The highest frequency of Milioloidea (including *Adelosina* spp., *Quinqueloculina seminula*, *Quinqueloculina* spp. and *Triloculina trigonula*) is recorded within this biofacies (average value of 23.8%). All the mentioned taxa show a significant positive correlation with CaCO₃ (Fig. 5). Moderate

concentrations of *A. tepida*-*A. parkinsoniana* (14.7% on average), *Criboelphidium* ex gr. *granosum* (11%, with more common *C. lidoense*) and *Criboelphidium* ex gr. *poeyanum* (9.5%, with prevailing *C. decipiens*) are also recorded.

4.2.4. Biofacies F4 (cluster 4)

Biofacies F4 gathers the stations distributed south of the Po Delta down to Pesaro at 23–35 m water depth (Fig. 4d–f) and is characterised by high organic matter (1.3–1.8%) and low sand concentrations (0.5–7%; Fig. 7). The most abundant frequencies are shown by *Bulimina* ex gr. *marginata*, (21.1% on average, with a marked predominance of

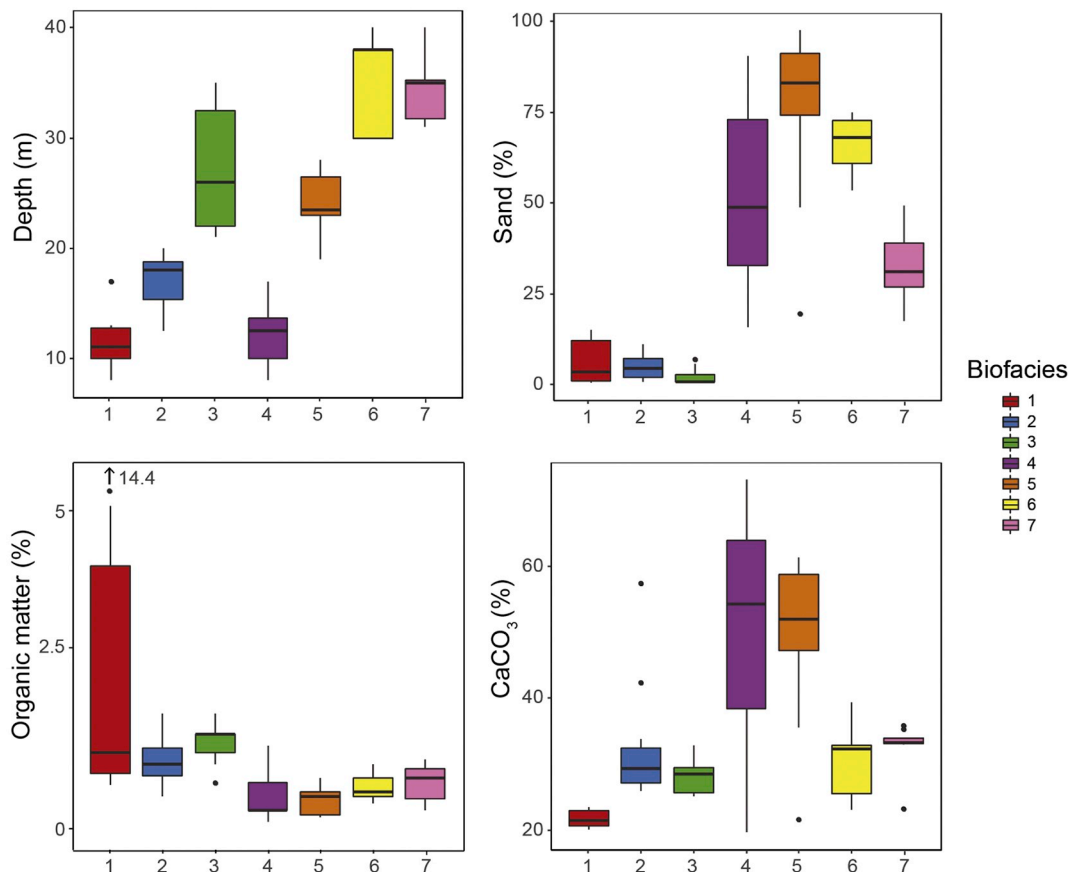


Fig. 3. Box plot summarising the values of the four environmental variables for each ostracod biofacies. The thick line within the box represents the median, and limits of the box represent the upper and lower quartiles.

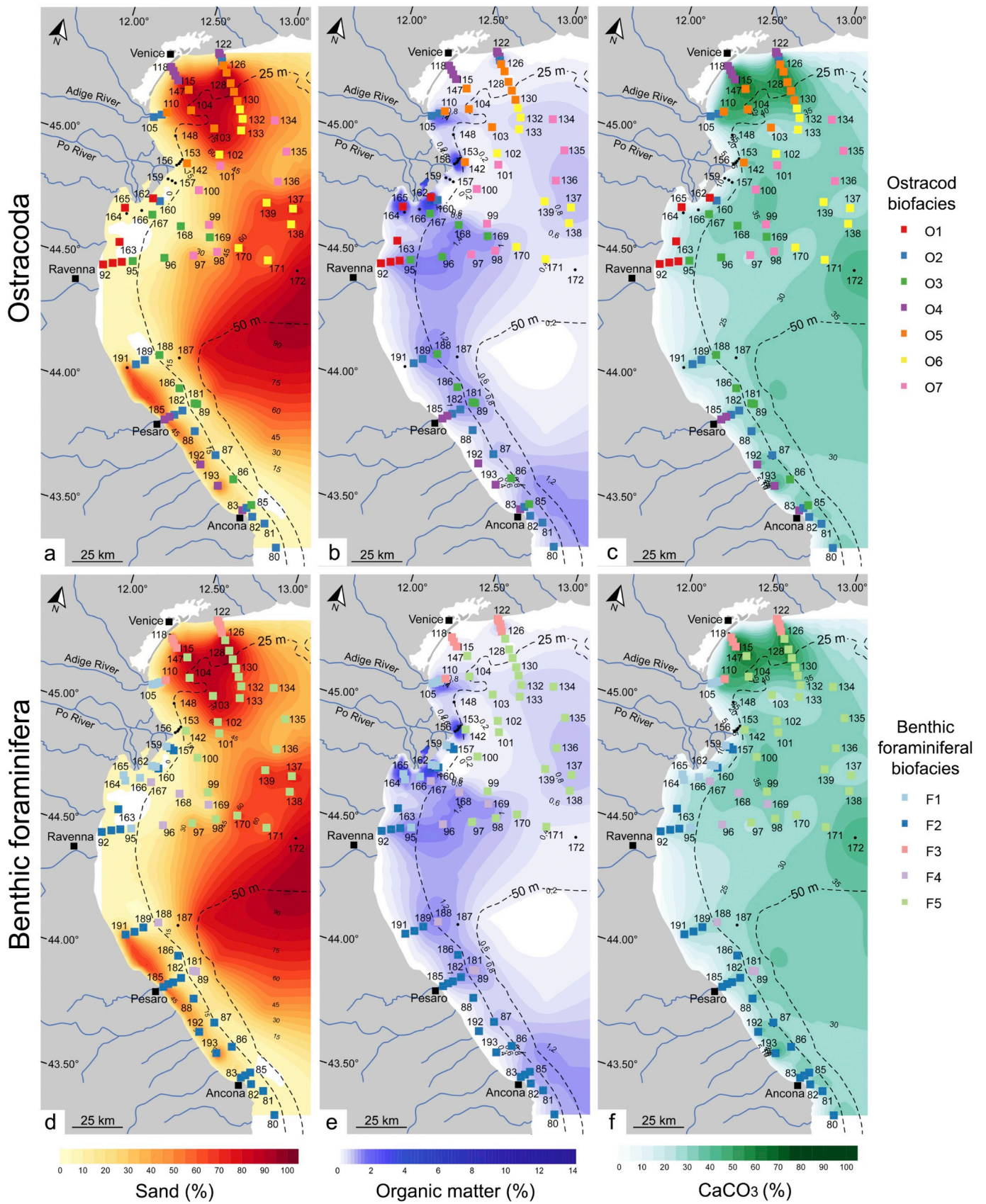


Fig. 4. Distribution of samples for ostracoda (a-c) and benthic foraminifera (d-f) coloured according to biofacies defined by the MRT, superimposed to the distribution of sand (a, d), organic matter (b, e) and calcium carbonate (c, f) concentrations.

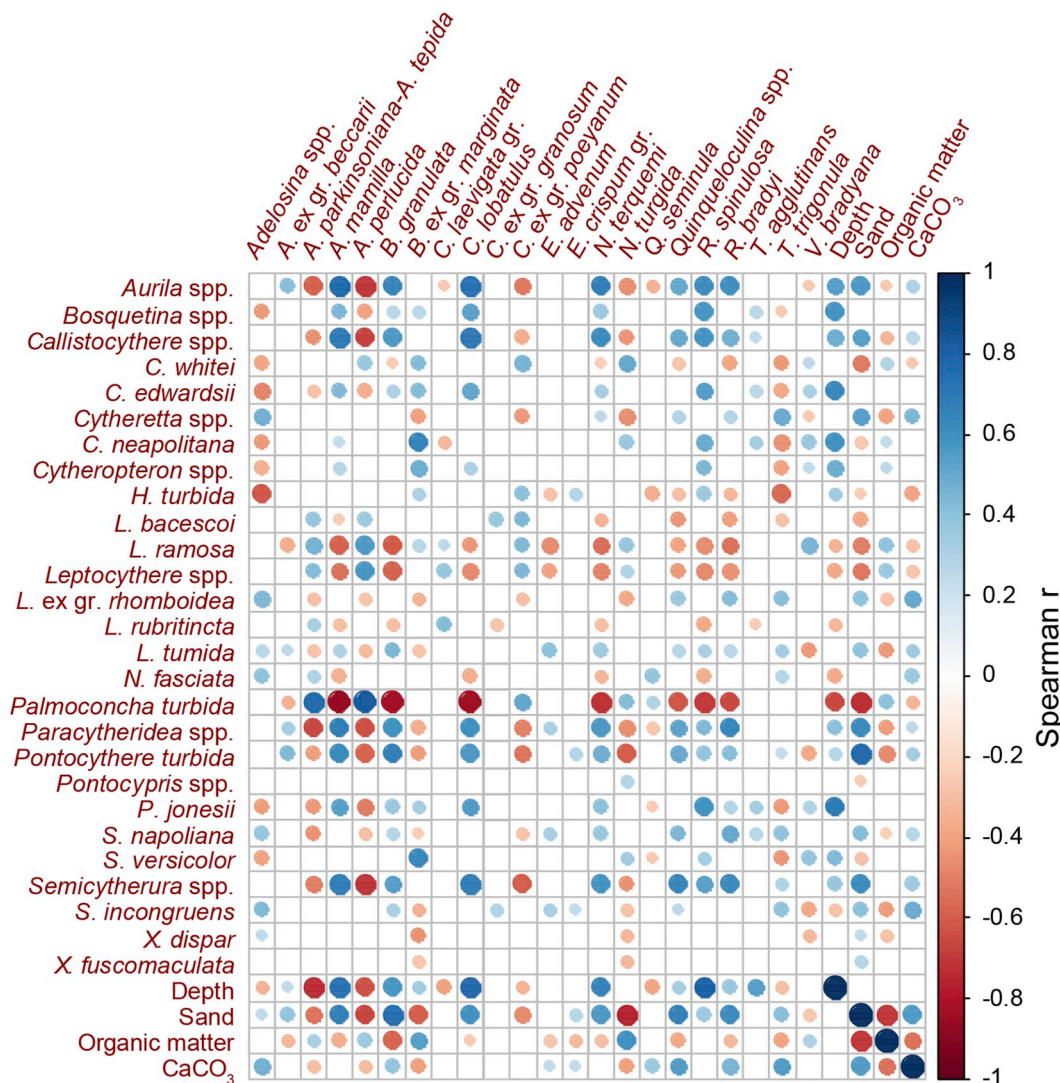


Fig. 5. Correlation matrix between abundances of ostracoda and benthic foraminifera and environmental variables. R-values (positive in blue and negative in red) are exclusively reported for significant correlations (p -values < .05, Supplementary Material 1 Table 6). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

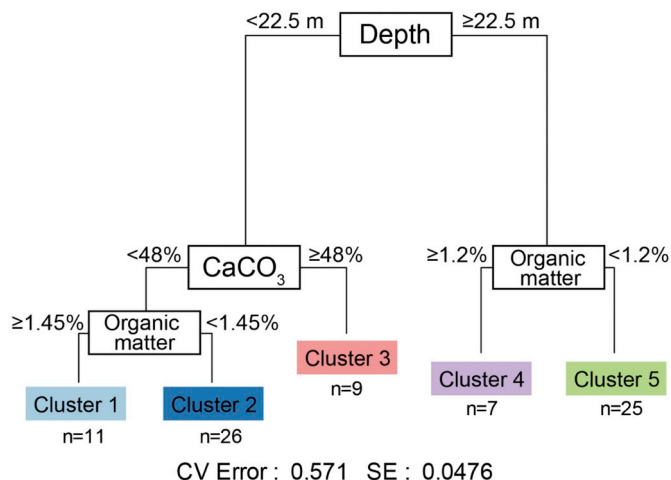


Fig. 6. Multivariate Regression Tree (MRT) obtained from the benthic foraminiferal matrix and four explanatory variables (concentrations of sand, organic matter, CaCO_3 and water depth in m). Discriminant variables and threshold values are reported at each node of the tree. Cross validation error and Standard error are also indicated.

Bulimina denudata), positively correlated to organic matter and depth, negatively correlated to sand and CaCO_3 (Fig. 5). Accompanying taxa are *Textularia agglutinans* (average frequency of 12.7%), *A. parkinsoniana-A. tepida* (12.6%), *Criboelphidium ex gr. poeyanum* (7.8%), *Criboelphidium ex gr. granosum* (6.4%) and *N. turgida* (5.9%). Even though with low frequencies, *Valvulineria bradyana* shows its maximum concentration within this biofacies (average value of 2.1%).

4.2.5. Biofacies F5 (cluster 5)

This biofacies occurs between 23 and 40 m water depth, relatively far from the North Adriatic coast (> 23 m water depth; Figs. 4d-f, 7). Stations of biofacies F5 show high percentages of sand (21.7–97.4%), moderate CaCO_3 (21.7–61%) and low organic matter content (0.2–1.1%; Fig. 7). The benthic foraminiferal fauna is highly diversified, mainly composed of taxa positively correlated to depth and sand and negatively correlated to organic matter (Fig. 5), such as *Buccella granulata* (average frequency of 11%), *Ammonia ex gr. beccarii* (8.4%), *Asterigerinata mamilla* (7.2%), *Cibicidoides lobatulus* (5.8%), *Neoconorbina terquemi* (3.4%) and *Rosalina bradyi* (1.9%). Moderate concentrations of *T. agglutinans*, *Criboelphidium ex gr. granosum* and *A. parkinsoniana-A. tepida* are also recorded within this biofacies.

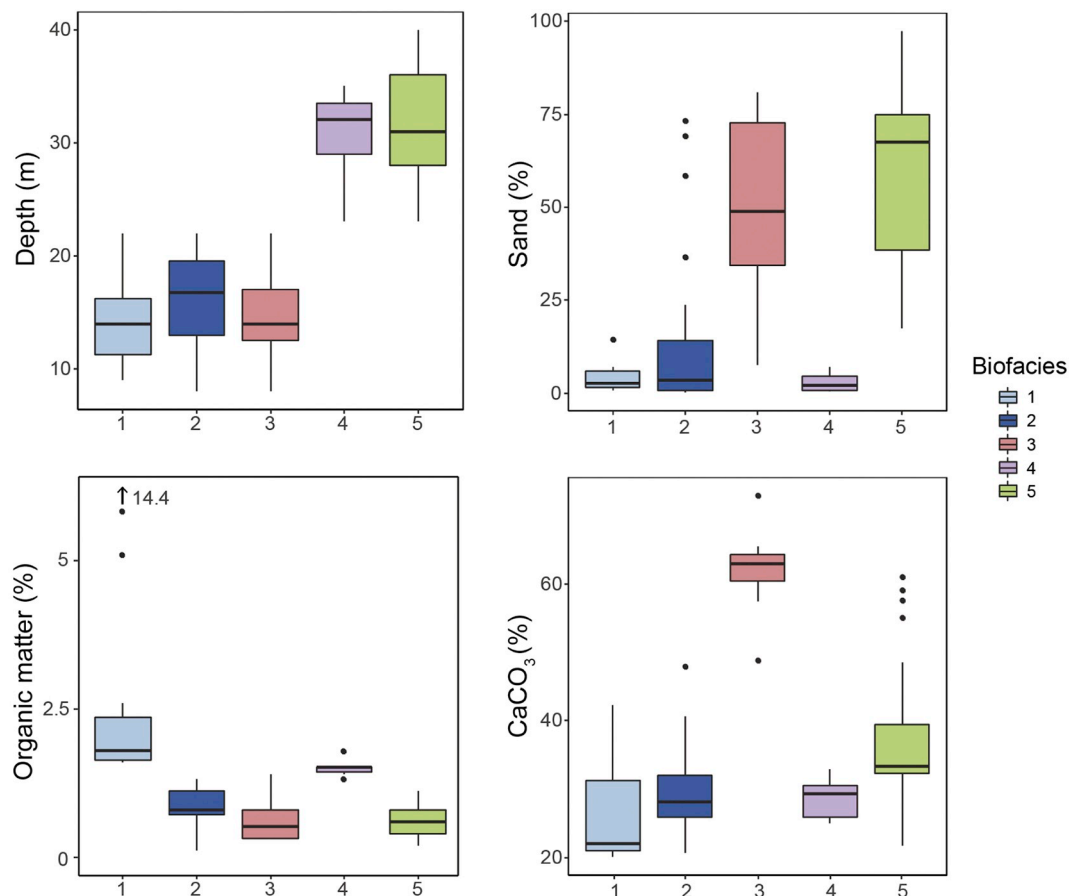


Fig. 7. Box plot summarising the values of the four environmental variables for each benthic foraminiferal biofacies. The thick line within the box represents the median, and limits of the box represent the upper and lower quartiles.

4.3. MDS analysis of the North Adriatic meiofauna

The application of MDS to the ostracod and benthic foraminiferal data (Fig. 8) refines the results obtained by the MRT, furnishing new insights on the species-environmental variables relationship (Figs. 2, 5, 6). Indeed, except for scattered samples, the distribution in the MDS graphs is consistent with the biofacies occurrence across the North Adriatic inner shelf (Figs. 4 and 8).

About ostracoda, the strong environmental gradient underlying the major axis of variation (axis 1 - MDS1 in Fig. 8) corresponds to the substrate grain-size (specifically, the sand concentration). Fitted vectors and contour plots clearly display that the arrangement of the samples from positive to negative eigenvalues of axis 1 (explaining 33.5% of variance) can be connected to an increase of sand content in the substrate. Biofacies characterised by a low sand content (O1-O3; Figs. 3, 4a-c) plot on the right side of the graph (< 20% of sand), whereas samples with intermediate (20–60%; biofacies O4-O7) and high (> 60%; biofacies O5-O6) percentages of sand are plotted towards the left side. As indicated by the direction of environmental vectors, axis 2 (MDS2, explaining 20.7% of variance) has a strong positive correlation with bathymetry. Samples belonging to biofacies O1, O2 and O4 plot in correspondence of low MDS2 values underlying water depths < 20 m; in contrast, biofacies O3, O5-O7 attain higher MDS2 values and water depths ranging between ca. 20–40 m.

Concerning benthic foraminifera, a high percentage of the total variance (42.5%) is explained by MDS axis 1, which is negatively correlated to the organic matter concentration in the substrate (Fig. 8). This is indicated by the low angle between this axis and the vector underlying the organic matter parameter, even if the strength of the gradient (i.e., the length of the arrow) is relatively low. According to

this interpretation, the position of biofacies (F1-F5) follows a negative organic matter gradient from negative to positive scores of MDS1 (Fig. 8). Biofacies F1, F2 and F4, with organic matter concentration (> 0.8%), plot on the left side of the graph, while biofacies F3 and F5 occur on the right corresponding to lower organic matter concentrations (Figs. 7 and 8). Conversely, a clear correlation between MDS axis 2 (explaining the 13.2% of the total variance) and any available environmental parameters is difficult to assess. None of the plotted environmental vectors can be easily related (i.e., is more or less parallel) to axis 2, therefore this axis could be directly correlated to a different environmental variable (or a combination of two or more variables) not included in the analysed database. Nevertheless, taking into account the direction of the vector corresponding to water depth, which was recognised by the MRT as the first parameter influencing benthic foraminiferal biofacies (Fig. 6), a distribution of biofacies along a bathymetric gradient from the upper-left (lower depths) to the lower-right (higher depths) corner of the graph (Fig. 8) is recognised.

5. Discussion

5.1. Drivers of changes in meiofauna composition across a river-influenced shelf

The employment of multiple statistical analyses on the modern ostracod fauna of the North Adriatic shelf suggests that the primary factor influencing biofacies composition and distribution is the substrate grain-size (i.e., sand content), while water depth represents the second most important environmental driver (Figs. 2, 8). Bathymetry seems to play a significant but not primary role also for the distribution of benthic foraminifera, that are mainly controlled by the organic matter

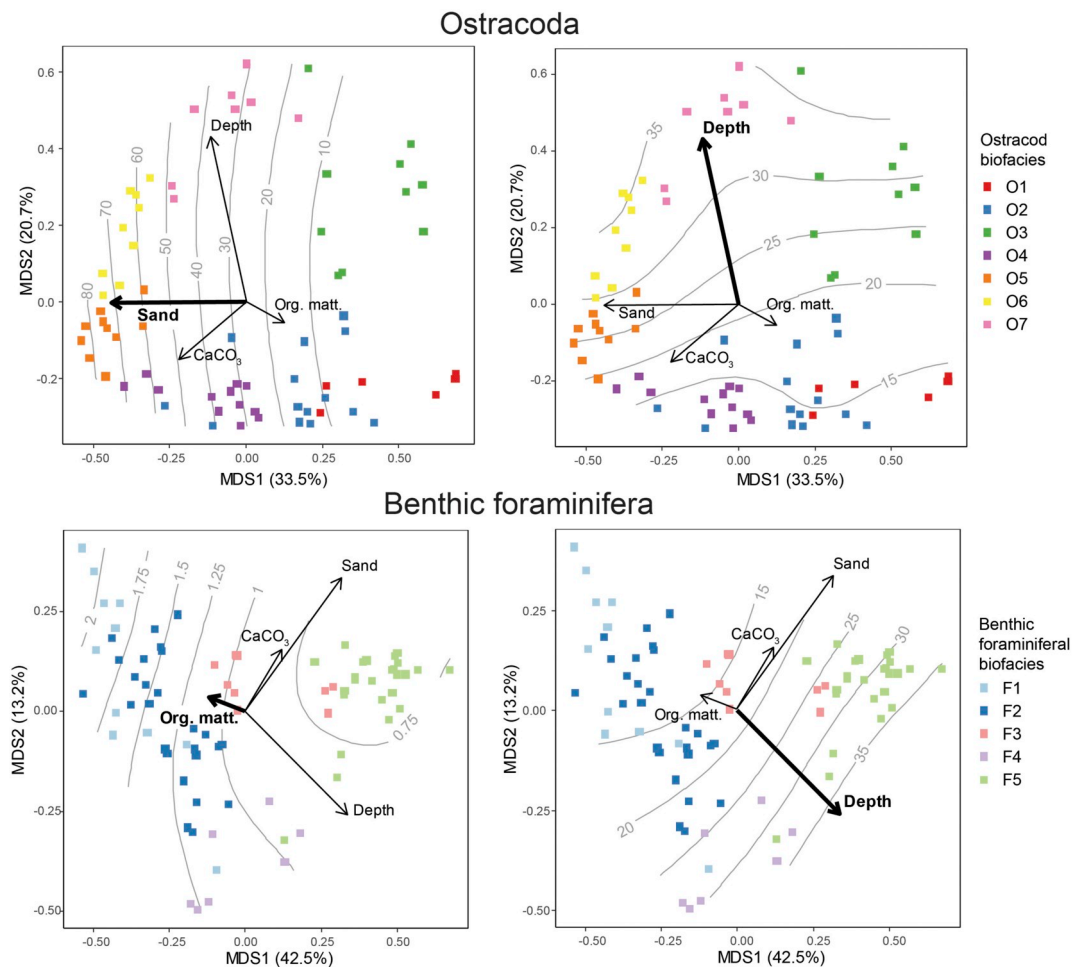


Fig. 8. Metric multidimensional scaling (MDS) for ostracod and benthic foraminiferal species composition of stations based on the Euclidean distance. Colours of groups are in accordance to biofacies defined by the MRT. Contours display the distribution of the main environmental drivers on assemblages: depth and sand for ostracoda, organic matter and depth for benthic foraminifera. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

content (Figs. 6, 8). Bathymetry is considered a complex gradient that commonly drives faunal distribution in modern and fossil marine settings (Scarponi and Kowalewski, 2004; Tyler and Kowalewski, 2014; Benito et al., 2016; Danise and Holland, 2017; Rossi et al., 2018). Although the water-depth distribution of ostracod and benthic foraminiferal species can vary from basin to basin, bathymetry was commonly identified as the main driver for the meiofaunal turnover from the coast to the lower continental slope (ca. 5–900 m water depth; Jorissen, 1987; Mendes et al., 2004; Avnaim-Katav et al., 2015; Bernasconi et al., 2018; Angue Minto'o et al., 2013), as well as from the inner to the middle-outer shelf depths (Hayward et al., 1999; Pascual et al., 2008; Azzarone et al., 2018). Also considering a narrower water-depth range on continental shelves facing delta systems, the zonation of meiofaunal assemblages seems to be related to bathymetry (e.g., Horton et al., 2003; Rossi and Horton, 2009; Frezza and Di Bella, 2015; Benito et al., 2016), but it should be remembered that water depth is a complex factor strictly related to many biotic (e.g., life strategy) and abiotic parameters (e.g., grain-size and vegetation cover of substrate, organic matter concentration, oxygen content). In turn, the distribution of these parameters is influenced by the geomorphological features and sedimentary dynamics of the basin, including the position of river mouths with respect to longshore currents and amounts of riverine input in terms of sediment and organic matter (Puig et al., 2007; Hanebuth et al., 2015; Liu et al., 2018). Therefore, in shallow marine, fluvial-influenced environments, bathymetry can be considered an indirect

influencing factor on the distribution of marine meiofauna that exclusively defines a specific location in the three dimensional space.

The employment of multiple statistical analyses on the modern ostracod fauna of the North Adriatic shelf suggests that the primary factor influencing biofacies composition and distribution is the substrate grain-size (i.e., sand content), while water depth represents the second most important environmental driver (Figs. 2, 8). Bathymetry seems to play a significant but not primary role also for the distribution of benthic foraminifera, that are mainly controlled by the organic matter content (Figs. 6, 8). Bathymetry is considered a complex gradient that commonly drives faunal distribution in modern and fossil marine settings (Scarponi and Kowalewski, 2004; Tyler and Kowalewski, 2014; Benito et al., 2016; Danise and Holland, 2017; Rossi et al., 2018). Although the water-depth distribution of ostracod and benthic foraminiferal species can vary from basin to basin, bathymetry was commonly identified as the main driver for the meiofaunal turnover from the coast to the lower continental slope (ca. 5–900 m water depth; Jorissen, 1987; Mendes et al., 2004; Avnaim-Katav et al., 2015; Bernasconi et al., 2018; Angue Minto'o et al., 2013), as well as from the inner to the middle-outer shelf depths (Hayward et al., 1999; Pascual et al., 2008; Azzarone et al., 2018). Also considering a narrower water-depth range on continental shelves facing delta systems, the zonation of meiofaunal assemblages seems to be related to bathymetry (e.g., Horton et al., 2003; Rossi and Horton, 2009; Frezza and Di Bella, 2015; Benito et al., 2016), but it should be remembered that water depth is a

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In the Mediterranean basin, among the several parameters underlying water depth, a strong influence on the distribution of present-day ostracoda seems to be played by the grain-size of the substrate (Bonaduce et al., 1975; Ruiz et al., 1997; Arbull et al., 2004; Frezza and Di Bella, 2015; Sciuto et al., 2015). However, to our knowledge, its effect was statistically validated in just one case (Pascual et al., 2008).

Sand concentration, which is the first influencing factor on ostracod assemblages of the North Adriatic Sea, defines two major groups of ostracod biofacies: the first is related to muddy substrates (biofacies O1-O3) and the second to more sandy sediments (biofacies O4-O7). Further subdivisions within these two groups of biofacies reflect minor changes in organic matter/CaCO₃ conditions along the bathymetric gradient (Figs. 2, 4, 8). Muddy substrates are formed by the deposition of fine-grained particles of river plumes rich in soil-derived organic matter (Tesi et al., 2007), mostly provided by the Po River (Cattaneo et al., 2003; Frignani et al., 2005), which are distributed in specific areas (and at well-defined bathymetric ranges) of the shelf by surficial currents (Harris et al., 2008; Fig. 1). Within these areas oxygen deficiency as well as dissolution phenomena, which determines low CaCO₃ values, can be developed in response to the high organic matter concentration (Van der Zwaan and Jorissen, 1991).

Organic matter is, indeed, an important controlling factor that exerts a primary influence on the distribution of benthic foraminifera in the North Adriatic Sea (Fig. 8), as previously assessed by Jorissen (1988). High concentrations of organic matter occur in areas subject to high accumulation of riverine sediments (Figs. 1, 4d-f), where a series of opportunistic taxa (sensu Jorissen et al., 2018) characterise benthic foraminiferal biofacies (i.e., F1, F2, F4). Conversely, where the input of riverine material is substantially negligible and the concentration of organic matter is lower (Figs. 1, 4d-f), benthic foraminiferal assemblages are more diversified and opportunistic taxa are scarce (biofacies F3, F5). This is consistent with several studies undertaken on other river-influenced shelves of the Mediterranean Sea (e.g., Rhone Delta and Ombrone Delta; Frezza and Carboni, 2009; Mojtabid et al., 2009; Goineau et al., 2011).

The contribution of other abiotic parameters, such as sand and CaCO₃, is less significant (Figs. 6, 8); however, a clear distinction between shallow-water (biofacies F1-F3) and relatively deep-water (biofacies F4, F5) assemblages is recognisable in the North Adriatic Sea (Figs. 4d-f, 8).

Among the additional abiotic parameters which were not provided in the analysed database, salinity is often regarded as one of the most important influencing factors on benthic assemblages from marginal marine settings (e.g., Murray, 2006; Frenzel and Boomer, 2005). Nevertheless, data from the Adriatic Sea indicate that its influence on meiofaunal benthic assemblages can be considered negligible. In fact, the lowest salinity values are recorded during major flood events, when high amounts of riverine water are delivered to the prodelta and water stratification is produced, especially in proximity to the Po River mouths (Frasconi et al., 2006). Under these conditions, cold, less saline waters characterise the upper layer of the water column, and salinity rapidly increases to values of 36 psu at ca. 8–9 m water depth (Fox et al., 2004; Frascari et al., 2006). Since the shallowest samples analysed in this work were collected at 8 m water depth, meiofaunal assemblages should not be affected by salinity variations related to

intense fluvial discharge.

An additional abiotic parameter that is worth considering is water temperature. In the North Adriatic Sea, a well-developed seasonal thermocline is present especially during spring and summer at ca. 30 m water depth, whereas it almost disappears in winter due to the complete cooling of the water column (Artegiani et al., 1997). Interestingly, this water depth limit matches well with a main node of the ostracod MRT that separates assemblages of sandy sediments at 29 m of water depth (Fig. 2), whereas such change is not reflected in benthic foraminiferal assemblages (Fig. 6). Water temperature is a significant driving factor on ostracod assemblages in oligohaline-mesohaline settings (e.g., Pint et al., 2016; Valls et al., 2016), but its influence is usually negligible on ostracoda of shallow marine environments (Perçin-Paçal and Balkis, 2015). In accordance with environmental thresholds of ostracod assemblages, the contribution of temperature as an influencing factor on ostracoda of the shallow North Adriatic Sea cannot be excluded, but it can possibly act in association with other parameters related to water depth in the study area.

5.2. Integrating ostracoda and benthic foraminifera: a multi-proxy tool for river-influenced depositional environments

In marine settings, riverine influence is considered a qualitative parameter primarily dependent on the amount of river supply (in terms of organic matter and sediment) and it defines a position in the basin with respect to the main source of fluvial material (Goineau et al., 2011). The linkage between meiofaunal assemblages and riverine influence was previously recognised even in the Rhône (Mojtabid et al., 2009; Goineau et al., 2011, 2012) and Ombrone prodelta (Frezza and Carboni, 2009; Frezza and Di Bella, 2015), but not fully explored combining the two groups in a quantitative framework. Our approach demonstrates that ostracoda and benthic foraminifera of the North Adriatic shelf are primarily related to different environmental parameters (i.e., grain-size and organic matter, apart from the water depth). Therefore, only their combination allows us to recognise different (palaeo)depositional environments within the water-depth range 8–40 m, as defined by a set of abiotic parameters (Fig. 9, Table 5), which depends on the sediment supply and relative position to the Po River mouths (i.e., riverine influence). In a stratigraphic perspective, changes in meiofauna structure and abundance of key species can track variations in riverine inputs within past sedimentary successions, highlighting lateral shifts and/or approaching of river mouths during highstand periods (Amorosi et al., 2019).

5.2.1. Prodelta in proximity of the main feeding mouths

Near the Po Delta at < 20 m water depth (Fig. 9), where the substrate is enriched in mud and organic matter, the maximum values of sediment accumulation are recorded (Frignani et al., 2005) and frequent hypoxic events occur due to the deposition of abundant organic matter of riverine origin coupled with scarce water circulation (Palinkas and Nittrouer, 2007; Alvisi et al., 2013). All these environmental conditions are marked by a peculiar meiofauna (biofacies O1 + F1), mainly composed of *Palmoconcha turbida*, *L. ramosa*, *A. tepida*, *A. parkinsoniana* and *N. turgida*. *Ammonia tepida* shows high concentrations in proximity to fluvial outlets under unstable environmental conditions (Mojtabid et al., 2009; Goineau et al., 2011, 2012). *Palmoconcha turbida* and *L. ramosa* prefer fine-grained substrates at shallow depths (Colalongo, 1969; Frezza and Di Bella, 2015) and the former is considered tolerant to low oxygen conditions (Bodergat et al., 1998). *Nonionella turgida* is common at the transition with the mud belt and, locally, south of the Po Delta where organic matter accumulates and periodical oxygen deficiency occurs (Van der Zwaan and Jorissen, 1991; Alvisi et al., 2013). This species thrives under strong inputs of fresh organic matter derived from riverine phytoplankton (Goineau et al., 2012), but it even survives in sediments enriched in low-quality organic matter near river mouths (Mojtabid et al., 2009; Goineau et al.,

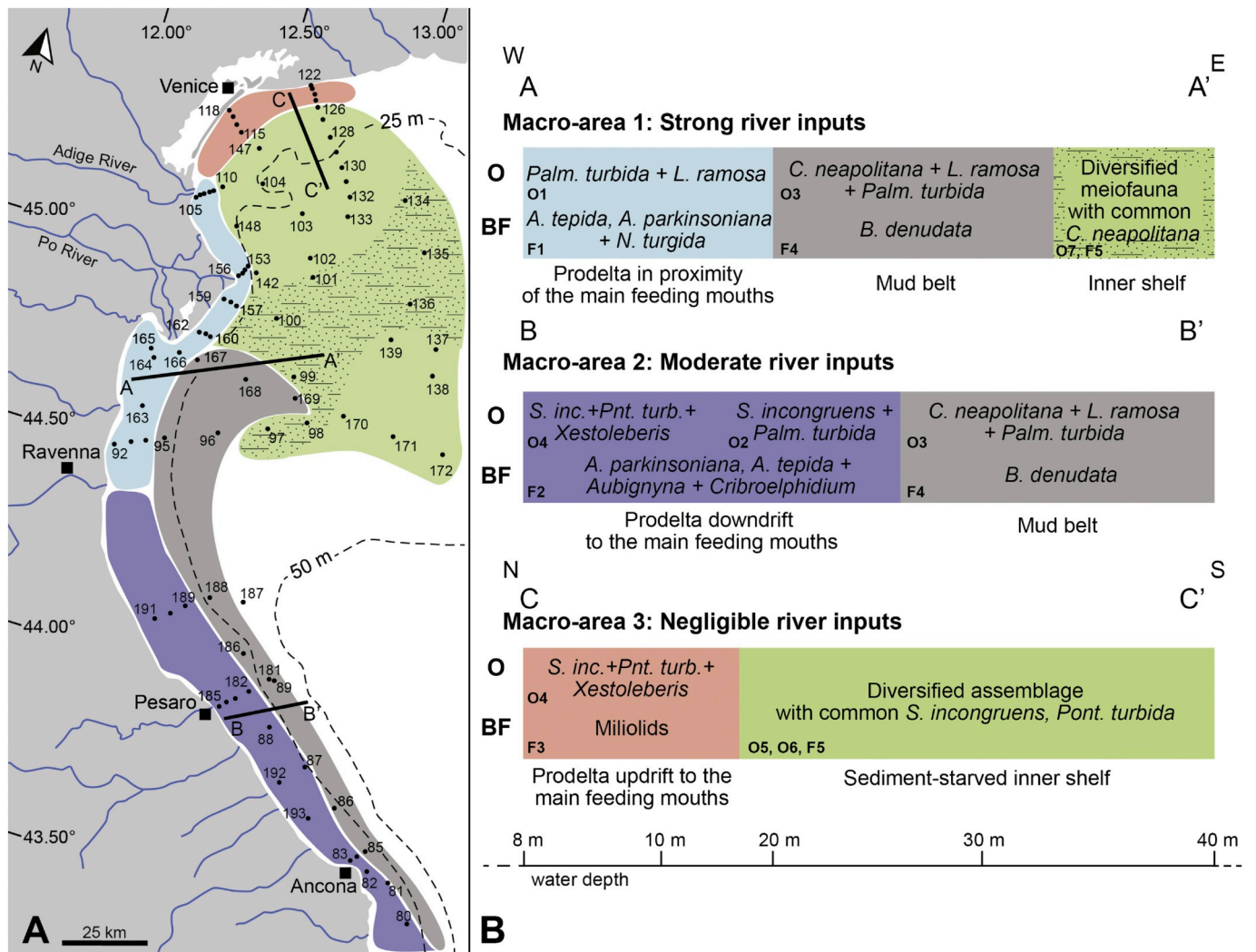


Fig. 9. A) Distribution of the five depositional environments defined by the combined application of ostracoda and benthic foraminifera on the shallow (< 40 m) North Adriatic Shelf. B) Variation of the meiofaunal biofacies along a bathymetric gradient for three macro-areas subject to different degrees of river inputs of the North Adriatic Sea.

Table 5

Depositional environments recognised on the basis of ostracod, benthic foraminiferal biofacies and environmental parameters on the shallow (< 40 m) North Adriatic shelf. A summary of the most significant environmental features, main characteristics of the meiofaunal assemblage and key ostracod and benthic foraminiferal taxa are reported for each depositional setting.

Depositional settings	Environmental conditions	Meiofaunal assemblage	Key species (D: dominant; S: secondary)
Prodelta in proximity of the main feeding mouths	High fluxes of OM and periodic oxygen deficiency Low sand content Very high accumulation rates	Ostracoda and foraminifera: mud-loving taxa tolerant to high OM and low oxygen conditions at shallow depths	<i>Palmoconcha turbida</i> (D), <i>Leptocythere ramosa</i> (D); <i>Ammonia tepida</i> , <i>A. parkinsoniana</i> (D); <i>Nonionella turgida</i> (S)
Prodelta downdrift of the main feeding mouths	Moderate fluxes of OM Variable sand content Moderate accumulation rates	Ostracoda: indifferent to grain-size. Foraminifera: tolerant to high OM; preferring clay sediments.	<i>Semicytherura incongruens</i> (D); <i>Pontocythere turbida</i> , <i>Palmoconcha turbida</i> (S); <i>Ammonia parkinsoniana</i> (D); <i>A. tepida</i> , <i>Aubignyna perlicuda</i> , <i>Criboelphidium</i> ex gr. <i>granosum</i> and <i>C. ex gr. poeyanum</i> (S)
Prodelta updrift of the main feeding mouths	Low fluxes of OM High sand content Moderate to low accumulation rates	Ostracoda: indifferent to grain-size. Foraminifera: preferring low OM.	<i>Semicytherura incongruens</i> (D); <i>Pontocythere turbida</i> (S); Miliolids (D); <i>Criboelphidium</i> ex gr. <i>granosum</i> and <i>C. ex gr. poeyanum</i> (S)
Mud belt	High fluxes of OM Low sand content High accumulation rates	Ostracoda and foraminifera: tolerant to high OM and low oxygen conditions at high depths	<i>Cytheridea neapolitana</i> (D); <i>Leptocythere ramosa</i> , <i>Palmoconcha turbida</i> (S); <i>Bulimina denudata</i> (D); <i>Nonionella turgida</i> (S)
Inner shelf	Low fluxes of OM Moderate to high sand content Low accumulation rates	Ostracoda and foraminifera: mainly indicative of low OM and indifferent to grain-size	Diversified assemblages with benthic foraminifera sensitive to organic matter

2011) under hypoxic conditions (Barmawidjaja et al., 1992).

In front of the main Po River outlets, the deposition of seasonal floods determines a non-steady state accumulation of sediment (Palinkas and Nittrouer, 2007). Here, ostracod assemblages are extremely poor (< 20 valves, not included in the statistical analyses) and usually include high percentages of transported brackish and freshwater taxa. In contrast, benthic foraminifera are characterised by more abundant assemblages, and mostly by the biofacies F1. This implies that unstable conditions in proximity of river outlets hamper the development of an autochthonous ostracod fauna, whereas benthic foraminifera are more abundant and dominated by the opportunistic *A. tepida* (Jorissen et al., 2018). However, it should be specified that at depths shallower than our minimum values (< 8 m), in correspondence of the Po delta front, both ostracod and benthic foraminiferal assemblages are very scarce (Colalongo, 1969; D'Onofrio, 1969).

5.2.2. Prodelta downdrift of the main feeding mouths

This prodelta area, located at < 20 m water depth from Ravenna to Ancona, is affected by the accumulation of sediments transported by the Apennine rivers and, subordinately, by the Po River (Fig. 9). The substrate has a variable grain-size (1.1–73.3% of sand), it is characterised by relatively high organic matter content (0.9% on average) and sediment accumulation rates are moderate (Frignani et al., 2005; Fig. 1). This area shows abundant concentrations of the ostracod *S. incongruens* (biofacies O2 and O4), a species distributed on all kind of sediments in the Adriatic Sea, even though it shows a slight preference for sediments enriched in sands. The characteristic benthic foraminiferal taxa are *A. parkinsoniana*, *A. tepida* and *A. perlucida* (biofacies F2), that tolerate relatively high organic matter concentrations and prefer muddy substrates (Fig. 5). The associated *Criboelphidium* ex gr. *granosum* and *Criboelphidium* ex gr. *poeyanum*, mostly represented by *C. lidoense* and *C. decipiens*, seem to be relatively indifferent to organic matter, in accordance with Jorissen (1988) and Jorissen et al. (2018). Within this area, ostracoda discriminate significantly different substrate conditions. Biofacies O4 occurs in the shallowest portion (ca. 8–13 m water depth), on sandy sediments (15.9–73.3%) with low organic matter content (0.6% on average) and includes, apart from *S. incongruens*, other species such as *Pontocythere turbida* and *Palmoconcha turbida*, both widespread in the Adriatic Sea between 5 and 40 m water depth. Even though they are abundant under different conditions (the former on sandy sediments and the latter on muddy substrates), they seem to be able to live on different substrate grain-size, as similarly observed in other Mediterranean shallow marine settings (Arbulla et al., 2004; Angue Minto'o et al., 2013; Frezza and Di Bella, 2015). The occurrence of the highest frequencies of two phytal species of the genus *Xestoleberis* (*X. dispar* and *X. fuscomaculata*; Lachenal and Bodergat, 1988; Triantaphyllou et al., 2005) indicates a vegetated prodelta setting.

Conversely, the deepest sector (ca. 13–20 m water depth) with more fine-grained bottoms (1.1–11.2% of sand) and higher organic matter concentration (0.9% on average; Fig. 4) is colonised by *Palmoconcha turbida* in association with *S. incongruens* (biofacies O2) and the above-mentioned benthic foraminifera (biofacies F2), pointing to a muddy prodelta not affected by hypoxic conditions. This interpretation is strongly supported by the occurrence of species, as *Aubignyna perlucida*, showing a limited tolerance for oxygen deficiency (Barmawidjaja et al., 1992; Donnici and Serandrei Barbero, 2002).

5.2.3. Prodelta updrift of the main feeding mouths

At shallow depths (< 20 m) in the northern Adriatic Sea (Fig. 9), the sediment accumulation is extremely low due to the negligible inputs provided by Alpine rivers, with the exception of the Adige River (Cattaneo et al., 2003; Frignani et al., 2005). Moreover, the efficient distribution of the riverine inputs by strong longshore currents prevents the sediment accumulation in proximity to river mouths (Harris et al., 2008). A peculiar benthic foraminiferal assemblage dominated by Milioloidea – biofacies F3 (i.e., *Adelosina* spp., *Q. seminula*,

Quinqueloculina spp. and *T. trigonula*) occurs in this depositional setting, characterised by high concentration of sand and CaCO₃ (respectively 49.7% and 62.0% on average). The ostracod fauna (biofacies O4) is consistent with a shallow marine area with vegetated bottoms.

5.2.4. Mud belt

South of the Po Delta at ca. 20–35 m water depth, the peculiar setting of the Adriatic mud-belt (Fig. 9) occurs and high abundances of *C. neapolitana* (biofacies O3) and *Bulimina* ex gr. *marginata* (biofacies F4, mostly represented by *B. denudata*) are recorded, along with subordinate *L. ramosa*, *Palmoconcha turbida* and *N. turgida*. These species thrive under eutrophic and hypoxic conditions typical of the clay belts (Donnici and Serandrei Barbero, 2002; Mendes et al., 2004; Di Bella et al., 2013; Frezza and Di Bella, 2015). *Sagmatocythere versicolor* and *V. bradyana* are additional characteristic taxa with environmental affinities similar to those of the most abundant species, such as a slight preference for muddy bottoms in relatively deep waters (Bonaduce et al., 1975; Frezza et al., 2005; Frezza and Carboni, 2009; Mojtahid et al., 2009; Frezza and Di Bella, 2015).

5.2.5. Inner shelf

Far from the river mouths at water depths > 20 m (Fig. 9), the organic matter content is low (0.6% on average) as well as the riverine influence in terms of sediment supply (Cattaneo et al., 2003; Frignani et al., 2005). Overall, ostracoda (biofacies O5–O7) and benthic foraminifera (biofacies F5) are highly diversified in terms of number and relative abundance of taxa. Widespread ostracod taxa indifferent to bottom grain-size such as *S. incongruens* and *Pontocythere turbida* are abundant and are associated with epiphytic benthic foraminifera such as *A. mamilla*, *B. granulata*, *C. lobatulus*, *N. terquemi*, *R. bradyi* (Sgarrella and Moncharmont Zei, 1993; Frezza and Carboni, 2009), sensitive to organic enrichment (Jorissen et al., 2018).

However, ostracod biofacies identify different areas in terms of sediment grain-size. Specifically, biofacies O7 shows a significantly lower sand concentration than biofacies O5–O6 (Fig. 3), which mark the sediment-starved portions of the inner shelf (Fig. 9). In front of the Po Delta, a minor portion of fine-grained riverine sediments is episodically transported by water currents (Harris et al., 2008). Here, the most common species is *C. neapolitana*, which is also abundant in the Adriatic mud-belt: this taxon does not seem to be disturbed by organic matter enrichment and oxygen depletion, rather its distribution seems to be related to the presence of fine-grained sediments at water depths > 20 m. Within this depositional setting, it is associated with several depth-related taxa, such as *B. carinella*, *Callistocythere* spp., *C. whitei*, *C. edwardsii*, *Cytheropteron* spp., *H. turbida*, *Pterygocythereis* spp. and *Semicytherura* spp. (biofacies O7), indicative of an open marine environment (Bonaduce et al., 1975; Faranda et al., 2007).

5.3. Patterns in the spatial turnover of meiofauna

The general distribution patterns of the meiofaunal biofacies reflect the presence of three macro-areas (Fig. 9) with peculiar environmental characteristics related to different degrees of river inputs from the coast to the basin, according to Frignani et al. (2005):

1. *Macro-area subject to strong river inputs: in front of the Po Delta, from the Adige outlet down to Ravenna.* Maximum values of sedimentation rates occur near the major source of river inputs (Fig. 1), where the meiofauna is characterised by mud-loving taxa tolerant to high organic matter and lowered oxygen content, such as *L. ramosa*, *Palmoconcha turbida*, *A. tepida*, *A. parkinsoniana* and *N. turgida*. At water depths > 20 m, fine-grained substrates enriched in organic matter (the Adriatic mud-belt sensu Van der Zwaan and Jorissen, 1991) are characterised by high frequencies of opportunistic taxa such as *C. neapolitana* and *B. denudata*, whereas deepward (> 25 m water depth) the meiofauna is diversified and typical of an inner shelf

setting. A similar pattern in terms of species and distribution of benthic foraminifera was identified across the Rhône prodelta under the influence of river plumes, from the main river mouths to the offshore (Goineau et al., 2011, 2015). As far as we know, no comparable ostracod patterns have been recorded in the Mediterranean area.

2. **Macro-area subject to moderate river inputs: from Ravenna to Ancona.** This area is subject to the riverine inputs provided by the Apennine rivers as well as to the deposition of slow-settling mud and organic matter particles provided by the Po River (Fig. 1; Frignani et al., 2005; Harris et al., 2008). The strong, persistent southward along-shelf WACC distributes at shallow depths (< 13 m) the coarse-grained sediments supplied by rivers (Puig et al., 2007; Fain et al., 2007). Such sandy substrates (Fig. 4; Brambati et al., 1983) are mainly colonised by *Semicytherura incongruens*, associated with the phytal taxa *Xestoleberis* spp. A small portion of sediment flux supplied by the Apennine rivers is deposited at 13–25 m water depth, where fine-grained bottoms are characterised by higher frequencies of the mud-loving species *Palmoconcha turbida*. Benthic foraminifera are indifferent to change in substrate grain-size and the assemblages are characteristic of shallow depths with dominance of taxa tolerant or indifferent to organic matter (e.g., *A. parkinsoniana*, *A. perlucida*, *C. lidoense* and *C. decipiens*). The Adriatic mud-belt is still present at 20–40 m water depth. A similar distribution of meiofauna was reported from the Tyrrhenian shelf in front of the Ombrone River (Frezza and Carboni, 2009; Frezza and Di Bella, 2015).
3. **Macro-area subject to low river inputs: the northern shelf of the Adriatic Sea, north of the Adige Delta.** Sandy substrates at 8–20 m water depth result from the low sediment inputs provided by Eastern Alpine rivers (Adige River excluded) coupled with the action of longshore currents (Fig. 1; Frignani et al., 2005). Here, the local riverine sediment supply is not overcome by the higher contribution of upstream rivers (Harris et al., 2008), determining a lower concentration of mud and organic matter, and a consequent enrichment in CaCO₃ reflected by the abundance of Milioloidea. The ostracod fauna is typical of sandy substrates and is similar to that recovered within the proximal prodelta of macro-area 2. The general geographical context prevents the basinward development of a continuous mud belt, and only scattered mud patches occur in front of the river mouths out of the investigated area (Fig. 1; Brambati et al., 1983; Frignani et al., 2005). Therefore, at ca. 20 m water depth, the meiofauna directly shifts towards an inner shelf assemblage typical of the sandy, sediment-starved North Adriatic shelf.

6. Conclusions

The availability of ostracod and benthic foraminiferal data from the same set of samples gave us the opportunity to compare the zonation of both groups in the northern sector of the Adriatic Sea, and to explore the environmental factors that control their spatial distribution over a river-influenced shelf in a deltaic progradational context.

- The integrated multivariate analysis of the North Adriatic modern meiofaunal databases revealed that communities are primarily controlled by different environmental drivers: ostracoda by grain-size and bathymetry, benthic foraminifera by organic matter.
- The combined application of the seven ostracod biofacies and the five benthic foraminiferal biofacies allowed the identification of five depositional environments determined by their position with respect to the Po River: 1) In proximity of its mouths, the meiofauna is dominated by species tolerant to muddy substrates, high organic matter inputs and slight deficiency in oxygen such as *Palmoconcha turbida*, *L. ramosa*, *A. tepida*, *A. parkinsoniana* and *N. turgida*. 2) Downdrift of the main fluvial mouths, generalist ostracoda in terms of grain-size (*S. incongruens*) are associated with benthic foraminifera tolerant to moderate levels of organic matter (*A.*

parkinsoniana, *A. tepida*, *A. perlucida*, *C. lidoense* and *C. decipiens*). Here, ostracoda discriminate between shallower sandy sediments (*Pontocythere turbida*, *Xestoleberis* spp.) and deeper fine-grained bottoms (abundant *Palmoconcha turbida*). 3) Updrift of the fluxes of riverine material, shallow-marine ostracoda typical of sandy substrates and Milioloidea occur. 4) In the shallow Adriatic mud belt, species tolerant to high organic matter concentrations and oxygen deficiency (*C. neapolitana*, *L. ramosa*, *B. denudata* and *N. turgida*) dominate. 5) On the inner shelf, meiofaunal assemblages are well-diversified and ostracoda mark changes of substrate grain-size in relationship with sediment inputs (sediment-starved areas enriched in sand vs. fine-grained bottoms subject to episodic riverine inputs).

- Distinct sequences of depositional environments are recognised from coastal to offshore locations on three macro-areas of the North Adriatic shelf subject to different degrees of riverine inputs.
- Ostracoda and benthic foraminifera have proven to be complementary indicators on river-influenced shelves, allowing a refined characterisation of depositional environments in relationship with the main riverine inputs. Therefore, they represent a useful tool to investigate the evolution of fine-grained sedimentary successions in deltaic progradational contexts.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

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