



Ostracods as indicators of organic enrichment in marine sediments (Adriatic Sea, Mediterranean): ecological groups and applications in palaeoenvironmental studies

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ABSTRACT

Ostracods represent valuable proxies in palaeoenvironmental reconstructions and environmental monitoring, yet their ecological response to organic enrichment remains poorly quantified compared to other benthic groups such as macrofauna and benthic foraminifera. Here, we propose the first large-scale assessment of ostracod species' tolerance to total organic carbon (TOC) in the Adriatic Sea (western Mediterranean), based on a previously published, extensive dataset of 298 samples analyzed using a weighted-averaging approach. Ninety marine species are assigned into five canonical Ecological Groups (EGs): twenty-six sensitive (EG I), thirty-one indifferent (EG II), twenty third-order opportunists (EG III), ten second-order (EG IV), and three first-order opportunists (EG V). This classification allowed the development of a novel Ostra-AMBI index, a modified version of the AZTI Marine Biotic Index (AMBI), based on species-specific tolerance to organic matter enrichment. The reliability of species assignment is supported by significant positive correlations between Ostra-AMBI and both TOC ($R^2 = 0.59$) and Foram-AMBI ($R^2 = 0.75$), calculated on an independent testing dataset. Besides promoting ostracods as reliable marine (palaeo)ecological indicators, results reveal a clear link between ostracod EGs distribution and the Adriatic sediment routing system, reflecting the interplay between river plumes, current-driven sediment dispersal, and organic matter accumulation. Sensitive and indifferent species dominate the coastal belt and north-central shelf, whereas opportunistic taxa prevail in TOC-enriched deposits (i.e., Adriatic Mud Wedge and deep basins). Although further studies are needed to refine the Ostra-AMBI index, this work highlights the importance of integrating biological and sedimentological processes for both environmental and stratigraphic studies.

1. Introduction

Marine environments are increasingly threatened by climate change, human exploitation, and several sources of pollution that undermine their ecological functionality and biodiversity (IPCC, 2019), including chemical contaminants such as heavy metals and hydrocarbons, as well as municipal effluents and plastics (Chen and Liao, 2006; Thompson et al., 2004; Wang et al., 2013). The effects of anthropogenic activities on marine ecosystems are exacerbated by the accumulation of organic and inorganic pollutants produced on land, released by rivers and then redistributed by the sea currents even far away from the fluvial mouths, following the sediment routing systems (Kane and Fildani, 2021;

Pellegrini et al., 2023; Saliu et al., 2023; Rossi et al., 2024).

Quantitative assessment of the Ecological Quality Status (EcoQS) is essential to implement sustainability action plans as well as recovery and mitigation strategies. An ecosystem-based approach including biological indicators (Markert, 2007; Zaghoul et al., 2020) is mandatory as also indicated by marine legislations (i.e., Water Framework Directive, 2000; Marine Strategy Framework Directive, 2008/56/EC), but it is still a challenging issue due to the complex interaction between biota and physico-chemical parameters. Therefore, a deep understanding of the processes is crucial (e.g., Pavlidou et al., 2019; Smith et al., 2021) and site-specific reference conditions should be known to effectively quantify the deviation from a natural, pristine-like state by the application of

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the Ecological Quality Ratio (EQR; Borja et al., 2012; Borja et al., 2014).

Numerous ecological indices based on the structure and composition of soft-bottom benthic communities have been developed and applied worldwide during the last decades (Borja et al., 2004; Diaz et al., 2004; Dong et al., 2023; Laut et al., 2024). Among these, diversity and sensitivity indices are the most widely applied and critically evaluated for their strengths and limitations. Since the pioneering work on macrofauna by Borja et al. (2000), the AZTI Marine Biotic Index (AMBI) based on species sensitivity to organic enrichment has been widely adopted also involving organisms with a fossilizable shell, like molluscs and foraminifers (Alve et al., 2016; Dietl et al., 2016; Jorissen et al., 2018, among others). The high sensitivity of these groups to several environmental stressors, including organic enrichment (Murray, 2006; Moraitis et al., 2018), is well-known and the AMBI application opens the opportunity to track changes in the EcoQS back in time (PaleoEcoQS; Dolven et al., 2013). Moreover, this approach improves the EQR quantification through the analysis of well-dated, cored successions that bridge the gap between past and present (e.g., de Jesus et al., 2020; O'Brien et al., 2021).

Within the marine benthos, ostracods (microscopic crustaceans) represent a remarkable group sharing the key features of reliable (palaeo)ecological indicators (e.g., Frenzel and Boomer, 2005; Gliozzi et al., 2015; Mohammed Nishath et al., 2017; Hong et al., 2019; Schmitz et al., 2025): i) high preservation and fossilization potential of the bivalve carapace, ii) specific ecological requirement and quick response to environmental stressors, iii) high biodiversity and wide geographical and environmental distribution, and iv) high abundance in the sedimentary record. Indeed, ostracods have been used for the assessment of ecological conditions within various transitional-shallow marine environments (Ruiz et al., 2005; Yasuhara et al., 2012), like estuaries and bays (Pascual et al., 2002; Cronin and Vann, 2003; Ruiz et al., 2004; Yasuhara and Yamazaki, 2005; Yasuhara et al., 2007; Irizuki et al., 2015; Gildeeva et al., 2021; Francescangeli et al., 2024), as well as coastal lakes and lagoons (e.g., Barut et al., 2015; Tan et al., 2021). Recently, the review by Schmitz et al. (2025) has further highlighted the great potential of ostracods as bio-indicators of anthropogenic impact, including eutrophication (i.e., excess of nutrient load) and deoxygenation, across several aquatic environments.

In the Mediterranean Sea, studies combining ostracods with other microorganisms and/or physico-chemical parameters of recent sediments show that assemblage changes can be a valuable tool to unravel the environmental deterioration (Triantaphyllou et al., 2003; Balassone et al., 2016; Mangoni et al., 2016; Aiello et al., 2020; Salvi et al., 2015, 2020). A similar approach has also been applied to molluscs, further demonstrating the value of benthic fauna to assess ecological changes (Gallmetzer et al., 2017; Fuksi et al., 2018; Scarponi et al., 2023; Berensmeier et al., 2025). However, specific responses of ostracod species to organic enrichment are not available to date, nor are their assignments to Ecological Groups (EGs) sensu Borja et al. (2000). These limitations have impaired the application of ostracods in the assessment of environmental impact over time and prevented the development of the Ostra-AMBI index.

This study aims to help fill the knowledge gap by investigating the possibility of assigning ostracod species to the five EGs commonly used for molluscs and benthic foraminifers (Alve et al., 2016; Dietl et al., 2016; Jorissen et al., 2018). We present the first large-scale analysis of the relationship between ostracod species and organic enrichment, quantified as Total Organic Carbon (TOC), a parameter commonly used to assess EcoQS, using an extensive database from the Adriatic Sea (central Mediterranean) published by Breman (1975). This database (Fig. 1) contains approx 300 samples distributed from a few meters to more than 1200 m water depth, and includes both abiotic parameters (depth, sand percentage and organic matter) and ostracod data (total assemblage at the collection time). Although we are aware that the living fauna is the best mirror of seafloor conditions, studies on Mediterranean ostracod biocoenosis are rare and restricted to relatively small

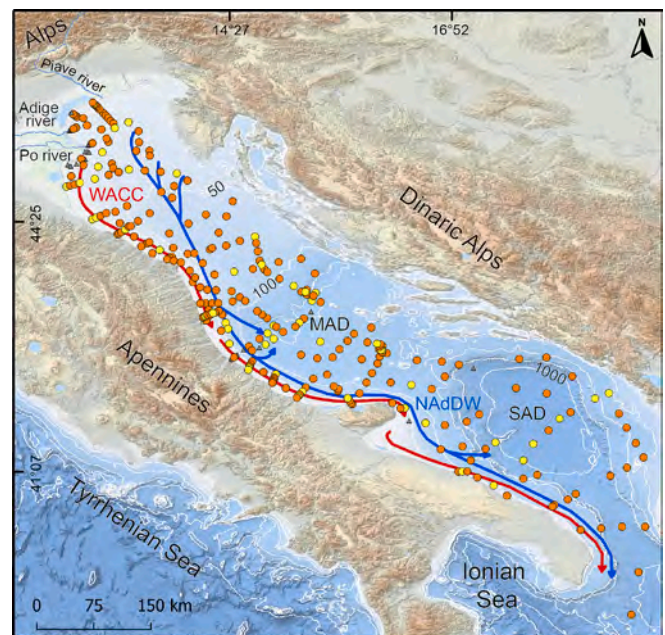


Fig. 1. “Spatial distribution of samples by Breman”. Spatial distribution of samples by Breman used for the study: samples used for the EG attribution (orange), test samples (yellow). Grey triangles show excluded samples (see subsection 3.2). The red line corresponds to the WACC (Western Adriatic Coastal Current); the blue line corresponds to the NAdDW (North Adriatic Dense Water current). The MAD (Mid Adriatic Deep) and SAD (South Adriatic Deep) are also highlighted. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

areas (Sciuto et al., 2015; Salvi et al., 2020). Specific goals of this study are: i) to expand the toolbox available to ecologists, environmental scientists and geologists, as the EGs assignment can improve palaeoenvironmental reconstructions, ii) to explore the connectivity between ostracod ecological groups distribution and the sediment routing system at a basin scale, and iii) to provide input on the potentialities and limitations of the assigned EGs in (palaeo)environmental quality evaluation, also in view of an integrated Ostra- and Foram-AMBI application and taking advantage from the availability of foraminiferal data from the same samples (Jorissen, 1988; Jorissen et al., 2018).

2. Study area

The Adriatic Sea is a northwest-southeast elongated, narrow epicontinental basin (about 200 × 800 km), semi-enclosed by the Italian and Balkan peninsulas and connected with the Mediterranean Sea through the Otranto Strait, whose sill is 850 m deep (Zavatarelli and Pinardi, 2003; Fig. 1). The seafloor morphology reflects processes that were active during the Last Glacial Maximum, when a broad alluvial plain occupied the shelf area (Amorosi et al., 2016), and during the present interglacial (Trincardi et al., 2014). Three main domains are identified (Cattaneo et al., 2003; Trincardi et al., 2014; Fig. 1):

1. the Northern Adriatic corresponds to a SE-dipping shelf, characterized by shallow depths averaging 35–40 m (maximum depth approx. 75 m) and a low topographic gradient of approx. 0.02°;
2. the Central Adriatic, with an average depth of 100 m, shows the steepest shelf gradient (approx. 0.5°) along the margin of the Mid Adriatic Deep (MAD), which reaches a depth of about 260 m;
3. the Southern Adriatic hosts a large, bathyal basin, known as the South Adriatic Deep (SAD), approx. 1200 m deep.

Seafloor grain-size varies as a function of bathymetry and oceanographic circulation. Both the MAD and SAD are predominantly mud-

covered, whereas sand is abundant in the Northern-Central sectors of the Adriatic Sea (Trincardi et al., 2014) and in correspondence of bottom relief; differently, more heterogeneous grain-size patterns characterize the Balkan coasts (Vrdoljak et al., 2021).

Under a microtidal regime, sediment distribution along the Italian side is mainly driven by the interactions between river input (i.e., Po River and other Alpine and Apennine rivers), waves and two main SE-directed currents (the Western Adriatic Coastal Current: WACC and the North Adriatic Dense Water current: NAdDW) related to the cyclonic circulation (Artegiani et al., 1997; Fig. 1). The NAdDW current splits into branches that reach variable depths downslope in the Central and Southern Adriatic, sinking towards the Mid and South Adriatic Deep (MAD and SAD; Trincardi et al., 2007; Marini et al., 2016; Rovere et al., 2019). The SAD is also affected by a denser and salty water mass that forms in the Levantine Basin (the Levantine Intermediate Water - LIW) and enters the Adriatic Sea through the Otranto Strait.

The Po River is by far the largest Adriatic river (drainage basin: approx. 74,500 km²; Correggiari et al., 2005) and, therefore, the main source of both inorganic and organic particles into the basin. It provides, on average, 12.22 Tg/yr of sediments with significant seasonal fluctuations (peaks in late autumn and late spring; Frignani et al., 2005), and about 13.4×10^4 t/yr of particulate organic carbon (Pettine et al., 1998). At present, the Po River accounts for ~50% of the total nutrient input into the Northern Adriatic, owing to the Po Plain high agricultural (and aquaculture) productivity (Degobbi and Gilmartin, 1990), and its load is high enough to contribute to organic-enrichment trends (Giordani et al., 2002; Paganelli et al., 2011). Although the organic matter detected within shelf surficial (0–1 cm) sediments shows multiple sources, a substantial fraction is derived from terrestrial, soil-origin organic matter (i.e., mineral-associated, degraded plant material delivered by rivers; Tesi et al., 2007). This reflects the preferential degradation of labile marine organic matter at the sediment–water interface, resulting in the relative enrichment and preservation of refractory terrestrial carbon (Tesi et al., 2007).

The basin-oceanographic setting determines the accumulation of fine-grained, riverine material beyond coastal sands, leading to the development of a highstand, tens of meters-thick mud wedge interpreted as a subaqueous prodelta that extends south of the modern Po Delta (also known as the Adriatic Mud Wedge: AMW; Correggiari et al., 2001; Cattaneo et al., 2003, 2007; Dalla Valle et al., 2024). Several peaks in mass accumulation rates are recorded in proximity of the Po prodelta (Frignani et al., 2005), mainly fed by the Po di Pila branch since the end of the 19th century (Correggiari et al., 2005). North of the Po Delta, the mud wedge is poorly developed, due to lower riverine sediment supply to the shelf (Barbieri et al., 2019).

Seaward, sediment-starved conditions are documented by remains of glacial alluvial deposits and by patches of transgressive, back-barrier and coastal deposits developed during the Holocene transgression and recognized down to approx. 90 m water depth in the Northern and Central Adriatic Sea (Trincardi et al., 1994; Correggiari et al., 1996; Storms et al., 2008).

3. Material and methods

3.1. The Adriatic Sea dataset

The ostracod data were retrieved from the database produced by Breman (1975). In 1962, a total of 360 samples - grab samples and core tops - were collected, and a set of environmental parameters was considered at all sampling stations (original data from Van Straaten, 1970): depth (m), content of sand (%), calcium carbonate (%) and organic matter (LOI – Loss On Ignition).

Only 298 of the samples collected were prepared and examined for micropalaeontological purposes: the treatment of samples is described in Breman (1975). Quantitative analyses were performed on the residue >150 µm, considering that most adult valves commonly occur in the

150–450 µm fraction (Breman, 1975). Each sample records multiple biotic parameters: i) the relative abundance (%) of 192 species, with some taxa grouped (e.g., *Cushmanidea elongata* and *C. turbida*; *Pro-pontocypris dispar* and *P. intermedia*; *Callistocythere adriatica* and *C. diffusa*); ii) the number of valves per split fraction; iii) species diversity, calculated as the number of ostracod species divided by the number of valves (after Breman, 1975); iv) the number of species; and v) the number of valves per 100 g of sediment. Allochthonous, brackish and freshwater-hypohaline taxa are also present in the dataset (Breman, 1975).

Despite some limitations mainly due to the publishing date (i.e., the adopted protocol of investigation), the richness and the unique spatial coverage of the data (approx. 97,000 km²; Fig. 1) make this historical dataset suitable for our aims as it provides a valuable opportunity to investigate species–environment relationships at the basin-scale (e.g., Adriatic Sea). Under the assumption that these relationships have remained consistent through time (Horne et al., 2012), the use of historical datasets for ecological interpretations is supported, as also demonstrated by the successful application of the same Adriatic samples to the ecological group assignment of Mediterranean benthic foraminifera (see Jorissen et al., 2018).

3.2. Statistical analyses

To evaluate preferred organic matter ranges for each species, the matrix was pretreated considering the dataset characteristics and the protocols proposed by Alve et al. (2016) and Bouchet et al. (2021):

- the organic matter content was converted to TOC using the formula: $LOI = \sim 2 \text{ TOC}$ (Frangipane et al., 2009);
- only samples with more than 50 specimens were considered;
- only species present in at least 5% of samples (i.e., 14 samples) were kept for the analyses;
- species showing frequency $\geq 2\%$ in at least one sample were examined.

Moreover, twenty-six taxa identified only at the genus level using open nomenclature (e.g., *Pontocypris* spp., *Henryhowella* sp.), for which a species-level identification was not possible, were excluded from the analyses. Species names are reported according to the World Ostracoda Database - *World Register of Marine Species* (Brandão et al., 2025), and their list is shown in Supplementary material 1.

The final dataset consists of 269 samples encompassing 90 different marine ostracod species (Vecchi, 2026a). This dataset was successively split into two datasets: a) a calibration (80% of the samples) dataset consisting of 214 samples, and b) a testing (20% of the samples) dataset including 53 samples, selected from the original dataset to cover the widest possible range of TOC, water depth and sand content (Fig. 1).

Using the calibration dataset, the weighted average (WA) optimum and tolerance range were calculated for the TOC content (%) for each taxon (Vecchi, 2026b). To better understand the species–environment relationships, the same parameters were also computed for additional variables known to influence ostracods' distribution (i.e., seafloor grain-size and water depth; Barbieri et al., 2019 and references herein). The weighted average optimum and tolerance range are a theoretically robust and widely used method to assess species-specific indicative values of preferred environmental conditions (Birks et al., 1990). The calculated optimum value is the average of all values of the chosen environmental variable for the samples in which the taxon occurs, weighted by the taxon's relative abundance (WA regression, Birks et al., 1990) and thus represents the value of the environmental variable in which the taxon thrives best. Differently, the tolerance range defines the interval between the lower and upper limits beyond which the species experiences environmental stress. The narrower the tolerance range, the more specialized the taxon, as it can tolerate only small variations in the specific environmental variable (Smith and Smith, 2015).

The WA optimum and tolerance range for each species were calculated using R software (R Core Team, 2023) and the *optimos.prime* R package (Sathicq et al., 2020). Data calculation and results visualization were performed using the *op.calculate()* and the *op.plot()* function included in the package.

Multiple scatter plots for each species highlight the relationship between taxon abundance and selected environmental parameters (*in primis* TOC; Vecchi, 2026b). Species-TOC scatter plots presented here do not include one sample (sample 162), which showed an anomalous TOC content of 7.2%, in front of the Po River mouth. This value was considered an outlier with respect to all the samples analyzed (maximum value: 1%) and literature values (Miserocchi et al., 2007).

For each graph, a locally weighted smooth regression line was fitted to investigate the species-variable relation. For each regression line, the confidence interval around the curve is shown. The graphs were produced using R software (R Core Team, 2023) and the *geom_smooth()* function of the *ggplot2* R package (Wickham, 2016).

To further evaluate the potential collinearity among environmental variables and to disentangle their respective effects on ostracod distribution, a Canonical Correspondence Analysis (CCA) was performed, including TOC (%), sand content (%) and water depth (m). The statistical significance of the model and of individual environmental variables was tested using permutation-based ANOVA. Additionally, multicollinearity among predictors was assessed by calculating the Variance Inflation Factors (VIF). This approach allows for identifying whether environmental variables are redundant or provide independent explanatory variables in our dataset. All analyses were carried out using the R software (R Core Team, 2023) and the *vegan* package (Oksanen et al., 2022).

3.3. Criteria for defining and testing ecological groups of TOC tolerance

Following general criteria, we referred to seminal papers on the benthic macrofaunal (e.g., Grall and Glémarec, 1997; Borja et al., 2000; Fig. 2) and recent works on foraminiferal species, where assignment to specific EGs was based on the response to increasing TOC (e.g., Alve et al., 2016; Jorissen et al., 2018; Bouchet et al., 2021):

- Group I (EG I). “Sensitive species” cannot tolerate organic enrichment. Their relative abundance is highest at the lowest TOC values and drops to zero as the organic concentration increases;
- Group II (EG II). “Indifferent species” are present over a broad TOC range, from low to high values, but generally drop to zero towards the highest concentrations; they show no clear preference for a specific TOC sub-range;
- Group III (EG III). “Third-order opportunistic species” (sensu Jorissen et al., 2018) can tolerate an initial excess of TOC. They may occur at low TOC, increase in relative abundance under high TOC, but are absent at the highest concentrations;
- Group IV (EG IV). “Second-order opportunistic species” show a clear positive response to the organic enrichment and are usually absent at the lowest TOC values;
- Group V (EG V). “First-order opportunistic species” apparently prefer an excess in organic load. Their maximum abundance is at the highest TOC values, whereas they are absent at low to intermediate concentrations.

The assignment of Adriatic ostracod species to the five different ecological groups was performed, following Bouchet et al. (2021), through the integration of the WA optimum, the tolerance range and the regression line trend, considering also the frequency distribution (points) in the scatter plots (Fig. 2).

To test the species assignment to EGs and the relative response of these latter to TOC enrichment, the Ostra-AMBI index was calculated using the adapted AMBI formula (Borja et al., 2000).

$$\text{Ostra-AMBI} = \{(0 \times \% \text{EG I}) + (1.5 \times \% \text{EG II}) + (3 \times \% \text{EG III}) + (4.5 \times \% \text{EG IV}) + (6 \times \% \text{EG V})\} / 100.$$

for 53 test samples selected from the original dataset (Fig. 1). Test samples were not included in the calibration of the species assignment to avoid circular arguments (Alve et al., 2016). Following Borja and Muxika (2005), AMBI values are valid only if species assigned to ecological groups (EGs) account for more than 80% of the total association; thus, four samples were excluded from the calculation.

Finally, an effective comparison between the Ostra-AMBI and Foraminiferal AMBI indices was performed, as the same sampling stations were analyzed for both ostracods (Bremner, 1975) and benthic foraminifera

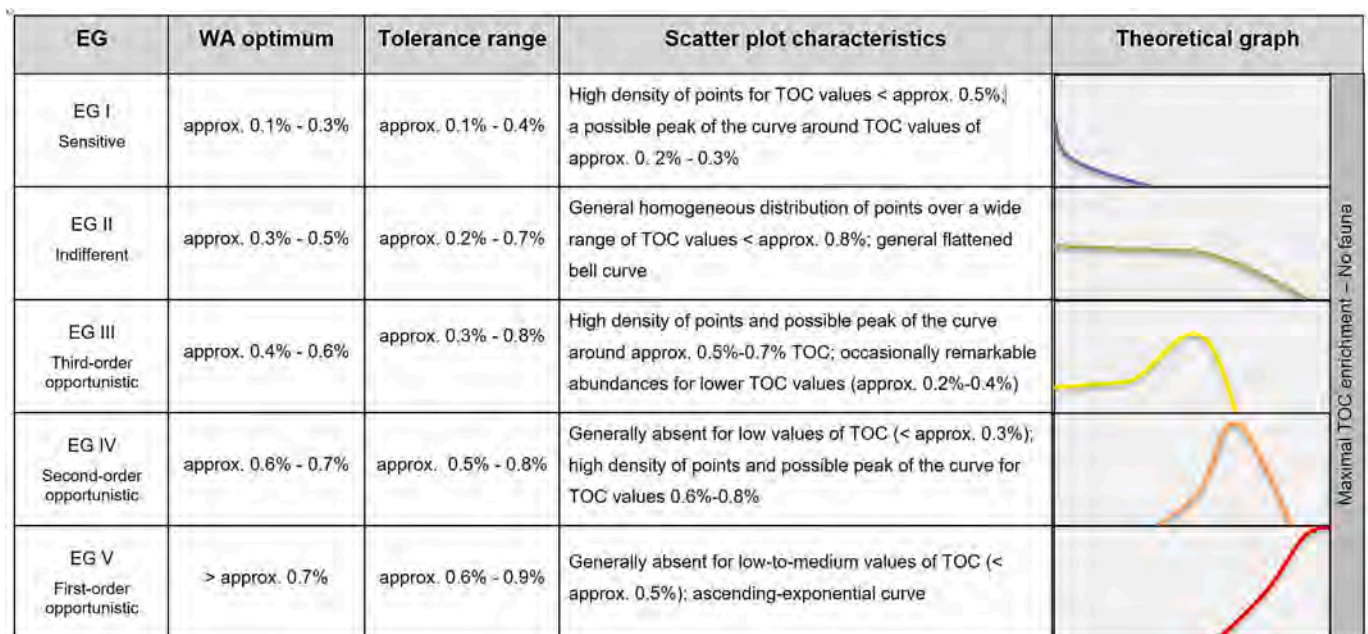


Fig. 2. “Criteria for EG assignment”. Criteria for assigning species to an Ecological Group (EG). For each category, WA optimum and tolerance range values are reported, along with scatterplot characteristics. Theoretical graphs illustrate species distribution along a gradient of organic-matter enrichment (slightly modified from Jorissen et al., 2018).

(Jorissen, 1988). This allows for a direct comparison of the two indices calculated for the same 53 test samples in both datasets. However, only 29 samples were retained for statistical comparison, as they met the eligibility criterion in both datasets, with at least 80% of the species assigned to an ecological group (EG), ensuring a reliable calculation of the AMBI indices (Borja and Muxika, 2005). The relationships between Ostra-AMBI and TOC, and Ostra-AMBI and Foram-AMBI values were investigated using the Pearson's correlation coefficient (R) calculated using the R software (R Core Team, 2023).

3.4. Definition of species-specific bathymetric ranges and substrate preference

Beyond organic enrichment, numerous other physical and chemical parameters can significantly influence ostracod species distribution in marine basins (e.g., Boomer and Eisenhauer, 2002). In the Mediterranean Sea and, specifically, in the Adriatic Sea, important drivers are water depth and seafloor grain-size (e.g., Arbuta et al., 2004; Angue Minto'o et al., 2013; Barbieri et al., 2019).

To contextualize the assignment of ostracod species to ecological groups (EGs) within the Adriatic sediment routing system, species' preferred substrate (in terms of sand percentages) and bathymetric range were evaluated. These were inferred from the trends of the regression curves, the distribution of points in the scatterplots, and the weighted average (WA) optimum and tolerance range for the specific parameter.

We specifically referred to four different morpho-bathymetric zones identified within the Adriatic basin (Van Straaten, 1970; Breman, 1975; Jorissen, 1988; Zavatarelli and Pinardi, 2003; Trincardi et al., 2014):

- i) inner shelf, with a water depth < 40 m;
- ii) outer shelf, from 40 m down to the shelf break, at 160 m;
- iii) continental slope, from 160 m to 800 m;
- iv) deep basin, with water depth > 800 m.

Species' substrate preference was based on classes from the modified Folk triangle (Kaskela et al., 2019); it's worth noting that the first two classes (i.e., the coarsest ones) were not recorded in the study area (western Adriatic Sea):

- i) rock and boulders;
- ii) coarse sediment (gravel $\geq 80\%$);
- iii) sand ($\geq 90\%$);
- iv) mixed sediment (sand <90%; mud 95–10%);
- v) muddy sand (sand 50–90%);
- vi) sandy mud (sand 10–50%);
- vii) mud (sand <10%).

4. Results

4.1. Species assignment to EGs

After filtering, 90 marine species belonging to 65 different genera were retained. Euryhaline-brackish and freshwater-hypohaline taxa were treated separately, as they represent allochthonous fauna. Despite the narrow TOC range typical of the commonly oligotrophic Mediterranean Sea (Boldrin et al., 2002), marine species were assigned to one ecological group (EG, sensu Borja et al., 2000; Table 1). For each EG, the key species response to TOC variations is illustrated in Fig. 3. All the species scatterplots are reported in Supplementary material 2, while Fig. 4 graphically illustrates the optimum (green dots) and tolerance range (bars) to TOC of ostracod species using a caterpillar plot.

The complex response of ostracods to environmental parameters and the scarcity of deep-water samples (> 160 m; Fig. 1) make the assignment of some species challenging (e.g., bimodal or particular distribution of frequencies along the TOC gradient), leading us to rely mainly on

Table 1

Species assigned to each EG, along with TOC optimum, preferred morpho-bathymetric zone and seafloor grain-size obtained by integrating the weighted average (WA) optimum and tolerance range.

Species	EG	TOC optimum	Morpho-bathymetric zone	Grain-size
<i>Aurila convexa</i>	I	0.30	outer shelf	muddy sands - sands
<i>Aurila speyeri</i>	I	0.30	outer shelf	muddy sands - sands
<i>Bythocythere turgida</i>	I	0.24	continental slope	indifferent
<i>Callistocythere flavidofusca</i>	I	0.23	inner shelf	indifferent - seems to prefer sandy
<i>Callistocythere rastrifera</i>	I	0.22	outer shelf	indifferent - seems to prefer sandy
<i>Cushmanidea elongata</i> and <i>C. turbida</i>	I	0.25	inner shelf	muddy sands - sands
<i>Cytheretta adriatica</i>	I	0.28	inner shelf	indifferent - seems to prefer sandy
<i>Cytheretta judaea</i>	I	0.25	inner shelf	indifferent - seems to prefer sandy
<i>Cytheropteron latum</i>	I	0.26	continental slope	indifferent - seem to prefer muddy sand
<i>Eucytherura complexa</i>	I	0.36	continental slope	indifferent
<i>Eucytherura mistrettai</i>	I	0.32	outer shelf	indifferent - seem to prefer sandy mud
<i>Loxococoncha rubritincta</i>	I	0.39	inner shelf	indifferent
<i>Microcytherura angulosa</i>	I	0.25	outer shelf	muddy sand
<i>Neocytherideis fasciata</i>	I	0.24	inner shelf	indifferent
<i>Neonesidea frequens</i>	I	0.28	outer shelf	muddy sand - sand
<i>Sagmatocythere napoliana</i>	I	0.28	inner shelf	indifferent
<i>Semicytherura acuta</i>	I	0.25	inner shelf	muddy sand - sand
<i>Semicytherura aff. Rara</i>	I	0.22	outer shelf	indifferent
<i>Semicytherura brachyptera</i>	I	0.24	outer shelf	indifferent - seem to prefer muddy sand - sand
<i>Semicytherura diafora</i>	I	0.26	outer shelf	indifferent
<i>Semicytherura inversa</i>	I	0.28	outer shelf	indifferent
<i>Semicytherura robusta</i>	I	0.31	outer shelf	indifferent - seems to prefer muddy sand - sand
<i>Semicytherura ruggierii</i>	I	0.31	outer shelf	indifferent - seems to prefer muddy sand - sand
<i>Semicytherura sulcata</i>	I	0.29	inner shelf	indifferent - seems to prefer sandy mud
<i>Semicytherura tergestina</i>	I	0.24	outer shelf	indifferent - seems to prefer muddy sand - sand
<i>Semicytherura ventricosa</i>	I	0.23	outer shelf	indifferent - seems to prefer muddy sand - sand
<i>Acanthocythereis hystrix</i>	II	0.34	continental slope	indifferent
<i>Archypolyclope demulderi</i>	II	0.51	continental slope	mud - sandy mud
<i>Bairdopillata supradentata</i>	II	0.50	continental slope	mud - (sandy mud)

(continued on next page)

Table 1 (continued)

Species	EG	TOC optimum	Morpho-bathymetric zone	Grain-size
<i>Bosquetina carinella</i>	II	0.49	outer shelf	mud - (sandy mud)
<i>Callistocythere adriatica</i> and <i>C. diffusa</i>	II	0.36	outer shelf	indifferent - seems to prefer sandy
<i>Callistocythere intricatoides</i>	II	0.36	outer shelf	indifferent - seems to prefer muddy
<i>Carinocythereis antiquata</i>	II	0.49	inner shelf	mud - sandy mud
<i>Cytherella</i> aff. <i>Vulgata</i>	II	0.51	outer shelf	mud - sandy mud
<i>Cytherella alvearium</i>	II	0.49	continental slope	mud - sandy mud
<i>Cytherois tiffenordei</i>	II	0.43	inner shelf	mud - sandy mud
<i>Cytheropteron hadriaticum</i>	II	0.35	continental slope	indifferent - seems to prefer sandy mud
<i>Cytheropteron monoceros</i>	II	0.46	outer shelf	indifferent - seems to prefer sandy mud
<i>Cytheropteron vespertilio</i>	II	0.54	outer shelf	mud - sandy mud
<i>Cytheropteron zinulusae</i>	II	0.53	continental slope	mud - sandy mud
<i>Hemicytherura defioerei</i>	II	0.28	outer shelf	muddy sand
<i>Hiltermannicythere turbida</i>	II	0.36	inner shelf	indifferent - seems to prefer mud
<i>Leptocythere rara</i>	II	0.28	outer shelf	indifferent
<i>Loxoconcha alata</i>	II	0.39	outer shelf	indifferent
<i>Loxoconcha concentrica</i>	II	0.44	outer shelf	indifferent
<i>Loxoconcha rhomboidea</i>	II	0.40	inner shelf	indifferent - seems to prefer sandy
<i>Loxoconcha tumida</i>	II	0.35	inner shelf	indifferent - seems to prefer sandy mud
<i>Monoceratina mediterranea</i>	II	0.38	continental slope	indifferent
<i>Paracythereis striata</i>	II	0.32	continental slope	indifferent - seems to prefer sandy mud
<i>Paradoxostoma triste</i>	II	0.54	continental slope	mud - sandy mud
<i>Pontocyprina spinosa</i>	II	0.51	continental slope	mud - sandy mud
<i>Pseudocythere caudata</i>	II	0.45	continental slope	indifferent - seems to prefer sandy mud
<i>Sagmatocythere littoralis</i>	II	0.34	outer shelf	sandy mud
<i>Semicytherura incongruens</i>	II	0.32	inner shelf	indifferent - seems to prefer muddy sand - sand
<i>Xestoleberis communis</i>	II	0.46	outer shelf	indifferent - seems to prefer sandy mud
<i>Xestoleberis dispar</i>	II	0.36	inner shelf	indifferent - seems to prefer sandy mud
<i>Xestoleberis fuscomaculata</i>	II	0.33	inner shelf	indifferent - seems to prefer sandy mud
<i>Bosquetina</i> aff. <i>Rhodiensis</i>	III	0.59	continental slope	mud - (sandy mud)
<i>Buntonia textilis</i>	III	0.59	continental slope	mud
<i>Costa edwardsii</i>	III	0.49	outer shelf	mud - (sandy mud)
<i>Cytheridea neapolitana</i>	III	0.57	outer shelf	mud

Table 1 (continued)

Species	EG	TOC optimum	Morpho-bathymetric zone	Grain-size
<i>Eucythere curta</i>	III	0.41	outer shelf	indifferent - seems to prefer sandy mud
<i>Henryhowella asperima</i>	III	0.55	continental slope	mud - sandy mud
<i>Heterocythereis albomaculata</i>	III	0.41	inner shelf	indifferent
<i>Krithe keyi</i>	III	0.54	continental slope	mud - sandy mud
<i>Leptocythere bacescoi</i>	III	0.53	inner shelf	mud - sandy mud
<i>Leptocythere ramosa</i>	III	0.51	inner shelf	mud - sandy mud
<i>Leptocythere tenera</i>	III	0.55	inner shelf	mud - sandy mud
<i>Loxoconcha pellucida</i>	III	0.58	continental slope	mud
<i>Loxoconcha versicolor</i>	III	0.54	outer shelf	mud - sandy mud
<i>Palmoconcha turbida</i>	III	0.49	inner shelf	mud - sandy mud
<i>Paracythereis mediterranea</i>	III	0.45	outer shelf	indifferent
<i>Polycopse reticulata</i>	III	0.55	continental slope	mud - sandy mud
<i>Propontocypris dispar</i> and <i>P. intermedia</i>	III	0.57	outer shelf	mud - sandy mud
<i>Pterygocythereis ceratoptera</i>	III	0.43	outer shelf	indifferent - seems to prefer sandy mud
<i>Pterygocythereis jonesii</i>	III	0.53	outer shelf	mud - sandy mud
<i>Rectobuntonia miranda</i>	III	0.50	continental slope	mud - sandy mud
<i>Cytheropteron alatum</i>	IV	0.64	continental slope	mud
<i>Cytheropteron garcanicum</i>	IV	0.61	continental slope	mud
<i>Cytheropteron rotundatum</i>	IV	0.61	outer shelf	mud
<i>Cytheropteron venustum</i>	IV	0.60	continental slope - deep basin	indifferent
<i>Polycopse tholiformis</i>	IV	0.63	continental slope - deep basin	mud
<i>Polycopse vasfiensis</i>	IV	0.60	continental slope	mud - sandy mud
<i>Polycopsis quadridentata</i>	IV	0.63	continental slope - deep basin	mud - sandy mud
<i>Pseudopolycopse striata</i>	IV	0.66	continental slope - deep basin	mud
<i>Robustoargilloecia acuminata</i>	IV	0.63	continental slope - deep basin	mud
<i>Thracella bartonensis</i>	IV	0.69	outer shelf	mud
<i>Anchistrocheles tenera</i>	V	0.83	deep basin	mud
<i>Bythocypris obtusata</i>	V	0.72	continental slope - deep basin	mud
<i>Loxoconcha</i> aff. <i>Agilis</i>	V	0.71	outer shelf	mud

optimum and tolerance range values. For each species, EG assignment and TOC optimum are reported in Table 1, along with preferred morpho-bathymetric zone and seafloor grain-size. Water depth and sand optima, as well as tolerance ranges for all the analyzed parameters, are shown in Supplementary material 1.

For each category, the most common species (e.g., occurrence within more than 50 samples and frequencies > 10%) showing a typical distribution along the TOC gradient (sensu Borja et al., 2000 and Jorissen et al., 2018) are presented below, along with species typified by peculiar scatterplots (Fig. 3).

4.1.1. Sensitive species (EG I)

Twenty-six species, such as *C. elongata* and *C. turbida* (Fig. 3a) and

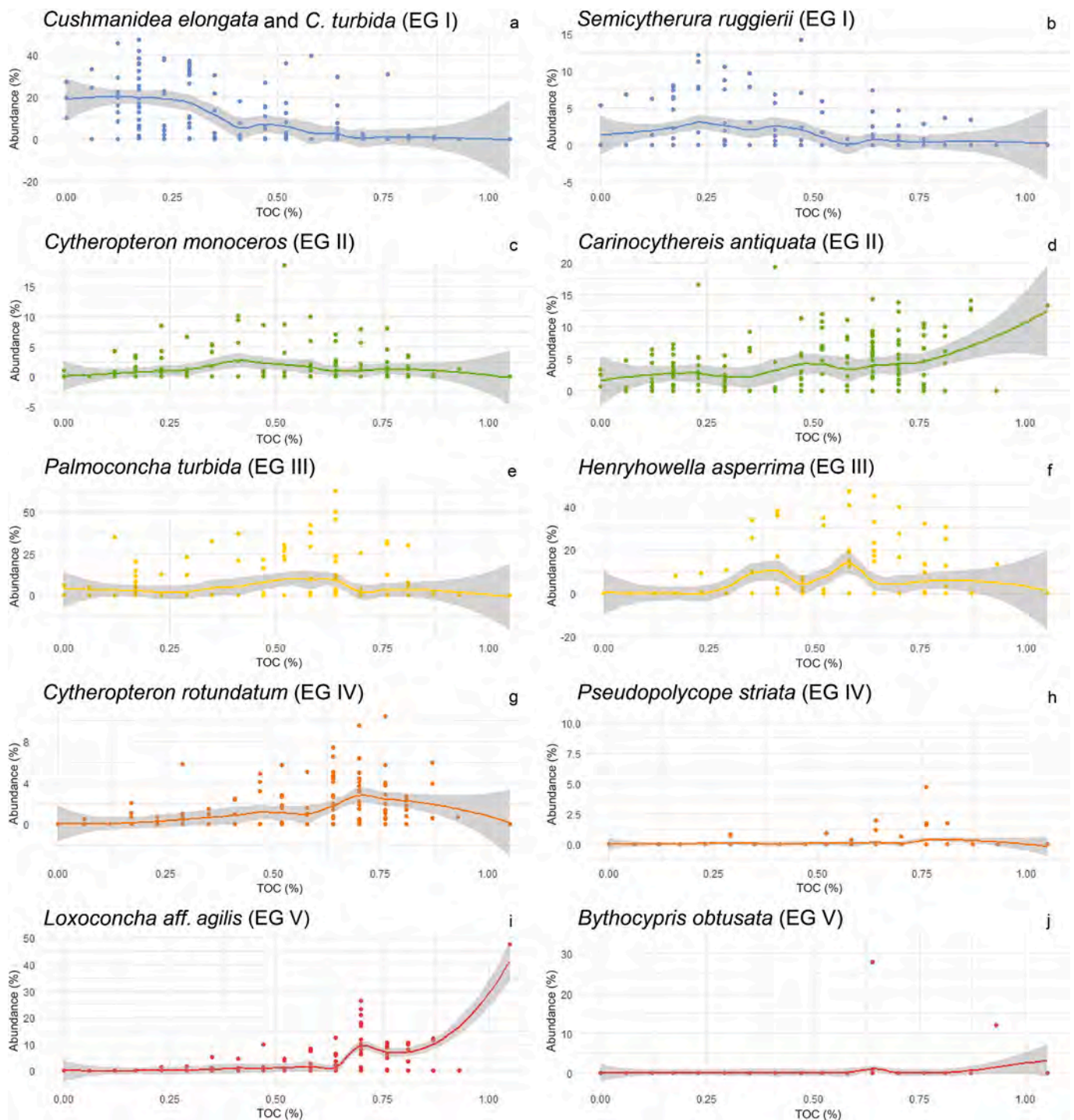


Fig. 3. “Scatterplots of key species”. Scatter plot of key species fitted with a locally weighted regression line (shaded area is the 95% confidence interval) to visualize typical and peculiar responses along a TOC (%) gradient for each ecological group: respectively, (a) *Cushmanidea elongata* and *C. turbida* and (b) *Semicytherura ruggierii* for EG I, (c) *Cytheropteron monoceros* and (d) *Carinocythereis antiquata* for EG II, (e) *Palmoconcha turbida* and (f) *Henryhowella asperrima* for EG III, (g) *Cytheropteron rotundatum* and (h) *Pseudopolycope striata* for EG IV, and (i) *Loxoconcha aff. agilis* and (j) *Bythocypris obtusata* for EG V.

Cytheretta judaea, are assigned to EG I and mostly exhibit a typical descending distribution pattern of the regression curve. Whereas other species, including *Microcytherura angulosa*, *Cytheretta adriatica* and *Aurila* species, show high densities of data points for low TOC values. Most *Semicytherura* species are also considered sensitive, but some of them show distinctive distribution patterns. For example, *S. diafora* is characterized by a bimodal distribution, while *S. ruggierii* is present over a wide range of TOC values (Fig. 3b). Nevertheless, both species are classified under EG I, due to their very low optima (0.26% and 0.31%,

respectively; Table 1) and high density of data points towards the lowest TOC values (tolerance range approx. 0.1% - 0.5%; Supplementary material 1 and Fig. 4).

4.1.2. Indifferent species (EG II)

Most of the thirty-one species assigned to EG II show a typical flattened regression curve: examples include *Bairdoppilata supradentata* and *Cytheropteron monoceros* (Fig. 3c). The assignment of other species to EG II is more difficult: *Carinocythereis antiquata* shows remarkable



Fig. 4. “Caterpillar plot for TOC”. Caterpillar plot graphically illustrating the optimum (green dots) and tolerance range (bars) to TOC of the 90 marine ostracod species assigned to an EG. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

frequency in one sample with high TOC (1.1%; Fig. 3d), but the overall distribution and calculated optimum (0.49%; Table 1) support its classification as an indifferent species. Similarly, *Hiltermannicythere turbida* displays two peaks along the TOC gradient, but is considered indifferent due to its optimum (0.36%; Table 1) and tolerance range (approximately 0.3%–0.9%; Supplementary material 1 and Fig. 4). Despite a descending regression curve, the only *Semicytherura* species considered indifferent is *S. incongruens*. Indeed, its high frequencies across a broad TOC range (tolerance approximately 0.1%–0.7%; Supplementary material 1 and Fig. 4) and slightly higher optimum (0.32%; Table 1) compared to other *Semicytherura* species, support its attribution to EG II.

4.1.3. Third-order opportunistic species (EG III)

Out of the twenty species assigned to this category, the most abundant are *Cytheridea neapolitana*, *Palmoconcha turbida*, and *Henryhowella asperrima*. The first two species show a typical peak of the regression curve for high TOC values (Fig. 3e), whereas the latter displays a distinctive bimodal distribution (Fig. 3f). Other common EG III species are *Loxoconcha versicolor* and *Pterygocythereis ceratoptera*, along with

Costa edwardsii and *Bosquetina* aff. *Rhodiensis*. Although *C. edwardsii* exhibits an atypical double peak in its regression curve and *Bosquetina* aff. *Rhodiensis* lacks a clear peak at high TOC values, the optima of these two species (0.49% and 0.59%, respectively; Table 1) and the occurrence of lower frequencies at low TOC values support their classification as third-order opportunistic.

4.1.4. Second-order opportunistic species (EG IV)

Most of the ten species assigned to EG IV exhibit the typical TOC regression curve, as illustrated by *Cytheropteron rotundatum* (Fig. 3g). This category also includes common species, such as *Robustoaargilloecia acuminata* and *Thracella bartonensis*, alongside most *Cytheropteron* species (*C. alatum*, *C. garganicum*, *C. rotundatum*, and *C. venustum*) and the majority of *Polycopse* species, including *P. tholiformis* and *P. vasfiensis*. Differently, the attribution of *Pseudopolycope striata* is challenging. Despite lacking a pronounced peak in its regression curve at high TOC values (Fig. 3h), it is attributed to EG IV due to i) high optimum (0.66%; Table 1) and ii) high density of data points at the upper end of the TOC gradient (tolerance range approximately 0.5%–0.9%; Supplementary

material 1 and Fig. 4).

4.1.5. First-order opportunistic species (EG V)

Only three species were assigned to EG V, all of which show an ascending-exponential regression curve along the TOC gradient. *Anchistrocheles tenera* and *Loxoconcha* aff. *Agilis* (Fig. 3i) are associated with higher contents of organic matter and show the highest optima values in the whole dataset. *Bythocypris obtusata* is a rare species (observed in only 11 samples) attributed to EG V due to its high calculated optimum (0.72% in Table 1; Fig. 3j).

4.2. Testing species assignment

The resulting Ostra-AMBI values obtained from the testing samples (Sect. 3.3; Fig. 1) range from 0.4 to 3.8, with the highest values commonly observed in samples where TOC exceeds 0.4%. The Ostra-AMBI is positively and significantly correlated with TOC ($R = 0.77$, $R^2 = 0.59$, $p = 8.6 \times 10^{-11}$; Fig. 5a). The correlation between the two variables can be considered strongly positive, particularly considering that the variables are greatly influenced by multiple different factors. Indeed, both ostracods and TOC are interrelated with seafloor grain-size and bathymetry, as a muddy substrate tends to be more organic-enriched than sandy ones (De Falco et al., 2004).

The validity of the species assignment is also supported by the strong positive correlation between the Ostra-AMBI and Foram-AMBI calculated for the shared 29 samples in the testing dataset ($R = 0.88$, $R^2 = 0.75$, $p = 5.3 \times 10^{-10}$; Fig. 5b). The Foram-AMBI spans from 0.3 to 3.4, and higher values generally correspond to an increase in Ostra-AMBI.

4.3. Bathymetric distribution and substrate preference of ostracod EGs

According to Breman (1975), 59 out of the 90 assigned species

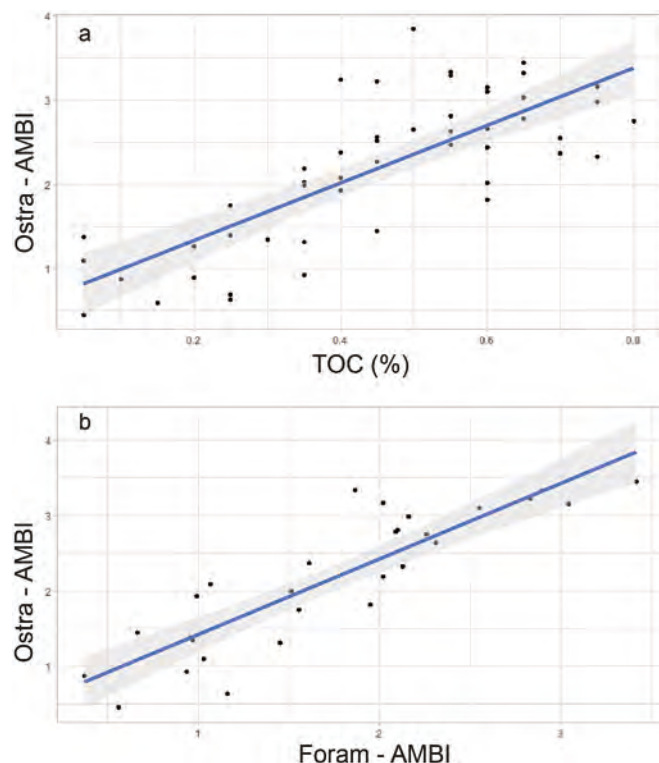


Fig. 5. “Correlation of Ostra-AMBI with TOC and Foram-AMBI”. Relationship between (a) Ostra-AMBI and TOC, and (b) Ostra-AMBI and Foram-AMBI for the test sub-dataset. Linear regression lines are depicted in blue, along with the 95% confidence interval (grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

commonly inhabit the shelf, whereas only 31 prefer deeper environments (> 160 m). This imbalance between shelf and deep-water (i.e., continental slope and deep basin in Table 1) species likely reflects the morphology of the Adriatic Sea and the spatial distribution of sampling stations, which tend to concentrate along the Italian coastline with sparse coverage in the deepest areas of the basin (Fig. 1). Among the 26 species considered sensitive, only three species are present at depth > 160 m, yet their optimum never exceeds approx. 200 m (Supplementary material 1). Out of the 23 species thriving in shallower environments, nine inhabit the inner shelf, whereas the remaining fourteen typically colonize the outer shelf (Fig. 6a; ASupplementary material 1). Sensitive species are commonly found on mixed sand-mud substrates (i.e., sandy muds and muddy sands), with sand content varying from 26% to 81% (Fig. 6b; Supplementary material 1).

A homogeneous distribution in terms of both water depth and grain-size typifies ostracods belonging to EG II (Fig. 6). Indeed, nineteen out of the 31 species assigned to this ecological group show depth optima values within the shelf environment (i.e., 20–144 m), whereas twelve species prefer deeper settings never exceeding ~ 230 m (Fig. 6a; Supplementary material 1). Moreover, indifferent species occur across a

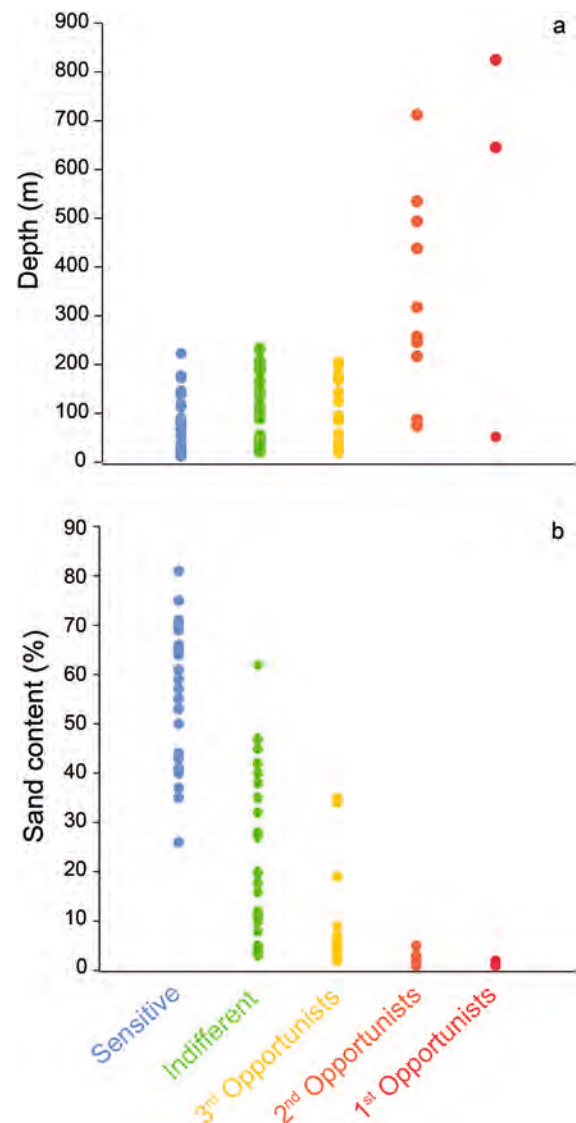


Fig. 6. “Jitterbox for each EG”. Jitterbox reporting the preferred (a) bathymetric range and (b) sand content for each ecological group. Data points represent the weighted average optimum values for each species assigned to a specific EG.

wide range of substrates, from muds to muddy sands, as their sand optima values range from 2% to 62% (Fig. 6b; Supplementary material 1).

Differently, thirteen species considered as third-order opportunists inhabit the shelf area (depth optima values from 18 m to 146 m) and only six species show optima values greater than 160 m (maximum value: 205 m; Fig. 6a; Supplementary material 1). However, most species assigned to EG III prefer muddy bottoms (sand optimum from 1.6% to 10%) and only two species show a sand optimum greater than 20% (i. e., sandy mud; Fig. 6b; ASupplementary material 1).

Most of second- and first-order opportunistic species prefer deep environments and muddy bottoms (sand optima maximum value of approx. 5%; Fig. 6b; Supplementary material 1). Specifically, eight out of the ten species assigned to EG IV show optima water depths between 200 m and 700 m, whereas only two species inhabit the outer shelf (i.e., 40 m–160 m; Fig. 6a; Supplementary material 1). Two of the three species considered as first-order opportunists prefer the deepest environments (optimum values of 600 m and 800 m), whereas only one shows a water depth optimum of 51 m (Fig. 6a; Supplementary material 1).

4.4. Distribution of allochthonous ostracods

In the Adriatic Sea, allochthonous ostracods, not considered for the EGs assignment (Sect. 4.1), are represented by euryhaline-brackish and freshwater-hypohaline species that are commonly found in inner-shelf samples (Fig. 7). Freshwater-hypohaline taxa (*Candona* spp., *Ilyocypris bradyi*, *Limnocythere inopinata* and *Darwinula stevensoni*) are commonly found in proximity of river mouths, with the highest abundances (up to approx. 43%, 20%, 6% and 2% respectively) in front of the Po Delta (Fig. 7a). Similarly, euryhaline-brackish species (*Cyprideis torosa*, *Cytheromorpha fuscata* and *Loxoconcha elliptica*) are mainly recorded close to the Po outlets and other Alpine river mouths (up to approx. 34%, 25% and 3% respectively). However, they are also encountered with lower abundances at greater water depths, rarely exceeding 100 m (Fig. 7b).

5. Discussion

5.1. Ostracods as bio-indicators of organic enrichment gradients

Our results show that in a basin strongly affected by fluvial inputs, like the Adriatic Sea, the interplay between river plumes and sea currents represents the main driver for the distribution of ostracods, similarly to what has been observed for foraminifera (Van der Zwaan and Jorissen, 1991). Specifically, proximity to major organic sources (i.e., Po River and other Alpine and Apennine rivers) is not the only factor to consider, as sediment dispersal mechanisms (Adriatic sea currents) control the accumulation of fine-grained inorganic and organic particles that can also promote primary production (Tesi et al., 2006, 2007; Giani et al., 2009). This leads to a patchwork of seafloor conditions in terms of organic matter and mud accumulation along the sediment routing system and across bathymetric gradients from shallow to deeper environments (Fig. 8a,b).

To evaluate the relative contribution of these variables within the Adriatic dataset, a Canonical Correspondence Analysis (CCA) was performed, including TOC, sand content and water depth. The CCA model is statistically significant (permutation test, $p = 0.001$; Supplementary material 3, Table C3), indicating that the relationships between ostracod assemblages and environmental variables are not random (see Supplementary material 3, Tables C1–C2 for detailed CCA results). Among the environmental variables, water depth represents the primary driver of species distribution, followed by sand content and TOC, which shows a statistically significant contribution ($p = 0.013$; Supplementary material 3, Table C4).

Variance Inflation Factor (VIF) values close to 1 (Supplementary material 3, Table C5) indicate the absence of problematic multicollinearity, suggesting that TOC, sand content and depth provide independent explanatory contributions to the observed ecological patterns. These results are consistent with the observed distribution of ecological groups (EGs), which show distinct bathymetric and substrate preferences (Fig. 6).

As for the Adriatic shelf, a variety of both sensitive (23 species) and opportunistic (sixteen species) ostracods are encountered (Fig. 5a).

Species here assigned to EG I (e.g., *Aurila*, *Semicytherura* and

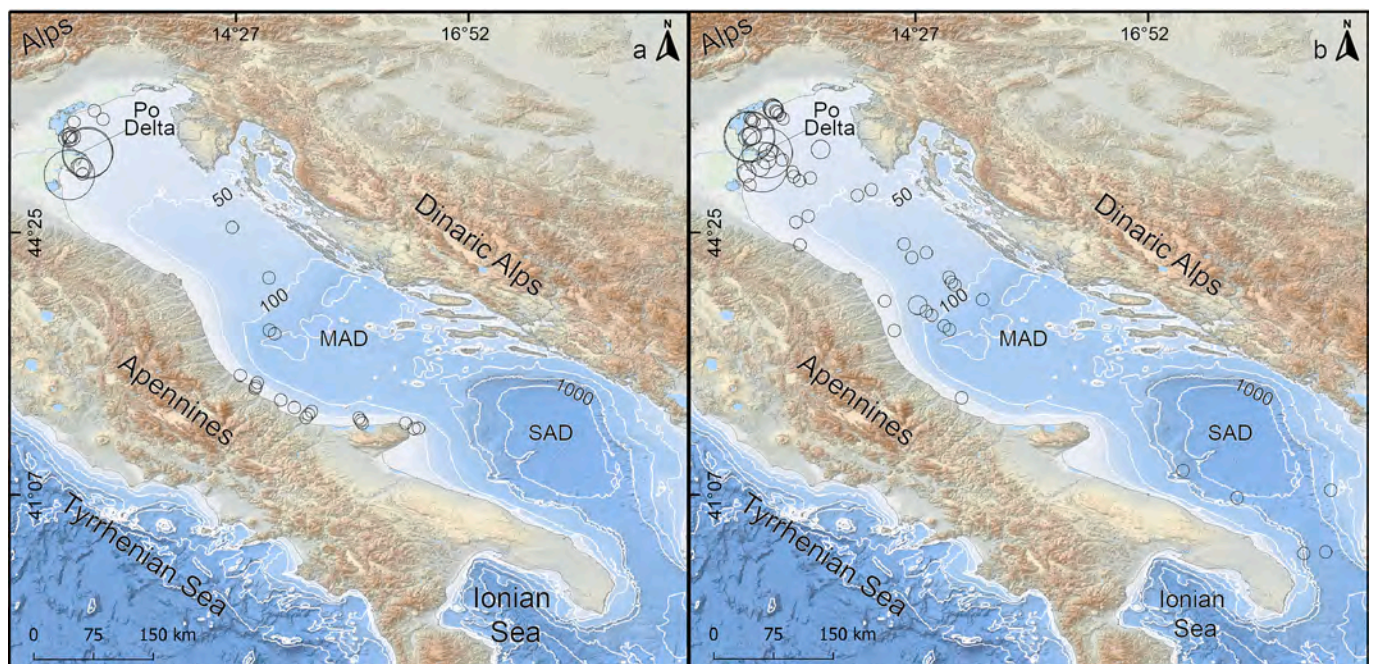


Fig. 7. “Distribution of allochthonous species”. Distribution of allochthonous species: (a) freshwater-hypohaline and (b) euryhaline-brackish species. Smaller circles: < 20%; larger circles: > 20%.

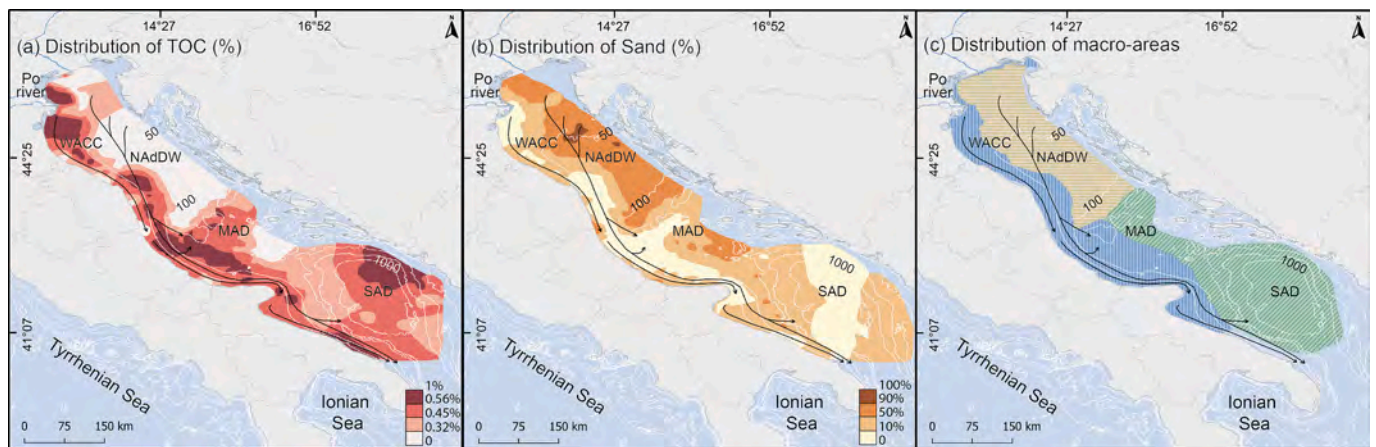


Fig. 8. “Environmental distribution and macro-area classification across the Adriatic Sea”. (a) Spatial distribution of TOC (%). (b) Spatial distribution of sand content (%). (c) Location map of the macro-areas identified based on the distribution of ostracod ecological groups (EGs). Colored domains indicate the Adriatic Mud Wedge (AMW; blue with vertical hatching), the coastal belt and sediment-starved shelf (yellow with horizontal hatching), and the slope and pits (MAD and SAD; green with diagonal hatching). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Cytheretta species, *Sagmocythere napolitana* and *Neocytherideis fasciata*) are known to prefer sandy substrates and oligotrophic conditions and include phytal taxa typical of low turbidity waters (e.g., Guernet et al., 2003; Aiello et al., 2006, 2018; Sciuto et al., 2015). Although considered opportunistic in the Adriatic Sea (Colalongo, 1969), *C. elongata* and *C. turbida* display a typical EG I behavior (Fig. 3a). This apparent discrepancy likely arises from the use of the term “opportunists” as a synonym for stress-tolerant, emphasizing the ability of these species to thrive under coastal, highly hydrodynamic conditions.

In this study, the degree of opportunism of Mediterranean ostracods has been quantitatively assessed along a TOC gradient, and taxa have been formally assigned to ecological groups (EGs). Previous interpretations were mainly based on qualitative observations, such as species occurrence or an increase in abundance under high organic-matter fluxes. The proposed approach enables a more robust and objective evaluation of species ecological responses, with significant palaeoenvironmental implications. EG III represents more than 80% of opportunistic species on the Adriatic shelf (Fig. 6a). According to literature (Frezza and Di Bella, 2015; Aiello et al., 2018; Salvi et al., 2020), many of these species are reported to be able to persist under organic-enriched and hypoxic conditions, frequently associated with muddy substrates and high fluvial runoff (e.g., *P. turbida*, *C. neapolitana*, *P. ceratoptera* and several *Leptocythere* species), or under stressed physico-chemical conditions (*Costa edwardsii*; Aiello et al., 2018). The assignment to EG V of the outer shelf *Loxoconcha* aff. *Agilis* is consistent with previous studies describing some *Loxoconcha* species as tolerant, able to persist in organic- and nutrient-enriched environments, commonly displaying a “survivor-type” response under severe environmental stress (e.g., Alvarez Zarikian et al., 2000; Cronin and Vann, 2003; Yasuhara et al., 2007). Other taxa commonly thriving on Mediterranean shelves on a variety of substrates and under different degrees of river influence (e.g., *Semicytherura incongruens*, *Xestoleberis* species, *C. antiquata* and *H. turbida*; Aiello et al., 2006; Frezza and Di Bella, 2015; Salvi et al., 2020) are here classified as indifferent (EG II) and, thus, able to extensively colonize the Adriatic shelf.

The ostracod distribution in Adriatic deeper environments (>160 m) appears to be monotone, as opportunistic species are invariably dominant with the prevalence of EG IV and EG V, particularly beyond the isobath 250 m (Fig. 6a). This is consistent with a relatively homogeneous seafloor typified by fine-grained sediments with a preservative absorption of carbon fluxes (Fig. 8a,b; Giordani et al., 2002). Deep-water species classified here as opportunist (i.e., *Bythocypris obtusata*, *Krithe keyi*, *Henryhowella asperima*, and *Cytheropteron*, *Polycoppe* and *Argilloecia* species; Table 1) are typically associated with muddy bottoms and

abundant nutrient fluxes across the Mediterranean Sea (Angue Minto'o et al., 2013; Sciuto and Rosso, 2015; Bassetti et al., 2010; Fanget et al., 2016).

Additionally, several studies from the North Atlantic and other deep-sea and continental margin settings have shown that genera such as *Krithe*, *Cytheropteron*, *Polycoppe*, and *Argilloecia* may display opportunistic behavior under conditions of increased organic matter flux and enhanced productivity (e.g., Yasuhara et al., 2008; Alvarez Zarikian et al., 2009, 2022; Huang et al., 2019; Jöst et al., 2018).

High organic-matter inputs may periodically lead to reduced oxygen levels. In previous studies regarding ostracods' ecology, different degrees of tolerance have been assigned to opportunistic taxa (EG III-V), highlighting a complex response to this co-occurring factor. For instance, deep-water genera *Henryhowella* and *Cytheropteron* appear to prefer oxygen-rich waters, whereas *Argilloecia*, *Polycoppe*, and *Krithe* are considered tolerant of hypoxic conditions (Yasuhara et al., 2008, 2012; Alvarez Zarikian et al., 2009; Bassetti et al., 2010; Aiello et al., 2018; Angue Minto'o et al., 2013; Jöst et al., 2018; Huang et al., 2019). Among shelf species, *Palmoconcha turbida* (ex *Loxoconcha turbida*) has been reported to tolerate low-oxygen conditions and increased nutrient supply (Bodergat et al., 1998). However, the Bremen dataset does not include any information on bottom-water oxygen conditions, preventing a thorough discussion of the relationship between ostracods, organic enrichment and oxygen levels.

The overall consistency of previously published ecological data, including life strategies observed in ostracod biocoenosis from different Mediterranean areas, further strengthens the application of the ecological groups (EGs) assignment proposed in this study (Table 1) on a Mediterranean scale. Although potentially subjected to local specific variations, these EGs can be a useful tool to track organic enrichment gradients (and sinks) at different water depths.

5.2. The fingerprint of the Adriatic sediment routing system on ostracod assemblages

Following a source-to-sink perspective, the spatial distribution of marine depositional environments from the coastal region to the deep basin reflects the transport pathways and storage of sediments supplied by rivers (Sømme et al., 2009; Spagnoli et al., 2021). In the western Adriatic Sea, seismic-stratigraphic studies have documented the occurrence of areas characterized by specific processes and chemical-physical conditions, also in terms of organic enrichment (ISPRA, 2001, 2010a-e).

The distinctive assemblages of ostracod ecological groups (Table 1) effectively discriminate three macro-areas (Figs. 8c and 9):

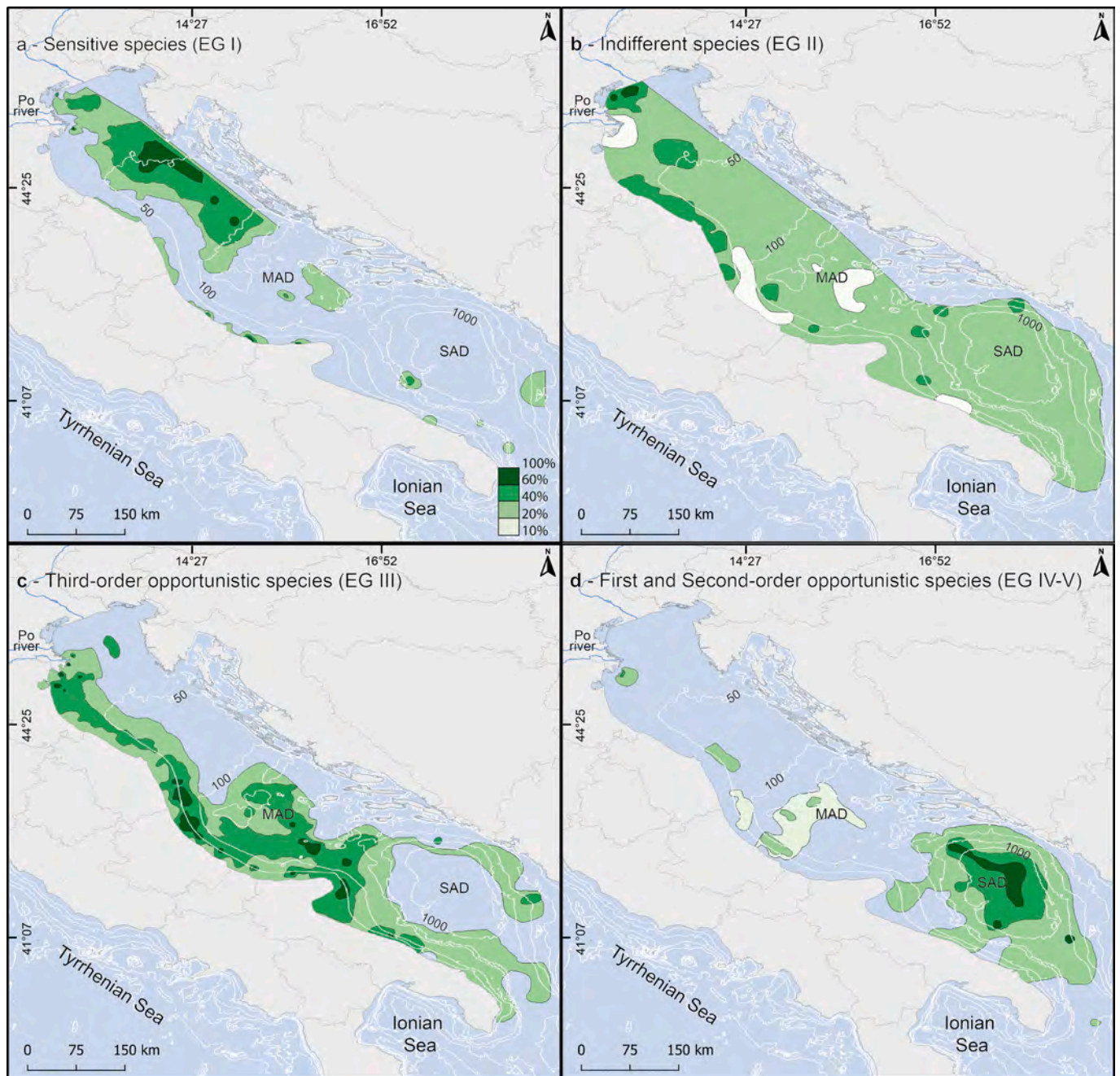


Fig. 9. “Distribution of EGs within the Adriatic Sea”. Distribution maps of (a) sensitive species (EG I), (b) indifferent species (EG II), (c) third-opportunistic species (EG III) and (d) second and first order opportunistic species (EG IV-V).

- 1) coastal belt and sediment-starved shelf;
- 2) Adriatic Mud Wedge;
- 3) slope and pits.

This distribution enhances the ecological relevance of species classification and improves our understanding of the relations between depositional processes and marine fauna, representing a fundamental step towards a comprehensive evaluation of environmental quality and its spatial and temporal variability.

The spatial distribution of grain-size and TOC (Fig. 8a,b) further supports this zonation, highlighting the importance of sediment transport pathways in controlling the depositional patterns across the basin. Coarser sediments are mainly confined to the coastal belt along the Italian coastline at water depths <10 m and to the sediment-starved

shelf of the Northern and Central Adriatic. Specifically, coastal sands accumulate under the action of wave-driven currents, which remove the finest particles and promote their transport and accumulation farther basinwards (Fig. 8a; Frignani et al., 2005; Tesi et al., 2007; Harris et al., 2008). In contrast, sandy substrates in deeper environments (Fig. 8a) result from limited sediment supply from Eastern Alpine rivers, compared to the Po and Apennine rivers, combined with the general southward alongshore redistribution of riverine sediments driven by the Western Adriatic Coastal Current (WACC) and the North Adriatic Dense Water (NAdDW; Figs. 1, 8a,b; Frignani et al., 2005; Harris et al., 2008). These factors together determine sediment-starved conditions over a vast shelf area, covering a wide water-depth range (from approx. 12 m to the shelf break; Fig. 8; Sect. 2).

As a result, fine-grained, organic-rich deposits from Alpine (mainly

the Po River) and Apennine rivers are not retained nearshore but are preferentially transferred offshore. This material accumulates between the coastal belt and the sediment-starved shelf within the Adriatic Mud Wedge (AMW), which acts as a major organic sink from north to south up to the Gargano Promontory, and is further redistributed towards the deepest parts of the basin (Fig. 8a,b; Correggiari et al., 2001; Cattaneo et al., 2003, 2007; Tesi et al., 2013; Pellegrini et al., 2021; Dalla Valle et al., 2024). In the Middle and South Adriatic Deep (i.e., MAD and SAD), organic matter transported downslope by dense water cascading and along-slope currents contributes to the formation of additional sinks (Fig. 8a,b), which are largely fed by lateral inputs rather than by local surface productivity (Giordani et al., 2002).

This suggests that the organic matter supplied by rivers is not simply deposited near river mouths, but is redistributed across the basin by coastal currents, following the pathway of the WACC and the NAdDW (Figs. 1 and 8; Artegiani et al., 1997; Trincardi et al., 2007; Marini et al., 2016; Rovere et al., 2019). As a result, TOC does not follow a typical and continuous proximal-to-distal gradient from river mouths, but instead accumulates in distinct depocenters. In the Adriatic Sea, TOC distribution reflects a source-to-sink system controlled by sediment dispersal and accumulation processes, leading to the development of preferential sinks of organic-rich, fine-grained sediments within the AMW and the MAD–SAD system (Fig. 8).

Terrestrial inputs and hydrodynamical patterns are also tracked by the distribution of allochthonous valves (non-marine species; Fig. 7), as they mainly accumulate via flood-driven currents near river outlets (particularly the Po River) within coastal sands and prodelta muds of the AMW. The occurrence of these species may be useful to recognize palaeoflood events within shallow-marine successions, confirming observations from the Rhône Delta (Fanget et al., 2016). Moreover, euryhaline-brackish species are frequently found in offshore sandy deposits of the Northern and Central Adriatic (i.e., the sediment-starved shelf). This distribution may be attributed to the presence of relict back-barrier systems (Storms et al., 2008) developed during the post-glacial sea-level rise or to sediment transport associated with major flood events, whose plumes can extend farther offshore in a west-east direction (Boldrin et al., 2005).

5.2.1. Coastal belt and sediment-starved shelf

Despite differences in bathymetry and depositional processes, both the coastal belt (water depth < 10–15 m) and a large portion of the north-central Adriatic shelf host an ostracod assemblage dominated by sensitive (EG I; average value of approx. 33%; max value approx. 77%) and indifferent species (EG II; average value of approx. 39%; max value approx. 80%; Fig. 9a–b). Third-order opportunists (EG III) occur with modest percentages (average value of approx. 18%), but they can locally reach higher values (up to 30%) close to the mud-wedge or to the slope (Sect. 5.2.2 and Sect. 5.2.3; Fig. 9c). Second- and first-order opportunistic species (i.e., EG IV and EG V) are almost absent (Fig. 9d). Overall, this community reflects the interaction between river plumes and sea currents, which impairs the deposition of fine-grained TOC-enriched sediments (Fig. 8b–c). The coastal belt is mainly colonized by selected EG I (*C. elongata* and *C. turbida*, *L. rubritincta*, *N. fasciata* and *Cytheretta*) and EG II species (*S. incongruens*, *H. turbida* and *Xestoleberis* spp.).

On the sediment-starved shelf of the North and Central Adriatic (Fig. 8), similar assemblages (Fig. 9a–b) occur over a wider bathymetric range, with minor variations related to depth. These include: i) the partial substitution of *L. rubritincta* and *N. fasciata* (EG I) with *S. napoliana* and *Aurila* species (EG I), and ii) the diffused appearance of *B. carinella* (EG II).

5.2.2. Adriatic Mud Wedge

The Adriatic Mud Wedge (AMW) represents a major shelf depocenter and organic sink characterized by fine-grained, TOC-enriched sediments (Fig. 8a).

In this area, the ostracod fauna is dominated by third-order

opportunists (EG III; average value of approx. 45%; max value approx. 90%; Fig. 9c), mainly represented by *Leptocythere* species, *P. turbida*, *C. neapolitana*, *P. jonesii* and *H. asperrima* along a bathymetric gradient. Indifferent species (e.g., *C. antiquata*, *B. carinella* and *B. supradentata*) occur as a secondary group (average value of approx. 30% and max value approx. 68%; Fig. 9b), while sensitive (EG I; Fig. 9a) and second- to first-order opportunists (i.e., EGs IV–V; Fig. 9d) commonly show low abundances (approx. 6–7% as average value). However, a few samples display a higher content of EG I (mainly *C. elongata* and *C. turbida*) or EG V (*Loxoconcha* aff. *agilis*) species. The former commonly correspond to sandy substrates, whereas the latter possibly reflect areas of higher accumulation of fine-grained organic-enriched material (Fig. 9d). These sites correspond to the AMW depocenter, located on the mid-shelf (Pellegrini et al., 2021), and to the shelf area south of the Po Delta, where a high sediment input from the Po River promotes TOC deposition (Fig. 8a; Frignani et al., 2005; Tesi et al., 2013).

5.2.3. Adriatic slope and pits (MAD and SAD)

The Adriatic slope and, in particular, the Mid and South Adriatic Deep (MAD and SAD) represent the main deep organic sinks of the Adriatic Sea, characterized by muddy substrates and high organic matter accumulation (Fig. 8). These conditions favor the colonization of opportunistic species belonging to EG III (average value of approx. 27% and max value approx. 60%; Fig. 9c) and EGs IV–V (average value of approx. 23% and max value approx. 70%; Fig. 9d). EG III comprises a few species (Fig. 6a): *H. asperrima*, *Bosquetina* aff. *Rhodiensis* and *P. reticulata*. In contrast, second- and first-order opportunistic species, which reach the highest abundances in this macro-area, include several species (Fig. 6a) of *Cytheropteron* and *Polycopse*/*Polycopsis*/*Pseudopolycopse*, as well as *R. acuminata*. Within the deepest basin (SAD; water depth > 250 m), EG V species (*B. obtusata* and *A. tenera*) also occur (Fig. 6a) with the concomitant disappearance of indifferent (EG II) species. This distribution is consistent with the model by Borja et al. (2000), who suggested that indifferent species can tolerate initial stages of organic enrichment, but are unable to tolerate excessive TOC accumulation.

5.2.4. Application in environmental monitoring: Potentialities and limitations

In total, approximately 56% of the species retained after the pre-treatment of the matrix have been assigned to a specific ecological group (EG; 90 species out of 192). Beyond the percentage value, the species list of Table 1 is potentially valuable also for monitoring studies as only four samples in the testing dataset were excluded from the validity analyses, indicating that a sufficient number of common species are assigned to a specific category for a reliable application of the Ostra-AMBI index (Sect. 3.3). Moreover, Ostra-AMBI shows a significantly positive correlation with TOC (Fig. 5a), further highlighting its ability to reflect environmental changes even along a relatively narrow TOC gradient, such as the one observed in the Adriatic Sea. Notably, the coefficient of determination for the Ostra-AMBI–TOC relation ($R^2 = 0.59$) is comparable to or even exceeds those reported for Foram-AMBI in other regions (e.g., Alve et al., 2016; Bouchet et al., 2021). For instance, Alve et al. (2016) reported R^2 values of 0.52 and 0.42 in two separate test sub-datasets from the North-East Atlantic and the Arctic fjords, respectively. Similarly, Bouchet et al. (2021) found R^2 values of 0.67 for the Mediterranean Sea (Harbor of Cagliari) and 0.42 for the English Channel (Pertuis Charentais).

Consistent with previous works (e.g., Aiello et al., 2006; Aiello et al., 2020; Yasuhara et al., 2012; Salvi et al., 2015; Salvi et al., 2020; Schmitz et al., 2024; Schmitz et al., 2025), our findings reveal that ostracods could offer reliable insights into the environmental quality of marine sediments, making them an additional, viable proxy for assessing the (Palaeo)EcoQS of benthic ecosystems. On condition that the sedimentary environments are taken into account, the value of ostracods as (palaeo)ecological sentinels is particularly well-grounded in relation to

organic enrichment, a parameter frequently associated with both natural and anthropogenic environmental pressure (Figs. 8 and 9; Sects. 5.1 and 5.2). Understanding sediment transport, depositional patterns, and their relationships with ostracod fauna is therefore essential to accurately infer the signal they provide, including environmental quality evaluation.

It should be noted that many taxa assigned to ecological groups IV–V are predominantly associated with deeper environments, and their response to organic enrichment may not be evidenced in shallow-water settings, potentially limiting the detection of high levels of organic matter in cored successions lacking deeper depositional environments. However, the scarcity of second- and first-order opportunistic species thriving on the shelf is not limiting in itself, as environmental changes linked to organic fluxes can still be effectively detected through shifts in the relative abundance of EG III taxa and/or sensitive and indifferent species. This underscores the importance of interpreting Ostra-AMBI results within their bathymetric and sedimentological context. Although the dataset used in this study (Bremner, 1975) has proved to be a robust and valuable source of information, capable of providing an essential baseline for the assignment of species to EGs also within the framework of the AMBI applicability, some methodological limitations should be acknowledged. Since the spatial distribution of sampling stations is uneven, with most sites concentrated along the western Adriatic shelf and sparse coverage in the southeastern and deeper sectors, some species may not have been detected or may have suffered from poor information availability during the assignment process (low number of samples/data points, particularly for deep-water species). However, from a monitoring perspective, the main limitations concern the use of total ostracod assemblages (dead and living specimens) and their origin from a single sampling campaign, thus not accounting for seasonal species variability (Schmitz et al., 2025).

Therefore, future studies incorporating newly collected and more spatially balanced datasets, with a distinction between live and dead specimens and seasonal sampling, will be of great value to improve the species lists compiled in this work, as well as to validate and refine the species categorization in light of the Ostra-AMBI index. Additional information on physico-chemical parameters at sampling stations, in particular oxygen concentration, and the assessment of the source and quality of food on the seafloor would further improve our understanding of the ecological dynamics of benthic fauna, as documented for foraminifera by Lo Giudice Cappelli et al. (2019).

This is particularly true for ostracods, being more complex organisms than other bio-indicators as benthic foraminifera. According to Schmitz et al. (2025), ostracods may show more diverse and pronounced responses to environmental changes and disturbances, likely also related to their efficient mobility (Athersuch et al., 1989). For instance, in the Adriatic Sea, high energy levels or high sediment accumulation rates typical of submerged delta environments commonly hamper the colonization of autochthonous ostracods, whereas benthic foraminifera can tolerate such conditions (Barbieri et al., 2019).

In this regard, despite the explained limitations and the differences in behavior between ostracods and benthic foraminifera, the strong positive correlation in the Adriatic sub-dataset between Ostra-AMBI and Foram-AMBI ($R^2 = 0.75$; Fig. 5b) supports the combined future application of these indices to more effectively monitor environmental degradation over time. This integrated approach could also improve the comparison of present and past ecological conditions and the ecological quality Ratio (EQR) quantification by leveraging the well-documented ability of foraminifera to track organic enrichment (Alves Martins et al., 2019; de Jesus et al., 2020; Da Silva et al., 2022, among others) and the here proven sensitivity of ostracods to track TOC changes.

6. Conclusions

This proof-of-concept provides, for the first time, the assignment of 90 Mediterranean ostracod species to Ecological Groups, supporting and

strengthening the use of ostracods as bio-indicators of organic enrichment gradients and sinks in marine settings. This has been achieved by defining the weighted-averaging optimum and tolerance range to TOC of each species on an Adriatic calibration dataset composed of 214 samples, analyzed for the total assemblage by Bremner (1975).

The statistical modelling of species preferences about seafloor grain-size (sand percentage) and water depth, along with the basin-scale contextualization of the cumulative distribution of individual ostracod EGs, documents the need for a cross-disciplinary bio-sedimentological perspective to fully interpret fauna data in both the modern and past records.

Overall, the spatial patterns of Adriatic ostracod EGs clearly reflect the sediment routing system guided by the interaction between river inputs and the oceanographic regime, allowing the identification of different depositional settings along the sediment routing system and across bathymetric gradients from shallow to deeper environments, as well as the distinction between shallow-water (prodelta – Adriatic Mud Wedge) and deep-water organic sinks.

Specifically, the coastal belt (water depth < 10–15 m) and a large portion of the north-central Adriatic shelf are dominated by sensitive (EG I) and indifferent (EG II) species, whereas opportunists are almost absent. This community reflects interaction between river plumes and sea currents, which impairs the sedimentation of fine-grained TOC-enriched deposits. Fine-grained, TOC-enriched deposits of the Adriatic Mud Wedge, an elongate prodelta body of the Western Adriatic between the coastal belt and the sediment-starved shelf, are dominated by third-order opportunists (EG III) and, only secondarily, by indifferent species (EG II). The Adriatic slope and pits represent major organic sinks fed by lateral inputs, besides the surface productivity, that are colonized by opportunistic species (i.e., EG III–V).

The application of the Ostra-AMBI, an ostracod-based modified version of the AMBI index, on a testing dataset of 53 independent samples shows a positive and significant correlation to TOC, further highlighting the great potential of ostracods to track environmental degradation (i.e., organic enrichment) even along a relatively narrow TOC gradient and in the past record.

The observed positive relationship between Ostra-AMBI and Foram-AMBI provides a robust baseline for the future integrated use of these indices, while highlighting the importance of the integration of newly collected and spatially balanced datasets, including additional physico-chemical parameters, such as bottom-water oxygen concentration and indicators of food source and quality on the seafloor, to further improve the ecological interpretation of benthic assemblages.

Open research

The data analyzed in this study were originally published in Bremner (1975). A digitized subset containing the data required to reproduce the analyses is publicly available in Zenodo at <https://doi.org/10.5281/zenodo.20072782>.

The analysis scripts used in this study are available on Zenodo at <https://doi.org/10.5281/zenodo.20072837>.

CRediT authorship contribution statement

Amanda Vecchi: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Stefano Claudio Vaiani:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Fabrizio Frontalini:** Writing – review & editing, Validation, Supervision, Methodology. **Alessandro Amorosi:** Writing – review & editing. **Veronica Rossi:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2026.113928>.

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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