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Quantitative paleoecology in shallow-marine settings: the value of ostracods and foraminifers from the Holocene North Adriatic record

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Keywords

Sequence stratigraphy; Po Delta; prodelta; micropaleontology

Abstract

Benthic ostracods and foraminifers are commonly applied as paleoenvironmental indicators in shallow marine successions, ignoring that individual meiofaunal groups could provide distinct information. We aim to shed light on the distinct paleoecological record of benthic ostracods and foraminifers by analyzing the shallow marine Holocene succession of the Po Delta (Italy) in a sequence stratigraphic fashion. Multivariate elaborations connecting the modern North Adriatic reference set to fossil data allowed to investigate community dynamics, obtain quantitative estimates of (paleo-)environmental drivers and assess the

meiofaunal response to coastal and delta dynamics through time and space under the influence of allogenic and autogenic factors. Benthic ostracods and foraminifers easily discern transgressive (TST) and highstand (HST) systems tract, and also discriminate between locations at different distance from paleo-river mouths under highstand conditions. Specifically, community changes reflecting shifts in delta regimes at distal locations suggest that lobe-fringe deposits are more indicated for paleoenvironmental purposes. We emphasize that a deep knowledge of the analyzed datasets should drive the interpretation of multivariate outputs, as reconstructed values from significantly similar deposits could be inappropriate, and the lack of true modern analogs could reflect authentic differences in community composition, or either pitfalls in the modern reference set. Our results show that ostracods evidence depositional regimes determined by the interplay of sediment supply and hydrodynamic energy in relationship with the position from main river outlets; on the other hand, foraminifers highlight changes in riverine inputs in terms of organic matter. Our findings demonstrate that shallow marine benthic ostracods and foraminifers provide distinct but complementary paleoecological information, and their integration allows to achieve high-resolution reconstructions.

1. Introduction

Ostracods and foraminifers represent a main component of the marine benthos (Murray, 2006; Horne et al., 2012; Yasuhara et al., 2017). Characterized by similar size ranges (from a few microns to millimeters), short life cycles and mostly possessing calcareous hard shells that ensure high preservation potential in the sedimentary record, they form abundant communities on the seafloor (Gooday, 2001; Schellenberg, 2007).

Nevertheless, the taxonomic positions of benthic ostracods (multicellular crustaceans) and foraminifers (unicellular protists) highlight remarkable biological and paleoecological differences. Benthic ostracods swim relatively fast (a few $\text{cm}\cdot\text{s}^{-1}$), whereas foraminifers move very slowly (a few $\mu\text{m}\cdot\text{s}^{-1}$) or can even be sessile (Murray, 2001; Sutherland et al., 2011). Although benthic ostracods can be subject to long-distance transport due to natural events or anthropogenic activities (Faasse, 2013; Tanaka et al., 2018), the lack of a nauplius larval stage determines a low dispersal potential (Rodriguez-Lazaro and Ruiz-Muñoz, 2012). Conversely, the

45 global distribution of propagules banks was hypothesized to explain the greater dispersion of benthic
46 foraminifers even in coastal settings (Weinmann and Goldstein, 2017). Concerning the growing mechanism,
47 ostracods perform several moults and discarded valves are preserved in the sediment, whereas benthic
48 foraminifers mainly add successive chambers on single tests (Mesquita-Joanes et al., 2012; Hohenegger, 2018).
49 Other biological differences, such as reproduction mechanisms and feeding strategies, could account for
50 distinct structure and composition of assemblages (Yasuhara et al., 2012).

51 Comparing the (paleo-)ecological response of benthic ostracods and foraminifers may shed new light on the
52 interaction among species, community patterns and environmental parameters, especially in shallow-marine
53 areas, where the interplay of many environmental factors may lead to high temporal and spatial heterogeneity.
54 Since the application of the meiofauna as paleoecological indicator is rooted in the principle of taxonomic
55 uniformitarianism, the micropaleontological investigation of past shelves dynamics should ideally start from
56 modern reference datasets. Unfortunately, heterogeneity in measured parameters and taxonomic resolution
57 has commonly prevented the development of integrated meiofaunal distribution models. Studies performed
58 on Mediterranean shelves mostly deal with single groups (e.g., Goineau et al., 2015; Sciuto et al., 2015; Benito
59 et al., 2016) and the few works performed on both benthic ostracods and foraminifers aimed to identify
60 ecological patterns in response to anthropogenic pressure (e.g., Triantaphyllou et al., 2005; Pascual et al., 2008;
61 Salvi et al., 2015). As a consequence, even though benthic ostracods and foraminifers have been extensively
62 employed in late Quaternary paleoenvironmental reconstructions (e.g., Carboni et al., 2002; Flaux et al., 2013;
63 Cacciari et al., 2019), paleoecological information has been extracted from separate modern datasets (e.g.,
64 Breman, 1975; Jorissen, 1988; Mendes et al., 2004; Frezza and Carboni, 2009; Frezza and Di Bella, 2015) and
65 reviews (e.g., Athersuch et al., 1989; Murray, 2006; Horne et al., 2012). An integrated analysis of present-day
66 benthic ostracods and foraminifers performed on the North Adriatic river-influenced shelf (Barbieri et al., 2019)
67 revealed that these two groups have distinct distribution patterns driven by specific environmental factors (i.e.,
68 bathymetry, substrate grain-size and organic-matter fluxes). The distribution model could serve as a basis to

investigate and quantify the response of shallow-marine benthic communities to allogenic (sea-level oscillations) or autogenic (e.g., delta lobe switching) factors acting on river-influenced shelves. The well-constrained chronostratigraphic framework of its inland counterpart (Ciabatti, 1967; Stefani and Vincenzi, 2005; Amorosi et al., 2017; Campo et al., 2017; Giacomelli et al., 2018; Amorosi et al., 2019) makes the Po Delta-North Adriatic system an excellent venue where to analyze and weight up the response of benthic ostracod and foraminifer communities to deposition dynamics across the Holocene. Although some paleoenvironmental studies integrated marine benthic ostracods and foraminifers from upper Quaternary shallow-marine successions of the Mediterranean area (Amorosi et al., 2008; Fanget et al., 2013, 2016; Angue Minto'o et al., 2016), a critical comparison of these groups has never been performed.

In the present work, we describe and compare the vertical distribution patterns of benthic ostracods and foraminifers throughout the shallow-marine deposits of three cores from the Po Delta area along a N-S oriented transect, crossing two adjacent ancient delta lobes (Fig. 1). Specifically, we frame meiofauna quantitative data within two well-recognized sediment units: (i) the transgressive systems tract (TST), formed during the Holocene transgression, and (ii) the highstand systems tract (HST), deposited in response to deltaic progradation of two delta lobes (Volano and Goro) that were governed by distinct sediment dynamics under overall high progradation rates (Amorosi et al., 2020). We investigate the analogies with the modern North Adriatic benthic ostracod and foraminifer biofacies and quantitatively estimate trends in selected environmental parameters through the application of multivariate elaborations. Finally, we extract specific paleoecological indications from the two benthic groups, with the objective of comparing their resolution potential in fossil shelves subject to defined coastal and delta dynamics through time and space.

2. Stratigraphic and geomorphological framework

The Holocene sedimentary succession of the Po delta plain, developed on top of upper Pleistocene continental deposits, was formed in response to relative sea-level rise (Amorosi et al., 2017). The lower TST (9.5-8.5 cal kyr B.P.) consists of back-barrier deposits that mark the landward migration of a wave-dominated

93 estuarine system (Bruno et al., 2017). Above a wave ravinement surface, the upper TST (8.5-7.0 cal kyr B.P.)
94 includes a deepening-upward succession of transgressive barrier sands and offshore muds that represent the
95 deepest conditions within the entire Holocene succession (Amorosi et al., 2008). The boundary between
96 offshore and overlying prodelta facies (maximum flooding surface, MFS) records the turnaround from back-
97 stepping (TST) to prograding (HST) depositional systems, which took place in response to relative sea-level
98 stabilization (Amorosi et al., 2019), around 8-7 kyr B.P. (Vacchi et al., 2016). Stratigraphic condensation at the
99 MFS (Scarponi et al., 2017) was associated to persistently low accumulation rates, as clastic input was trapped
100 at the head of the estuary (Amorosi et al., 2019). Due to its poor lithological expression, the MFS has been
101 defined by the maximum value of the ratio between open-marine and fluvial-influenced benthic foraminifers,
102 and by ostracods shifts towards assemblages with predominant taxa tolerant to salinity oscillations (e.g.,
103 Amorosi and Colalongo, 2005; Amorosi et al., 2008).

104 Thick prodelta clays (up to ca. 20 m) capped by delta front sands record a complex pattern of coastal
105 progradation under highstand conditions (Amorosi et al., 2020). Steps in delta progradation were controlled by
106 distributary-channel avulsions and by the interplay with longshore currents. Geomorphological (i.e., preserved
107 sand ridges; Fig. 1), historical and archeological data indicate that one of the oldest wave-influenced (arcuate)
108 deltas in the northern coastal plain was fed by the Po di Ariano (the present-day Po di Goro) in the Early Roman
109 Age (Ciabatti, 1967; Fig. 1). Towards the south, the Volano lobe mostly prograded from the Roman to the Early
110 Medieval Age (Ciabatti, 1967; Correggiari et al., 2005a). In the second half of the 12th century (800-750 cal yr
111 B.P.), the Ficarolo river avulsion shifted the Po in a northern position. The increased activity of the Goro branch
112 caused the rapid outbuilding of a cusped Po delta lobe, up to the XVI century, whereas the Volano river mouth
113 remained relatively stable (Ciabatti, 1967). Later, the Fornaci branch (the modern Po di Levante, Fig. 1) became
114 the main outlet and formed the first lobate delta of the Po River, marking the onset of the Modern-Age delta
115 characterized by several supply-dominated lobes prograding at rates even $>100 \text{ m yr}^{-1}$ (Correggiari et al.,
116 2005a).

117 Modern prodelta lobes show comparable size to their inland buried counterparts, with thickness up to ca.
118 15 m and lateral extension of 10-20 km. Their stratigraphic relations reflect activity of individual river branches
119 during the last centuries (Correggiari et al., 2005a, 2005b).

120 **3. Materials and methods**

121 *3.1 Experimental design and data collection*

122 Micropaleontological analyses were performed on Holocene shallow-marine deposits from three cores (Fig.
123 1) drilled by wire-line perforation in the southern portion of the modern Po Delta plain. Cores 187S4 (44°57'49"
124 N, 12°15'09" E), EM13 (44°51'50" N, 12°17'05" E) and 205S9 (44°46'71" N, 12°15'05" E) are 35-54 m long and
125 were specifically selected with approximately north-south orientation, in order to capture along-strike
126 paleoecological variations across two adjacent lobes (i.e., Volano and Goro) with documented activity in
127 historical times. Specifically, cores 187S4 and 205S9 were recovered in proximity to distributary channels,
128 whereas core EM13 is located far from river mouths (Fig. 1). Sedimentological features and concise
129 paleontological characteristics have been illustrated by Amorosi et al. (2003, 2017) and Campo et al. (2017),
130 whereas the benthic foraminifer distribution of core 205S9 is reported in Dasgupta et al. (2020). In this work,
131 we present quantitative benthic ostracod and foraminifer data from cores 187S4 and EM13, along with the
132 quantitative ostracod distribution from core 205S9, and provide novel multivariate elaborations. The
133 stratigraphic model by Amorosi et al. (2020) and surficial geological map by Ciabatti (1967) were used as a
134 geological framework to compare the record of benthic foraminifers and ostracods from distinct, locally
135 outcropping, Holocene beach-ridge sediment bodies.

136 Micropaleontological assemblages were recovered from (i) TST barrier sands and offshore clays, and from
137 (ii) the stratigraphically expanded HST of the Volano and Goro delta lobes. The chronologic framework relies on
138 14 published radiocarbon dates integrated with one sample from core 187S4 (Table 1), dated at the Korea
139 Institute of Geoscience and Mineral Resources (KIGAM, Republic of Korea). Calibration of conventional ¹⁴C ages

140 was performed with Oxcal 4.2 (Bronk Ramsey, 2009) using the IntCal13 and Marine13 curves (Reimer et al.,
141 2013) and a ΔR value of 139 ± 28 yr (Langone et al., 1996).

142 A total of 258 sediment samples of approximately 100-150 g of dry weight (151 from core EM13, 58 from
143 core 205S9 and 49 from core 187S4) were selected for micropaleontological analyses and treated following the
144 standard procedure adopted in other reference works from the study area (e.g., Rossi and Vaiani, 2008).
145 Samples were dried at 60 °C, soaked overnight in 10% H₂O₂, water-screened with a 63 µm sieve and dried again
146 for > 8 hours. Samples including abundant, well preserved microfossils were dry-sieved at 125 µm and divided
147 using a microsplitter. At least 300 benthic foraminifers and 100 ostracod valves (with carapaces considered as
148 two valves) were counted from the >125 µm fraction, otherwise, all the tests or valves were considered. Both
149 adult and juvenile ostracod valves with morphological characters sufficiently developed to perform an
150 identification at species level were counted. Literature adopted for taxonomic identification and structure of
151 meiofaunal matrices are reported in Text S1 and Table S1.

152 3.2 Data matrices

153 Microfossil data matrices were treated prior to the application of multivariate analyses, following specific
154 criteria in order to keep the data comparable to the modern reference set based on total assemblages (Barbieri
155 et al., 2019). Clearly transported freshwater and brackish water taxa were removed from the ostracod dataset
156 and only samples including >20 valves were retained, in accordance with other works from marine settings
157 (Azzarone et al., 2020; Barbieri et al., 2019; Bassetti et al., 2010; Cronin et al., 1999). Samples including <300
158 individuals were removed from the benthic foraminifer matrix. The contribution of the fragile agglutinated
159 taxon *Eggerella scabra* was discarded. Selected taxa with similar ecological characteristics were gathered up to
160 the genus level in order to reduce the dataset dispersion and taxa with relative abundance >5% in at least one
161 sample were retained. We harmonized variables and taxonomic nomenclature in modern and fossil datasets,
162 as reported in Table S2.

163 3.3 Multivariate analyses

164 Fossil data were subject to the Hellinger transformation, i.e. the square root of the relative abundance was
165 computed (Legendre and Gallagher, 2001). Then, multivariate analyses were separately performed on benthic
166 ostracod and foraminifer matrices using the Euclidean distance in order to obtain the Hellinger distance, a
167 measure recommended to detect community changes in short environmental gradients that gives low weights
168 to rare species (Legendre and Gallagher, 2001; Legendre and De Cáceres, 2013).

169 The contribution of taxa to the composition of sample groups was assessed by means of a Euclidean-based
170 similarity percentage analysis (SIMPER – Clarke, 1993) carried out on Hellinger-transformed data, whereas
171 average values were derived from relative abundance data in order to produce more straightforward outputs.

172 Paleoecological conditions were assessed through the application of the analogue matching technique (AM;
173 Simpson, 2007). AM identifies the k -closest modern sites to each fossil assemblage, and the degree of analogy
174 is estimated through the computation of dissimilarity values between each fossil and modern sample. Fossil
175 assemblages were compared to the modern North Adriatic ostracod and foraminifer biofacies determined
176 through quantitative thresholds of environmental parameters presented in Barbieri et al. (2019), synthetized in
177 Table 2 (geographic distribution in Fig. 2). This comparison also allowed the interpretation of the
178 paleoecological record in relation to the amount of riverine input and relative distance from the main feeding
179 channel. A threshold value to determine whether fossil samples have an adequate counterpart in the modern
180 reference set should be applied considering selected percentiles (up to 20th) of the distribution of modern
181 dissimilarities (Simpson, 2007). We chose the 20th percentile as a critical threshold to discriminate analog from
182 non-analog samples. Although this is considered an adequate value (Jackson and Williams, 2004), it is a bit
183 higher than those traditionally employed in other studies (Overpeck et al., 1985; Anderson et al., 1989). This
184 threshold was selected due to intrinsic properties of the distance measure and heterogeneity of the ostracod
185 datasets. Specifically, the Hellinger distance allows to manipulate percentage data (as expressed in the modern
186 datasets) and produces optimal results when samples share variables with intermediate frequencies (Legendre

187 and Gallagher, 2001). Nevertheless, it locally emphasized taxonomic discrepancies (e.g., taxa not recorded in
188 the modern dataset, Table S2), increasing the dissimilarity between fossil and modern datasets and leading us
189 to choose the 20th percentile as the threshold value for ostracods (Hellinger distance = 0.616). This value was
190 also applied to benthic foraminifers (Hellinger distance = 0.520) to keep the data comparable. Where several
191 modern analogs were found for a fossil assemblage, we retained the four modern samples with the lowest
192 dissimilarity values.

193 The distance between cores and modern assemblages was visualized through a weighted Principal
194 Coordinates Analysis (wPCoA), where core samples were passively plotted as trajectories in stratigraphic order
195 onto the ordination space defined by modern assemblages. To further refine the paleoecological
196 characterization, predicted values of environmental drivers on the distribution of modern North Adriatic
197 assemblages (Barbieri et al., 2019) and the associated standard error were extracted from microfossil
198 assemblages and plotted against core stratigraphy using a generalized additive model, as it is used
199 automatically in the wPCoA computation (Goring et al., 2009; Oksanen et al., 2019).

200 All the statistical elaborations were carried out in the R environment (version 3.6.1; R Core Team, 2019)
201 using the packages “vegan” (Oksanen et al., 2019), “analogue” (Simpson and Oksanen, 2020), “mgcv” (Wood,
202 2011), and “ggplot2” (Wickham, 2016) for graphical outputs, whereas the SIMPER analysis was performed with
203 PAST (PAleontological STatistics; Hammer et al., 2001).

204 **4. Results**

205 *4.1.1 Composition of fossil ostracod assemblages and analogies with modern North Adriatic sites*

206 Relatively high dissimilarity values were recorded between fossil and modern ostracod datasets, mostly due
207 to peak frequencies (>70%) of dominant taxa in fossil assemblages, in contrast to the relatively homogeneous
208 modern North Adriatic communities (maximum relative abundances <55%; Barbieri et al., 2019). Moreover,

209 fossil ostracod assemblages displayed relatively high abundances of species not recorded in the modern fauna
210 (Table S2).

211 The SIMPER routine performed on ostracods revealed an overall average dissimilarity of 0.64 (Table 3).
212 *Leptocythere ramosa*, *Pontocythere turbida*, *Semicytherura incongruens*, *Loxoconcha* ex gr. *rhomboidea*,
213 *Palmoconcha turbida* and other *Semicytherura* account for most of the differences (cumulative contribution
214 >55%).

215 Abundant statistically significant analogs were found for ostracod assemblages of transgressive deposits.
216 These are mostly represented by samples of the shallow, sediment-starved northern Adriatic shelf (biofacies
217 O5, Table 2), updrift of the main sediment input from the Po River (Figs. 2–4, Table S3). Scattered modern
218 analogs are represented by samples located at either lower (biofacies O4) or higher (biofacies O6) depths, in
219 areas with low-moderate river input. The lowest Hellinger distance values of the entire database indicate high
220 similarity between transgressive ostracod assemblages from the three cores (Fig. 5A, Table S4). Transgressive
221 ostracod assemblages are composed of similar frequencies of *S. incongruens*, *Pontocythere turbida*, other
222 *Semicytherura* and *Loxoconcha* ex gr. *rhomboidea* (Table 3), locally associated to *Sagmatocythere napoliana*
223 and *Cytheretta* spp.

224 A relatively low number of significant modern analogs was detected for the Volano ostracod assemblages
225 (Table 4). Specifically, the few significant modern analogs found in core 205S9 belong to biofacies O4, located
226 along the northernmost or central Adriatic coasts, where low to moderate river input is recorded. A single
227 sample (13 m core depth) was considered similar to a modern sample from deep-water relict sands (biofacies
228 O6; Fig. 2). A larger number of fossil assemblages is represented by significant modern analogs in core EM13
229 (Table 4, Fig. 3). In the lower portion of core EM13, one sample at 23.69 m depth was significantly similar to a
230 modern site of the sediment-starved shelf (biofacies O5). The upper part of the lobe includes relatively high
231 amounts of significant modern analogs, represented by shallow-water, mid-Adriatic sites with moderate river
232 input on either sandy (biofacies O4) or muddy bottoms (biofacies O2). A moderate dissimilarity (0.48, Table S4)

233 was recorded between the Volano ostracod assemblages of cores 205S9 and EM13, with *Pontocythere turbida*,
234 *S. incongruens* and *Palmoconcha turbida* representing the most abundant species (Fig. 5A, Table 3).

235 Ostracod assemblages from the Goro lobe in core 187S4 are represented by abundant modern analogs
236 along the shallow Adriatic coast, under moderate sediment supply (biofacies O4, subordinately biofacies O2;
237 Fig. 4). Concerning the Goro lobe ostracods from core EM13 (Fig. 3), one sample at 12.27 m core depth was
238 considered significantly similar to a modern site immediately south of the Po Delta, at shallow water depth on
239 fine-grained sediment enriched in organic matter under high sediment supply (biofacies O1). Non-analog sites
240 (i.e., the most similar sites, but exceeding the threshold value defined by the 20th percentile of modern
241 dissimilarities) for this interval were attributed to samples from the same area (biofacies O1) or, occasionally,
242 from a southern position on muddy substrates (biofacies O2). Ostracod assemblages from the Goro deposits
243 were characterized by high dissimilarity (1.1, Fig. 5A), due to the dominance of *L. ramosa* in core EM13 (68.4%
244 on average). On the other hand, the Goro sediments from core 187S4 show an ostracod composition with
245 common *Pontocythere turbida*, *S. incongruens*, *Palmoconcha turbida*, associated with moderate frequencies of
246 *Xestoleberis* spp. and *Loxoconcha* ex gr. *rhomboidea* (Table 3).

247 4.1.2 Composition of fossil benthic foraminifer assemblages and analogies with modern North Adriatic sites

248 Fossil and modern foraminifer datasets are taxonomically homogeneous, with a single taxon showing
249 frequencies >5% in fossil samples, but not in modern ones (*Haynesina* spp.; Table S2).

250 The overall dissimilarity between sediment units from each core is 0.42, as revealed by the SIMPER analysis
251 (Table 5). Most of the differences among sediment units from the three cores (>55%) were determined by
252 *Ammonia parkinsoniana* – *Ammonia tepida*, *Aubignyna perlucida*, *Quinqueloculina* group, *Porosononion* ex gr.
253 *granosum* and *Triloculina* ex gr. *trigonula*, representing the most abundant taxa.

254 Benthic foraminifer assemblages from transgressive deposits showed statistically significant analogs in the
255 modern North Adriatic (Figs. 2-4, Table 4). Specifically, transgressive assemblages from cores 187S4 and 205S9

are significantly similar to modern sites along the Adriatic coast, north of the Po Delta, under negligible organic matter inputs and strong longshore currents (biofacies F3; Table 2). On the other hand, many significant modern analogs of EM13 transgressive benthic foraminifer assemblages occur on the Adriatic shelf at high water depth (biofacies F5). Relatively low dissimilarity values were recorded between transgressive benthic foraminifer assemblages (Fig. 5B, Table S4), due to similar frequencies of the most common taxa, namely the *Quinqueloculina* group (Table S2), *Porosononion* ex gr. *granosum*, *Adelosina* spp. and *Textularia agglutinans*. The higher dissimilarity of transgressive assemblages from core EM13 was determined by the higher contribution of *Buccella granulata*, *Neoconorbina terquemi*, *Rosalina bradyi* and *Asterigerinata mamilla* (Table 5).

Benthic foraminifer assemblages from the Volano lobe show abundant significant modern analogs in core 205S9, whereas a lower number of significantly similar modern sites was detected from core EM13 (Figs. 2, 3). In core 205S9, between 25.25 and 23.50 m core depths, significantly similar modern sites are mostly located on the shallow northern Adriatic coast with low organic matter levels (biofacies F3) and subordinately south of the Po Delta on substrates with moderate organic matter (biofacies F2). Upwards, significant modern analogs are positioned along the mid-Adriatic coast (biofacies F2) or in proximity of the Po and Adige delta outlets (biofacies F1) under moderate to high organic matter inputs, respectively. In core EM13, up to 21.06 m core depth, the Volano lobe shows a low number of significant modern analog sites along the northern and middle Adriatic coasts (biofacies F3, F2). In the upper portion of the lobe, benthic foraminifers show high similarity to modern sites in proximity or south of the Po and Adige delta mouths (biofacies F1, F2). The Volano benthic foraminifer assemblages show a moderate dissimilarity between locations (0.39, Fig. 5B, Table S4), mostly driven by the lower frequency of *A. parkinsoniana* – *A. tepida* in core EM13, associated to relatively high concentrations of *A. perlucida*, *Porosononion* ex gr. *granosum* and *Quinqueloculina* group (Table 5).

A large number of significant analogs was found for benthic foraminifer assemblages from the Goro lobe (Figs. 3, 4). Significantly similar modern analog sites for core 187S4 were identified along the shallow mid-

280 Adriatic coast (biofacies F2) or near the Po and Adige river mouths (biofacies F1) under moderate to high
281 organic matter fluxes, with alternating trends along the prodelta succession. Oscillations in modern analogs
282 were also detected for assemblages of core EM13, but with a dominance of significantly similar sites from the
283 central Adriatic coast (biofacies F2). A very low dissimilarity (0.24; Fig. 5B, Table S4) was recorded between
284 benthic foraminifer assemblages from the Goro lobe, due to similar frequencies of *A. parkinsoniana* – *A. tepida*
285 (Table 5).

286 4.2 Quantitative paleoecological data from the fossil record

287 The distance between modern and core samples in terms of species composition was visualized through the
288 wPCoA, which also allowed to estimate paleoecological changes in relation to environmental drivers in the
289 modern North Adriatic ostracod and foraminifer biofacies (Figs.6-8).

290 In core 205S9, the trajectory of ostracod assemblages crosses the multivariate space of sites from biofacies
291 O5-O4-O2, and then turns back (Fig. 6B). This reflects a decrease in paleobathymetry from transgressive to
292 highstand assemblages (ca. $25-15 \pm 1$ m water depth), with a scattered higher water depth value at the delta
293 front transition (ca. 21 ± 1 m), paralleled by a similar trend in sand concentration (from ca. $62 \pm 3\%$ to $26 \pm 4\%$,
294 up to $>50\%$ in the delta front transition; Fig. 6A; Table 6). The trajectory of transgressive benthic foraminifers
295 from core 205S9 crosses the area of biofacies F3, F2 and F1, mirroring a progressive decrease in water depth
296 (from ca. 19 ± 1 m to 11 ± 2 m) and a parallel increase in organic matter (ca. $0.8 \pm 0.3-2.7 \pm 0.6\%$).

297 The trajectory of fossil ostracod assemblages in core EM13 extends through the upper multivariate space,
298 approximately parallel to the first axis of ordination, crossing biofacies O5-O4-O2-O1 (Fig. 7B). The
299 reconstructed bathymetry and sand evenly decrease throughout the core, from transgressive (27 ± 1 m water
300 depth, $75 \pm 4\%$ sand) to highstand (13 ± 1 m water depth, $4 \pm 4\%$ sand) deposits. Benthic foraminifers show a
301 zig-zag trajectory distributed through biofacies F5-F3-F2-F1, reflecting an overall decrease in paleo-water depth

302 (ca. from 27 ± 1 m in TST to 11 ± 2 m in HST) and increase in organic matter (ca. from $0.6 \pm 0.3\%$ in TST to $2.5 \pm$
303 0.6% in HST), with localized oscillations throughout the succession (Fig. 7A).

304 The trajectory of ostracods from core 187S4 resembles that of core 205S9, with a back and forth trend that
305 crosses sites from biofacies O5-O4 and comes back towards biofacies O5 (Fig. 8B). In terms of
306 paleobathymetry, it reflects decrease in water depth from transgressive (ca. 24 ± 1 m) to highstand (ca. 11 ± 1
307 m) assemblages, with a few oscillations within the Goro lobe. Estimated sand concentration decreases from
308 transgressive barrier (ca. $71 \pm 4\%$) to lower prodelta (ca. $30 \pm 4\%$) deposits and increases in the upper portion
309 of the Goro lobe (>50%). The relatively short core trajectory of benthic foraminifers that crosses biofacies F3,
310 F2 and F1 reflects higher paleobathymetry in TST (ca. 18 ± 1 m) and almost stable, lower water depths
311 throughout highstand prodelta deposits (ca. 12 ± 1 m). Accordingly, organic matter increases from TST to HST,
312 with relatively constant values across the Goro lobe (0.8 ± 0.3 – $2.6 \pm 0.6\%$, Fig. 8A).

313 Differences between study cores and systems tracts can be visualized in a main effects plot (Fig. 9), where
314 the centroids of each sediment unit are distributed in a multivariate space. Ostracod and foraminifer plots
315 display the maximum distance on a systems tract-scale, with the centroids of transgressive assemblages being
316 clearly separated from the highstand (delta lobe) ones. Concerning the study cores, centroids of 187S4 and
317 205S9 plot relatively close to each other showing negative PCoA axes scores for ostracods and positive values
318 for foraminifers. Core EM13 is distinctly separated in both plots, with positive values of both axes in the
319 ostracod plot and negative scores in the foraminifer PCoA.

320 5. Discussion

321 5.1 Know your setting: assessing the resolution of shallow-marine benthic ostracod and foraminifer records

322 The high contrast between centroids of systems tract in the main effects plot indicates that both ostracods
323 and foraminifers efficiently discriminate transgressive from highstand deltaic deposits (Fig. 9). Abundant
324 opportunistic taxa in deltaic sediments (i.e., *L. ramosa*, *Palmoconcha turbida*, *Pontocythere turbida* and *A.*

325 *parkinsoniana* – *A. tepida*; Lachenal and Bodergat, 1988, 1990; Jorissen et al., 2018) drive the high dissimilarity
326 with transgressive assemblages. Ostracods and foraminifers also highlight differences between cores,
327 discriminating core EM13, which geographically lies between two delta lobes, from the markedly similar cores
328 187S4 and 205S9 located near paleo-river mouths (Figs. 1, 9). The unique character of core EM13 is ascribed to
329 transgressive assemblages with abundant epiphytic foraminifers, i.e., *B. granulata*, *N. terquemi*, *R. bradyi* and
330 *A. mamilla* (Langer, 1993; Sgarrella and Moncharmont Zei, 1993; Table 5), influencing the centroid position
331 towards negative values of axis 1 (Fig. 7). Ostracods show marked dissimilarities in progradational deltaic
332 deposits of core EM13, due to the dominance of the mud-lover *L. ramosa* (Barbieri et al., 2019) in the Goro
333 lobe that determine a shift towards positive axis 1 values characteristic of highstand delta lobes. Core EM13
334 also shows the highest faunal turnover (Figs. 6B-8B), suggesting that paleoecological variations are better
335 recorded at distal locations.

336 The comparison between modern and fossil assemblages with the AM technique allowed to obtain further
337 insights in the paleoenvironmental record provided by each faunal group. In transgressive assemblages, the
338 significant similarity with sites on the shallow North Adriatic relict sand barriers (biofacies O5, Figs. 2-5) is
339 based on sand-related ostracods, such as *Semicytherura* spp. (including *S. incongruens*), *Pontocythere turbida*,
340 *Loxoconcha* ex gr. *rhomboidea*, *S. napoliana* and *Cytheretta* spp. (Bonaduce et al., 1975; Frezza and Di Bella,
341 2015). Ostracods track the same deposit in the Po Delta subsurface and in the northern Adriatic shelf, as
342 biofacies O5 is developed on sediment-starved sand ridges shaped from the reworking of relict transgressive
343 sands (Trincardi et al., 1994; Correggiari et al., 1996). Therefore, reconstructed values of water depth reflect
344 the geographic position of the deposit on the shelf instead of representing a true modern analog (Figs. 6A-8A).
345 Concerning benthic foraminifers, the similarity to modern sites depleted in organic matter (biofacies F3, F5) is
346 mostly driven by organic matter-sensitive taxa (*Triloculina* ex gr. *trigonula*, *Adelosina* spp., *Cycloforina* spp.,
347 *Siphonaperta aspera*, *B. granulata*, *N. terquemi*, *R. bradyi* and *A. mamilla*; Jorissen, 2018), widespread in the
348 modern, shallow North Adriatic shelf (Barbieri et al., 2019).

349 In prograding delta lobes, the similarity with modern assemblages is driven by abundances of opportunistic
350 taxa, particularly *Palmoconcha turbida*, *Pontocythere turbida*, *S. incongruens* and *A. parkinsoniana* – *A. tepida*.
351 The presence of non-analog samples (Figs. 2-5) is ascribed to differences in assemblage composition or to
352 under-representative modern dataset.

353 The paucity of significant modern analogs in the Volano lobe is determined by the marked compositional
354 differences with modern assemblages. Ostracod and foraminifer taxa abundant in the Volano assemblages
355 show contrasting ecological characteristics. Specifically, sand-related ostracods (*Pontocythere turbida*,
356 *Loxoconcha* ex gr. *rhomboidea*, *S. napoliana*, *Semicytherura* spp.) are associated to taxa preferring fine-grained
357 (*Palmoconcha turbida*, *S. versicolor*) or mixed (*Callistocythere* spp.) substrates (Bonaduce et al., 1975; Arbull
358 et al., 2004; Frezza and Di Bella, 2015). Similarly, benthic foraminifer assemblages from the lower Volano lobe
359 of core EM13 include moderate frequencies of species tolerant (*A. parkinsoniana* – *A. tepida*, *A. perlucida*,
360 *Criboelphidium* ex gr. *granosum*) and sensitive (*Triloculina* ex gr. *trigonula*) to organic matter (Jorissen et al.,
361 2018). Such microfossil assemblages chronologically overlap the development of wave-influenced cusped and
362 arcuate deltas characterized by a marked longshore transport component (Ciabatti, 1967; Amorosi et al.,
363 2019). In wave-dominated deltas, fine-grained sediments supplied by rivers can be reworked, integrated within
364 the delta or transported alongshore by wave-induced longshore currents. Even under high fluvial discharge
365 regimes, waves can strongly affect delta dynamics in case of episodic high-energy events (Anthony, 2015). In
366 the microtidal Mediterranean Sea, an example is represented by the Ombrone delta, where muddy sediments
367 brought by episodic floods are transported alongshore by wave-induced currents on the long term (Tortora,
368 1999). As a result, benthic ostracod and foraminifer assemblages from the shallow Ombrone prodelta are
369 composed of species with divergent ecological preferences (Frezza and Carboni, 2009; Frezza and Di Bella,
370 2015). Therefore, the absence of significant analogs in the Volano lobe still provides significant information,
371 specifically, the absence of similar processes currently acting in the modern reference set. In fact, the high
372 amount of riverine sediment and organic matter supplied by the lobate Po Delta represents the main forcing

373 on the meiofaunal zonation in the present-day North Adriatic system, whereas along-shore transport mostly
374 operates in the southern Adriatic, where low fluvial inputs are recorded (Frignani et al., 2005; Barbieri et al.,
375 2019).

376 A particular case is represented by the paucity of significant modern analogs for the Goro ostracod
377 assemblages in core EM13, determined by the higher abundance of *L. ramosa* in fossil assemblages (ca. 70% vs.
378 ca. 50% in modern communities). *Leptocythere ramosa* is one of the most opportunistic marine ostracods:
379 abundant in transitional settings subject to mixed marine-freshwater contribution, it is strongly positively
380 correlated with organic matter and prefers fine-grained bottoms at shallow depth (Uffenorde, 1972;
381 Montenegro and Pugliese, 1996; Barbieri et al., 2019). To our knowledge, very high concentrations (>60%) are
382 not reported from present-day environments. In sedimentary successions, *L. ramosa* is abundant at the
383 transition from lagoonal to deltaic deposits or in proximal prodelta intervals (Carboni et al., 2002; Rossi, 2009).
384 Studies on mollusks have shown that higher concentrations of opportunistic taxa in marine fossil assemblages
385 are connected to rapid multiple invasions that are hardly preserved individually in the stratigraphic record
386 (Levinton, 1970; Pearson and Rosenberg, 1978). Considering the paleoecological affinity of mollusks and
387 ostracods (Amorosi et al., 2014; Rossi et al., 2018), we cannot rule out that *L. ramosa*-dominated assemblages
388 in core EM13 were determined by comparable processes. In such nearshore river-influenced settings severely
389 impacted by organic enrichments, the estimated paleoecological information is not necessarily incorrect as
390 opportunistic population dynamics could greatly affect the dissimilarity with modern assemblages.

391 Finally, the lack of sites in the modern dataset could lead to biased assignments, as for the topmost prodelta
392 ostracod assemblages of core 205S9. The similarity with a modern site on relict sands at ca. 30-40 m water
393 depth (biofacies O6) is documented by the high abundance of *Pontocythere turbida*. However, this taxon is
394 reported as dominant in the shallow prodelta, delta front, and shoreface zones of the Western Adriatic coast
395 (Ruggieri, 1952; Colalongo, 1969), which were not sampled in the dataset used in the present work (>8 m water
396 depth; (Breman, 1975).

397 5.2 *Meiofauna-based paleoecological reconstructions: transgressive deposits*

398 Bathymetric estimates from transgressive benthic ostracods and foraminifers show some discrepancies
399 (Figs.6A-8A). Based on analogies with modern Adriatic sites (see section 5.1), we consider more reliable the
400 values provided by benthic foraminifers, which indicate an average water depth of ca. 18 ± 1 m at cores 187S4
401 and 205S9, and of 26 ± 1 m for EM13 (Table 6), in accordance with its distal position (Fig. 1). Significant modern
402 analogs for transgressive ostracod assemblages indicate the onset of sediment-starved conditions in the whole
403 study area during the last phases of transgression (ca. 8.5-7.0 cal kyr B.P.; Bruno et al., 2017), as also supported
404 by low organic matter concentrations indicated by foraminifers (Figs. 6A-8A). Comparable foraminifer
405 assemblages are reported from shallow-water, coarse-grained bottoms with low concentrations of refractory
406 organic matter, such as relict deltaic deposits subject to high-energy conditions and sediment reworking
407 (Goineau et al., 2015).

408 Paleoecological insights retrieved from transgressive microfossil assemblages are consistent with the early
409 Holocene paleogeography, when a backstepping wave-dominated estuary occupied the modern Po coastal
410 plain (Bruno et al., 2017). At the estuary mouth, transgressive barriers were affected by high-energy wave
411 action and offshore deposits developed under a reduced sediment influx due to sediment trapping in the
412 estuarine system (Bruno et al., 2017; Amorosi et al., 2019).

413 5.3 *Meiofauna-based paleoecological reconstructions: highstand delta lobe deposits*

414 In prodelta successions, ostracods and benthic foraminifers provide similar water depth estimates, tracking
415 a major decrease in paleobathymetry from bottom to top (Figs. 6A-8A). Overall, benthic foraminifers show
416 more regular trends and suggest slightly shallower water depths than ostracods (13 ± 1 m and 15 ± 1 m on
417 average, respectively), but these differences fall within the range of the standard error, with a few exceptions
418 mostly connected to the lack of significant modern analogs (Figs. 2-4, 6-8). No significant paleobathymetric
419 differences are recorded at proximal (core 205S9, 187S4) and distal (core EM13) locations. The different driving

factors that govern benthic ostracod and foraminifer distribution in the marine realm may account for local discrepancies in water depth and meiofaunal zonation (see section 5.1) (Yasuhara et al., 2012; Barbieri et al., 2019). Under highstand conditions, approaching river outlets due to delta progradation are consistent with a decrease in water depth, as observed in modern deltaic systems (Lavoie et al., 2014; Bomer et al., 2019), including the Po Delta (Correggiari et al., 2005b; Bosman et al., 2020). The relatively stable paleobathymetry recorded in ca. 10 m-thick upper prodelta deposits is ascribed to the rapid accumulation of riverine material that resulted in the deposition of expanded prodelta successions, with abundant opportunistic benthic ostracods and foraminifers that benefitted from continental organic matter inputs (Goineau et al., 2012; Frezza and Di Bella, 2015). High organic matter concentrations estimated from benthic foraminifers (2.1 ± 0.4 on average; Figs. 6A-8A) mostly linked to degraded, continental organic material are in accordance with data from the major deltaic systems of the Mediterranean (Goineau et al., 2011).

5.3.1 Volano lobe

Organic matter levels reconstructed from benthic foraminifers reflect the development of delta lobes. The good chronological resolution at core locations 205S9 and EM13 documents an increase in organic matter after the demise of the Roman Empire, when the countryside was abandoned and channel regulation ended, causing widespread inland flooding (Stefani and Vincenzi, 2005). Unstable river regime and high discharge are confirmed by relatively high organic matter concentrations (Figs. 4A, 5A), likely of continental origin that is typically associated to proximal prodelta settings with dominant *A. tepida* – *A. parkinsoniana* (Goineau et al., 2015). Nevertheless, abundant riverine organic inputs hardly reached updrift, distal locations at that time, as confirmed by the lower concentrations in core EM13 (1.5 ± 0.4 % vs. 2.1 ± 0.4 % in 205S9; Table 6).

High sand concentrations (Figs. 6-7A; Table 6) support considerable influence by longshore currents at both study sites, in accordance with the arcuate morphology of the Volano lobe (Fig. 1). In updrift position (EM13), a first phase of low sediment supply far from river outlets is suggested by analogy with ostracod assemblages on relict sands. After ca. 1.6-1.5 kyr B.P., ostracods track the approaching Volano lobe, with persistent longshore

444 currents and low to moderate sediment supply at shallow water depth (Figs. 3, 7). The increase of ostracod-
445 derived sand concentration in the upper prodelta and within delta front transition deposits at proximal
446 locations (core 205S9) is consistent with higher hydrodynamic conditions at the transition to the delta front in
447 microtidal Mediterranean deltas (Lavoie et al., 2014; Ciampalini et al., 2015).

448 High sand concentration estimated from ostracods that highlight strong hydrodynamic conditions, along
449 with increasing organic matter levels traced by benthic foraminifers, efficiently document the development of
450 the Volano lobe. The cusped morphology provides evidences for wave influence, nevertheless, abundant
451 sediment supply from the Po River is recorded by sediment geochemistry and high sedimentation rates
452 (Amorosi et al., 2020).

453 5.3.2 Goro lobe

454 Strong sediment and organic matter inputs of continental origin in proximity to a river mouth are consistent
455 with benthic foraminifers throughout prodelta deposits, both at the proximal location of core 187S4 and at the
456 distal EM13 site (Table 6, Figs. 7-8A).

457 In core 187S4, similarities with modern ostracod communities and high estimated sand concentrations
458 suggest an important longshore drift component, whereas an abundance of fine-grained sediments and
459 possible oxygen deficiency are recorded at the downdrift location (Figs. 3-4, 7-8).

460 The “Ficarolo avulsion” in the XII century AD caused a major switch from the Volano to Goro delta lobes.
461 This event is recorded by localized low organic matter levels from benthic foraminifers, without significant
462 associated paleobathymetric variations (Fig. 7A). The onset of the Goro lobe occurred at low water depth (<15
463 m), possibly due to decreasing accommodation after the progradation of the downdrift Volano lobe
464 (Correggiari et al., 2005a). Afterwards, the increased fluvial discharge in response to the late Middle Ages
465 climatic instability (including the Little Ice Age) and anthropogenic activity that led to the major Po delta lobe
466 outbuilding (Veggiari, 1990; Stefani and Vincenzi, 2005) is documented as changes in sediment dynamics by

ostracods (biofacies O1), which suggest increased riverborne sediment supply. Structure and composition of ostracod communities suggest unstable environmental conditions in a mud-dominated, shallow-marine environment subject to enrichment in continental organic matter, in accordance with the accumulation of thick flood layers that promoted the rapid progradation of the Goro lobe (Correggiari et al., 2005b). At seaward locations, extremely high sediment and organic-matter supplies are recorded by mud-belt microfossil assemblages (Rossi and Vaiani, 2008; Rossi, 2009; Barbieri et al., 2017) responding to both refractory and labile organic matter of continental and marine origin, respectively (Diz et al., 2006; Mojtahid et al., 2009; Goineau et al., 2012).

6. Conclusions

Integrated analyses of benthic ostracods and foraminifers from the marine Holocene succession of the Po Delta provide the opportunity to assess the paleoecological information recorded by individual microfossil groups in past river-influenced shelves. The comparison with the modern North Adriatic reference set through multivariate analyses revealed to be a powerful tool for investigating meiofaunal dynamics in relation to coastal and deltaic evolution. Specifically, we reconstructed and connected three environmentally significant parameters (water depth, sand and organic matter concentrations) that allow to characterize delta dynamics in shallow-marine, river-influenced settings.

- We demonstrated that benthic ostracods and foraminifers discriminate transgressive from highstand units. Furthermore, microfossils allow to identify locations at different distance from paleo-river mouths. Particularly, lobe-fringe deposits seem to be more suitable for paleoecological studies, as the highest faunal turnover in response to major changes in delta regimes is recorded distally.
- We stress that an extensive knowledge of the modern reference set should drive a critical interpretation of (non-)analogies with fossil assemblages. Significant modern analogs could mirror non-true environmental conditions (e.g., estimated water depth from transgressive relict ostracod samples). On the

other hand, the lack of significant modern analogs can be important, as in our study reflects wave-influenced deltaic conditions not recorded in the modern dataset. However, other factors, such as population dynamics and limitations in the modern reference set may also influence the detected paleoecological information.

- We show the complementarity of marine benthic ostracods and foraminifers as proxies for high-resolution paleoecological reconstructions in river-influenced successions. Ostracods provide insights into depositional regimes, furnishing an overview of bottom-water conditions in terms of sediment supply, hydrodynamic energy and, locally, oxygen conditions. Transgressive ostracod assemblages indicate sediment starvation, whereas highstand ostracods reflect position of the study site in relationship with the river mouth in the three-dimensional space (along-dip and along-strike) and delta regimes. Benthic foraminifers discriminate localized transgressive paleoenvironmental conditions and provide information about highstand changes in riverine input in terms of organic matter, in relationship with the position from river mouths.

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789

Core	Sample depth (m)	Dated material	Conventional 14C age (yr B.P.)	Calibrated age 2σ range (yr B.P.)	Calibrated age mean (yr B.P.)	σ	Laboratory	References
187 S4	25.45	Peat	8020 ± 70	9035–8635	8875	115	Beta analytic (FL, USA)	Sheet 187, Geological Map of Italy at 1:50,000 scale
187 S4	20.70	Shell fragments	1590 ± 24	1310–1185	1270	25	KIGAM (Korea)	This study
EM13	10.90	Shell	840 ± 40	650–510	580	40	KIGAM (Korea)	Amorosi et al., 2017
EM13	17.50	Wood	1060 ± 30	1055–925	975	35	KIGAM (Korea)	Amorosi et al., 2017
EM13	22.65	Shell	1900 ± 40	1700–1420	1570	50	KIGAM (Korea)	Amorosi et al., 2017
EM13	26.75	Wood	8040 ± 50	9090–8715	8900	100	KIGAM (Korea)	Amorosi et al., 2017
EM13	29.00	Peat	8500 ± 50	9545–9440	9500	30	KIGAM (Korea)	Amorosi et al., 2017
EM13	32.00	Wood	9080 ± 50	10385–10175	10250	50	KIGAM (Korea)	Amorosi et al., 2017
205 S9	8.40	Organic clay	2013 ± 57	1560–1285	1425	70	ENEA (Italy)	Amorosi et al., 2003
205 S9	22.40	Shell	2000 ± 40	1800–1570	1680	60	KIGAM (Korea)	Campo et al., 2017
205 S9	25.30	Shell	6440 ± 50	7225–6950	7080	70	KIGAM (Korea)	Campo et al., 2017
205 S9	26.95	Shells / Lentidium	7975 ± 30	8382–8192	8298	50	Keck-CCAMS (CA., USA)	Scarponi et al., 2013
205 S9	26.95	Shells / Varicorbula	8075 ± 30	8501–8316	8398	45	Keck-CCAMS (CA., USA)	Scarponi et al., 2013
205 S9	31.20	Plant fragments	9500 ± 80	11,110–10,570	10,840	160	ETH (Switzerland)	Amorosi et al., 2003
205 S9	35.30	Wood	18,830 ± 140	23,035–22,410	22,710	165	ETH (Switzerland)	Amorosi et al., 2003

791

792 **Table 1** – List of radiometric ages.

793

Benthic group	Modern biofacies	Color	Key taxa	Abiotic parameters' mean values				Geographic distribution	Environmental features
				Depth (m)	Sand (%)	Organic matter (%)	CaCO ₃ (%)		
Ostracods	O1		<i>Palmoconcha turbida</i> , <i>L. ramosa</i> , other <i>Leptocythere</i>	11.7	6.3	3.9	21.8	A few km south of the Po Delta	High sediment and organic matter supply determining recurrent oxygen deficiency at shallow depth
	O2		<i>S. incongruens</i> , <i>Palmoconcha turbida</i>	17.0	4.9	1.1	32.1	Adige river mouth; South of the Po Delta	Moderate sediment supply at intermediate water depth
	O3		<i>C. neapolitana</i> , <i>L. ramosa</i> , <i>S. versicolor</i>	27.5	2.2	1.4	28.1	Mud belt	High sediment and organic matter supply south of the feeding mouths at moderate water depth
	O4		<i>S. incongruens</i> , <i>Pontocythere turbida</i> , <i>Palmoconcha turbida</i> , <i>Xestoleberis</i> spp.	12.3	51.9	0.5	50.4	Along the coast, North and South of the Po Delta	Low to moderate sediment supply, sandy substrates with high CaCO ₃ subject to strong longshore currents at shallow depth, outside of the main feeding mouths influence
	O5		<i>S. incongruens</i> , <i>L. tumida</i> , <i>Cytheretta</i> spp., <i>Aurila</i> spp., <i>Semicytherura</i> spp., <i>L. neapolitana</i>	24.2	75.8	0.5	49.6	Shallower relict sands	Sediment starvation, very sandy substrate with high CaCO ₃ at moderate water depth
	O6		<i>Pontocythere turbida</i> , <i>Semicytherura</i> spp., <i>Aurila</i> spp.	35.0	66.4	0.7	30.6	Deeper relict sands	Sediment starvation, sandy substrate at high water depth
	O7		<i>C. neapolitana</i> , <i>Semicytherura</i> spp., <i>Callistocythere</i> spp., <i>Pterigocythereis</i> spp., <i>C. edwardsii</i> , <i>Cytheropteron</i> spp., <i>Bosquetina</i> spp.	34.4	32.7	0.7	32.5	Fine-grained shelf	Low sediment supply on mixed substrates at high water depth
Foraminifers	F1		<i>A. parkinsoniana</i> - <i>A. tepida</i> , <i>N. turgida</i>	14.3	4.2	3.3	26.5	In proximity to the Po and Adige river mouths	High organic matter supply near the main feeding mouths
	F2		<i>A. parkinsoniana</i> - <i>A. tepida</i> , <i>A. perlucida</i> , <i>Criboelphidium ex gr. granosum</i> , <i>Criboelphidium ex gr. poeyanum</i>	16.0	13.5	0.8	29.5	Along the coast, South of the Po Delta	Moderate organic matter supply at shallow water depth
	F3		<i>Q. seminula</i> , <i>Adelosina</i> spp., <i>T. trigonula</i> , other <i>Quinqueloculina</i> , <i>Criboelphidium ex gr. granosum</i> , <i>Criboelphidium ex gr. poeyanum</i>	14.5	49.7	0.6	62.0	Along the coast, North of the Po Delta	Low organic matter supply, strong longshore currents, high CaCO ₃ at shallow depth updrift of the main feeding sources
	F4		<i>N. turgida</i> , <i>V. bradyana</i>	30.7	2.9	1.5	28.6	Mud belt	High organic matter supply south of the feeding mouths at moderate water depth
	F5		<i>B. granulata</i> , <i>A. beccarii</i> , <i>A. mamilla</i> , <i>C. lobatulus</i> , <i>N. terquemi</i> , <i>R. bradyi</i>	31.6	59.7	0.6	36.8	Shelf	Low organic matter supply at high water depth

795 **Table 2** - List of the modern North Adriatic biofacies defined in Barbieri et al. (2019) through thresholds of
796 environmental variables. Modern biofacies are used in this work as reference for the comparison with fossil
797 assemblages.

798

Taxon	Aver age dissi m.	Contrib ution %	Cumulat ive %	Mean abundance						
				TST			HST - Volano lobe		HST - Goro lobe	
				187 S4	205 S9	EM13	205 S9	EM13	187 S4	EM13
<i>Leptocythere ramosa</i>	0.12	18.19	18.19	2.24	0.86	0.43	2.59	6.52	3.89	68.37
<i>Pontocythere turbida</i>	0.07	10.75	28.95	18.99	18.05	19.71	27.32	22.43	34.72	3.86
<i>Semicytherura incongruens</i>	0.06	10.09	39.04	20.44	30.59	24.95	15.18	16.68	15.08	2.73
<i>Loxoconcha ex gr. rhomboidea</i>	0.05	7.55	46.59	14.52	10.67	17.86	1.65	3.22	5.44	0.00
<i>Palmoconcha turbida</i>	0.04	6.81	53.39	1.92	1.62	1.48	10.91	9.98	9.27	11.71
Other <i>Semicytherura</i>	0.04	5.50	58.89	13.85	14.76	15.06	7.23	7.05	5.37	0.24
<i>Sagmatocythere versicolor</i>	0.03	5.25	64.14	2.24	2.59	1.07	3.41	7.46	2.46	0.00
<i>Sagmatocythere napoliana</i>	0.03	4.34	68.48	2.24	3.63	9.94	0.31	1.83	0.00	0.00
<i>Xestoleberis</i> spp.	0.03	4.04	72.52	1.76	1.44	0.41	3.38	3.96	6.33	2.15
<i>Hiltermannicythere turbida</i>	0.02	3.60	76.11	1.76	5.71	1.00	0.31	0.32	0.54	7.51
<i>Hiltermannicythere sphaerulolineata</i>	0.02	3.49	79.60	2.40	0.81	1.09	5.33	3.82	3.93	0.86
<i>Neocytherideis subulata</i>	0.02	3.10	82.70	0.00	0.52	0.36	3.87	2.52	2.66	1.25
<i>Carinocythereis whitei</i>	0.02	2.88	85.58	0.79	1.33	0.34	3.53	0.87	1.02	0.45
<i>Leptocythere bacescoi</i>	0.02	2.69	88.27	0.48	2.01	0.00	2.31	2.27	1.97	0.00
<i>Loxoconcha rubritincta</i>	0.01	2.25	90.53	0.96	1.04	0.00	1.86	0.00	1.41	0.00
<i>Loxoconcha</i> aff. <i>L. bonaducei</i>	0.01	2.01	92.54	0.48	0.00	1.43	0.97	1.78	0.08	0.00
<i>Callistocythere</i> spp.	0.01	1.84	94.37	1.59	1.62	0.70	0.76	0.35	1.94	0.00
<i>Cytheretta</i> spp.	0.01	1.71	96.08	7.94	0.00	0.20	0.44	0.00	0.00	0.00
<i>Hemicytherura</i> spp.	0.01	1.30	97.38	0.00	0.29	0.00	0.96	0.83	0.33	0.00
Other <i>Leptocythere</i>	0.01	0.80	98.19	0.00	0.00	0.24	0.31	0.87	0.00	0.00
<i>Pontocypris</i> spp.	0.00	0.71	98.90	0.00	0.00	0.14	0.00	1.08	0.00	0.00
<i>Paracytheridea</i> spp.	0.00	0.62	99.52	2.07	0.00	0.20	0.00	0.29	0.16	0.00
<i>Aurila</i> spp.	0.00	0.30	99.82	0.00	0.57	0.14	0.13	0.00	0.11	0.00
<i>Bosquetina</i> group	0.00	0.13	99.95	0.00	0.00	0.22	0.00	0.11	0.00	0.00
<i>Cytheridea neapolitana</i>	0.00	0.05	100.00	0.00	0.29	0.00	0.00	0.00	0.00	0.00

799

800 **Table 3** - Results of the SIMPER analyses performed on sediment units within each core, on Hellinger-
801 transformed ostracod data, with mean abundances expressed in percentage form. Grey cells evidence
802 characteristic mean frequencies of taxa with a marked paleoecological significance for each study interval.
803 Overall average dissimilarity: 0.64.

804

		Core	Ostracods	Foraminifers
TST		205S9	100.0%	100.0%
		EM13	81.3%	100.0%
		187S4	100.0%	100.0%
HST	Volano lobe	205S9	25.0%	90.6%
		EM13	38.9%	55.7%
	Goro lobe	187S4	69.0%	93.8%
		EM13	6.0%	100.0%

805

806 **Table 4** - Relative abundance of significant modern analogs per unit based on the four most similar modern
807 sites.

808

Taxon	Average dissim.	Contrib ution %	Cumulat ive %	Mean abundance						
				TST			HST - Volano lobe		HST - Goro lobe	
				187 S4	205 S9	EM13	205 S9	EM13	187 S4	EM13
<i>Ammonia parkinsoniana</i> - <i>A. tepida</i>	0.11	25.85	25.85	15.61	11.42	3.94	57.49	36.50	63.67	62.73
<i>Aubignyna perlucida</i>	0.03	8.07	33.92	2.82	1.28	0.00	6.59	11.09	5.98	17.21
<i>Quinqueloculina</i> group	0.03	7.62	41.54	14.11	15.82	17.34	4.91	8.05	4.61	1.03
<i>Porosononion</i> ex gr. <i>granosum</i>	0.03	7.41	48.95	10.68	13.76	12.54	3.56	10.49	3.49	9.22
<i>Triloculina</i> ex gr. <i>trigonula</i>	0.03	6.73	55.68	5.56	8.44	14.20	1.00	3.95	1.71	0.16
<i>Nonionella turgida</i>	0.02	5.50	61.17	0.90	1.59	0.40	1.99	4.55	1.10	0.17
<i>Ammonia beccarii</i>	0.02	4.90	66.07	1.51	3.81	2.32	3.78	0.44	1.04	1.00
<i>Textularia agglutinans</i>	0.02	4.76	70.83	8.03	4.54	4.75	1.06	1.88	0.77	0.00
<i>Haynesina</i> spp.	0.02	4.76	75.60	2.37	3.03	0.47	6.37	3.44	6.16	1.29
<i>Adelosina</i> spp.	0.02	4.00	79.60	9.79	7.26	6.74	1.89	3.33	1.89	1.15
<i>Criboelphidium</i> ex gr. <i>poeyanum</i>	0.01	3.29	82.89	7.29	5.08	2.81	3.91	2.04	4.06	3.31
<i>Elphidium advenum</i>	0.01	2.86	85.75	4.59	5.81	2.50	1.31	1.07	0.66	0.09
<i>Asterigerinata mamilla</i>	0.01	2.66	88.40	0.00	0.00	3.66	0.00	1.52	0.00	0.00
<i>Rosalina bradyi</i>	0.01	2.53	90.93	2.55	0.29	5.29	0.20	1.04	0.10	0.00
<i>Neoconorbina terquemi</i>	0.01	2.27	93.20	0.00	0.00	5.44	0.00	0.74	0.00	0.00
<i>Buccella granulata</i>	0.01	2.23	95.43	1.94	2.13	6.09	0.37	0.38	0.21	0.09
<i>Quinqueloculina seminula</i>	0.01	1.88	97.31	0.74	3.29	2.68	1.39	1.58	1.24	2.04
<i>Elphidium crispum</i>	0.01	1.37	98.68	1.79	1.50	1.24	0.41	0.23	0.19	0.00
<i>Reussella spinulosa</i>	0.00	0.60	99.28	0.30	0.00	0.16	0.03	0.42	0.03	0.00
<i>Cassidulina carinata</i>	0.00	0.32	99.60	0.15	0.00	0.00	0.15	0.01	0.11	0.05
<i>Bulimina marginata</i>	0.00	0.20	99.81	0.00	0.00	0.00	0.00	0.01	0.13	0.14
<i>Cibicoides lobatulus</i>	0.00	0.19	100.00	0.00	0.00	0.38	0.02	0.04	0.03	0.00
<i>Valvulineria bradyana</i>	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

810

811 **Table 5** - Results of the SIMPER analyses performed on sediment units within each core, on Hellinger-
812 transformed benthic foraminiferal data, with mean abundances expressed in percentage form. Grey cells
813 evidence characteristic mean frequencies of taxa with a marked paleoecological significance for each study
814 interval. Overall average dissimilarity: 0.42.

815

			Ostracods				Benthic foraminifers			
			Water depth (m)		Sand concentration (%)		Water depth (m)		Organic matter (%)	
			Estimated value	S.E.	Estimated value	S.E.	Estimated value	S.E.	Estimated value	S.E.
205S9	TST		23.3	1.1	58.3	3.5	18.4	1.3	0.8	0.3
	HST	Volano prodelta	15.3	1.3	35.1	3.8	13.1	1.5	2.0	0.4
		Volano delta front	14.8	1.2	42.0	3.8	12.2	1.5	2.2	0.4
EM13	TST		22.3	1.2	67.9	4.1	26.0	1.3	0.6	0.4
	HST	Volano prodelta	15.0	1.2	31.7	3.9	14.7	1.3	1.5	0.4
		Goro prodelta	14.0	1.3	3.6	4.3	12.2	1.5	2.3	0.4
187S4	TST		20.2	1.0	62.7	3.8	17.6	1.3	0.9	0.3
	HST	Goro prodelta	15.0	1.2	42.8	3.9	12.4	1.4	2.1	0.4

818 **Table 6** – Average values of estimated parameters *per* study unit within each core and associated standard
819 error (S.E.), considering only samples represented by significant modern analogs.

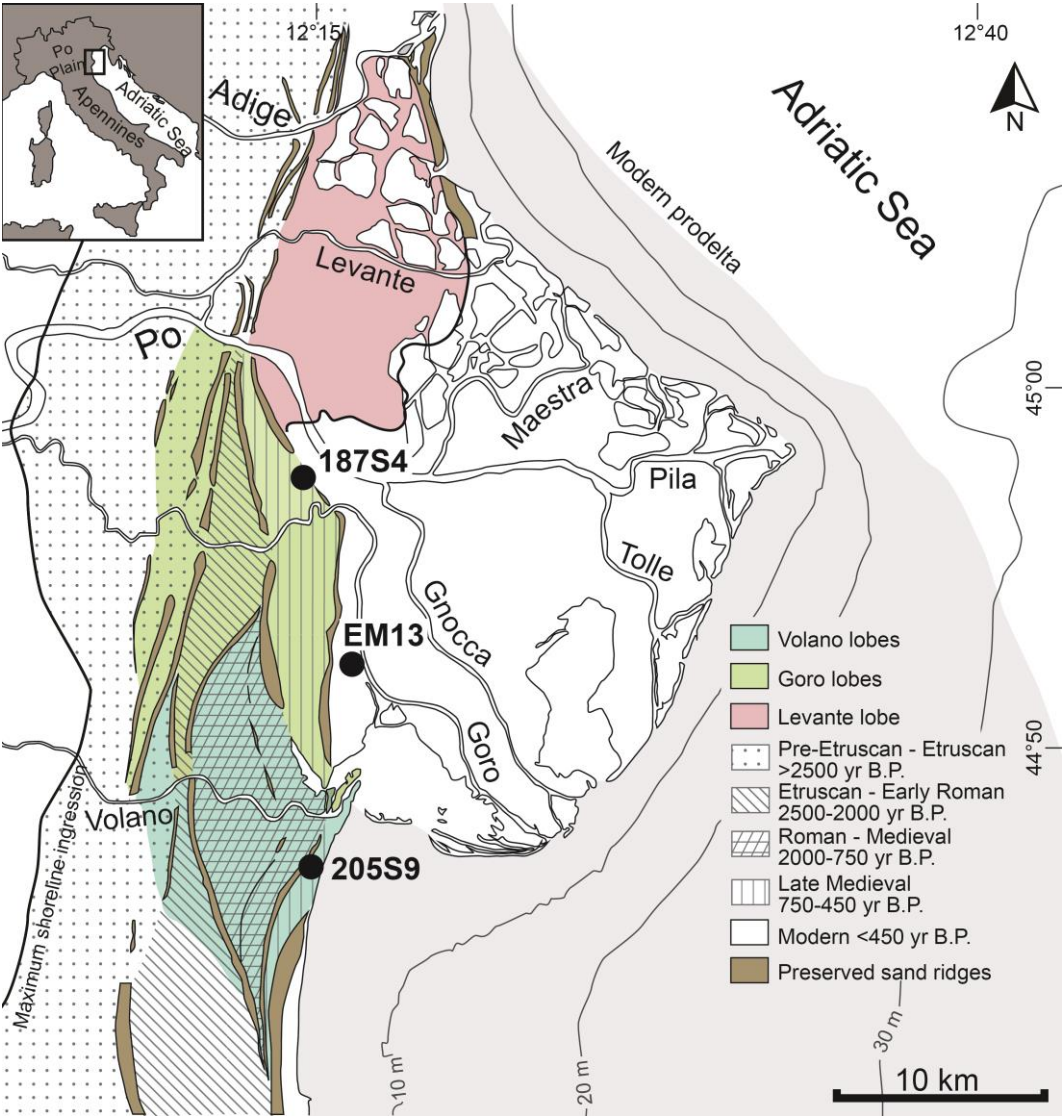


Figure 1 – Location of the three study cores and extension of Po Delta lobes based on preserved onshore sand ridges (from Ciabatti, 1967). Maximum shoreline ingression from Bruno et al. (2017), seaward extent of the modern prodelta from Correggiari et al. (2005a).

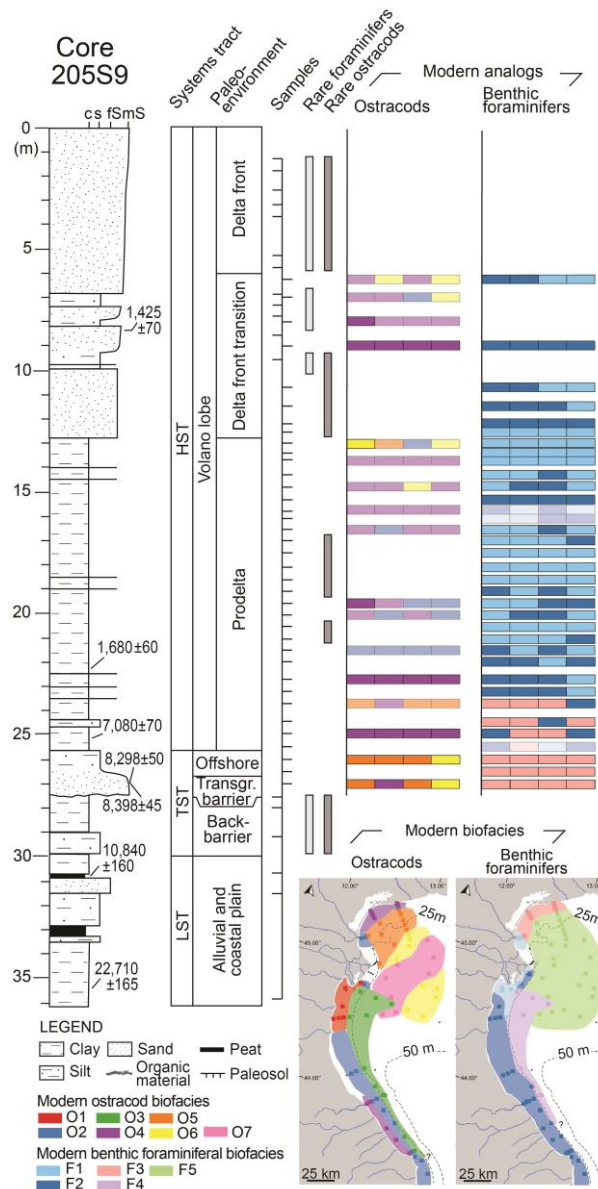


Figure 2 – Stratigraphy and modern analogs for benthic ostracods and foraminifers of core 205S9. On the right of the stratigraphic log, ages are reported as calibrated years B.P. Samples included in multivariate ordinations on the right of the sample column; on the left, samples inspected for quantitative analyses, but including a poor fauna. Significant modern analogs are reported in bold colors, whereas non-significant analogs, up to the fourth most similar sample, are reported in shaded tones. Colors are in accordance with modern biofacies defined in Barbieri et al. (2019), whose distribution is reported on the bottom of the figure.

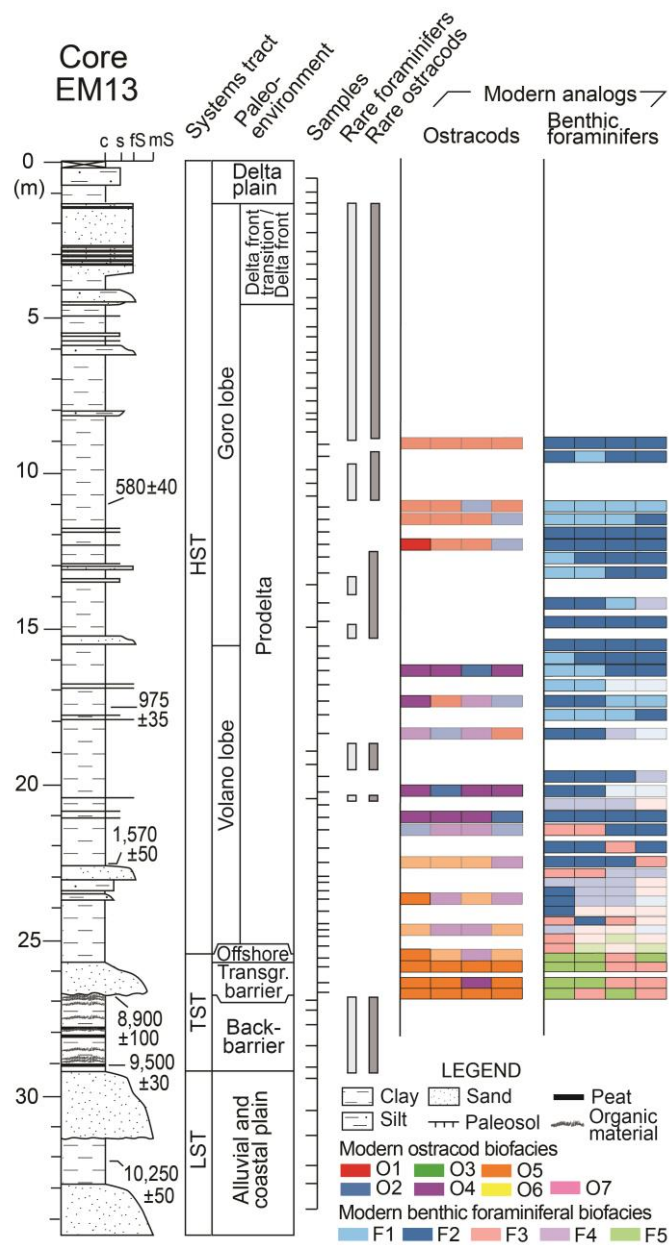


Figure 3 - Stratigraphy and modern analogs for benthic ostracods and foraminifers of core EM13. On the

right of the stratigraphic log, ages are reported as calibrated years B.P. For additional information, including the

distribution of the modern biofacies, the reader is invited to refer to Fig. 2.

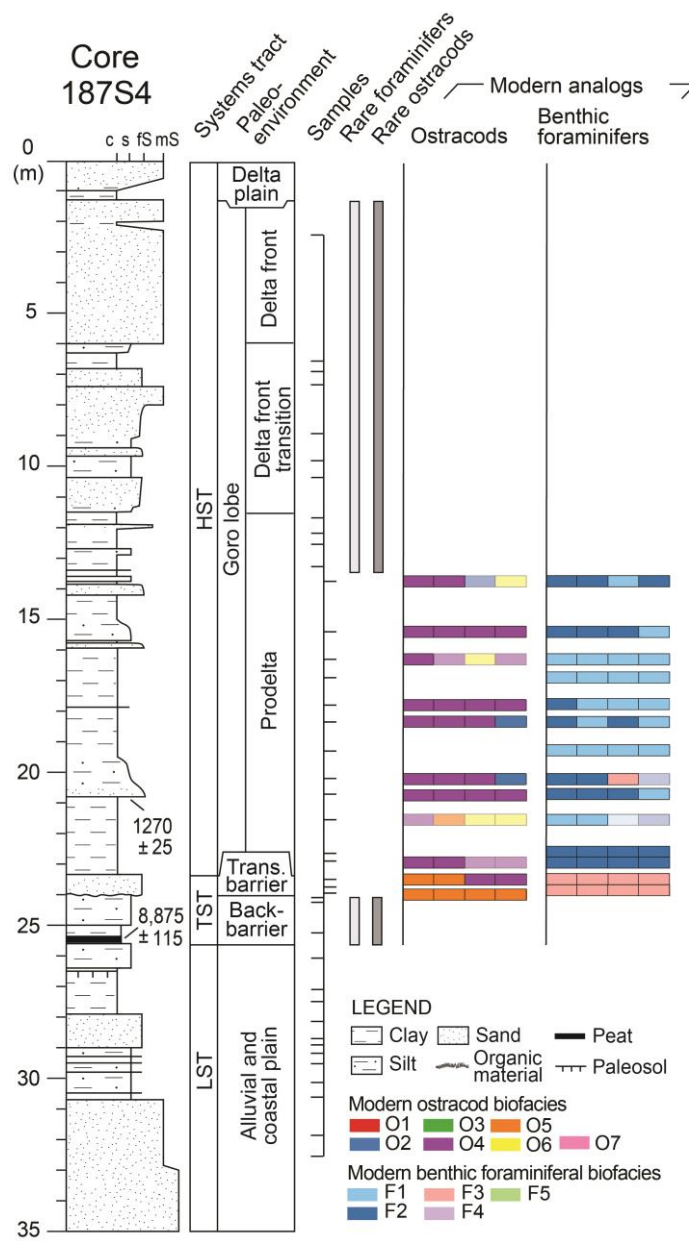
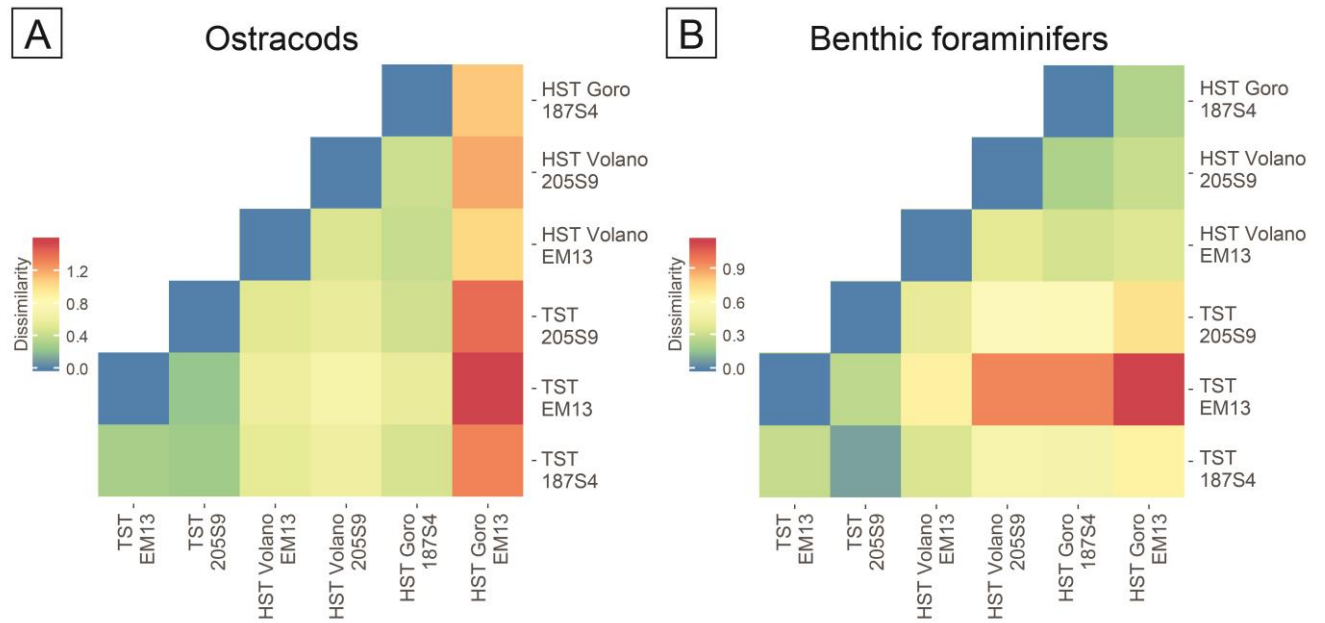


Figure 4 - Stratigraphy and modern analogs for benthic ostracods and foraminifers of core 187S4. On the right of the stratigraphic log, ages are reported as calibrated years B.P. For additional information, including the distribution of the modern biofacies, the reader is invited to refer to Fig. 2.



841

842 **Figure 5** – Graphic display of benthic ostracod (a) and foraminifer (b) dissimilarity matrices for transgressive

843 and highstand units of the Volano and Goro lobe in each core.

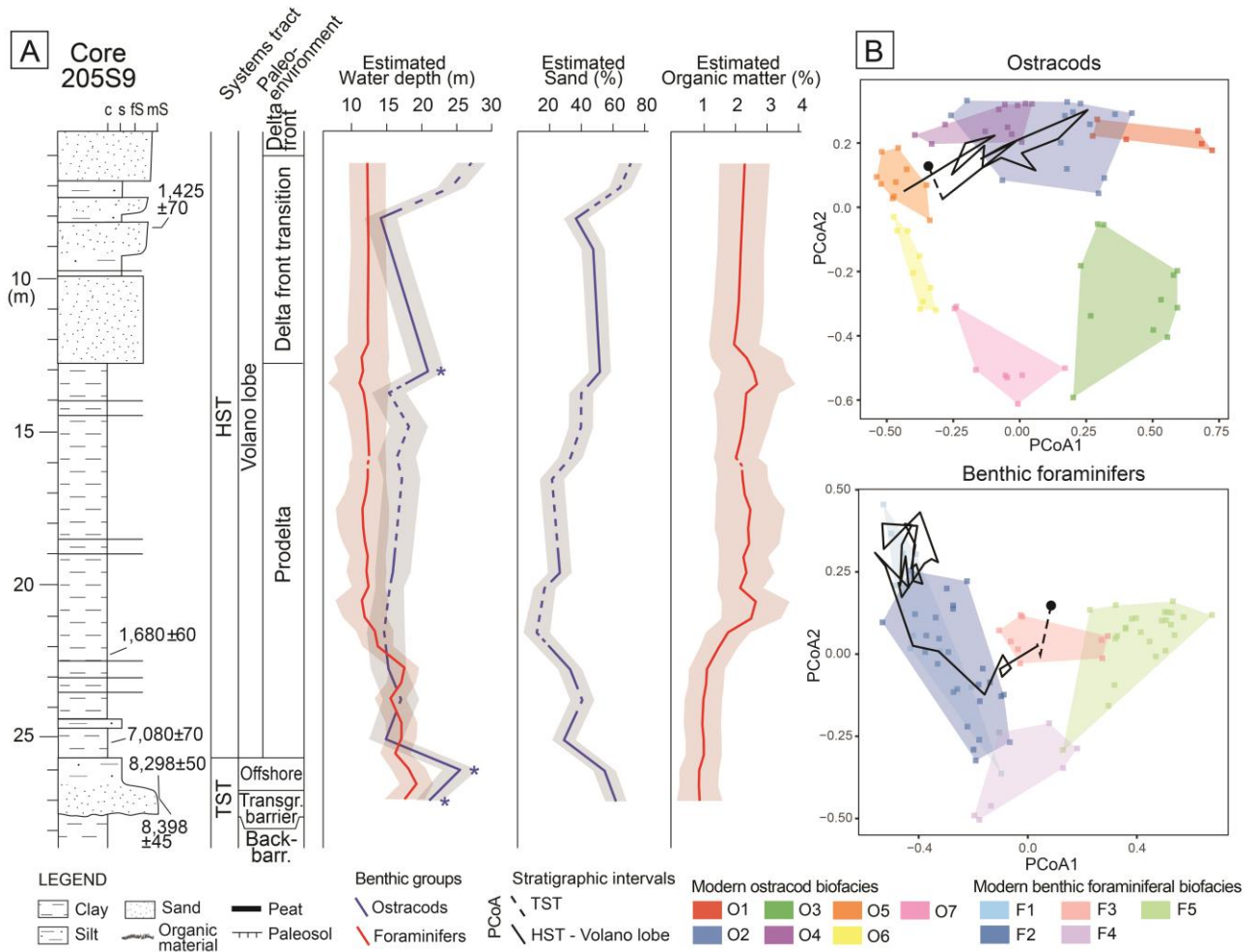


Figure 6 – (a) Estimated values of environmental drivers on the modern benthic ostracods and foraminifers (from Barbieri et al., 2019) extracted from the wPCoA of core 205S9. Estimated abiotic values that do not reflect true modern environmental conditions are marked by asterisks. Dashed lines indicate estimated values from samples with no significant modern analogs. On the right of the stratigraphic log, ages are reported as calibrated years B.P. (b) In the wPCoA, the core trajectory is indicated by a black line starting from a point and partitioned into study units. The core trajectory is superimposed over the distribution of modern sites on the multivariate space, grouped in accordance to modern biofacies.

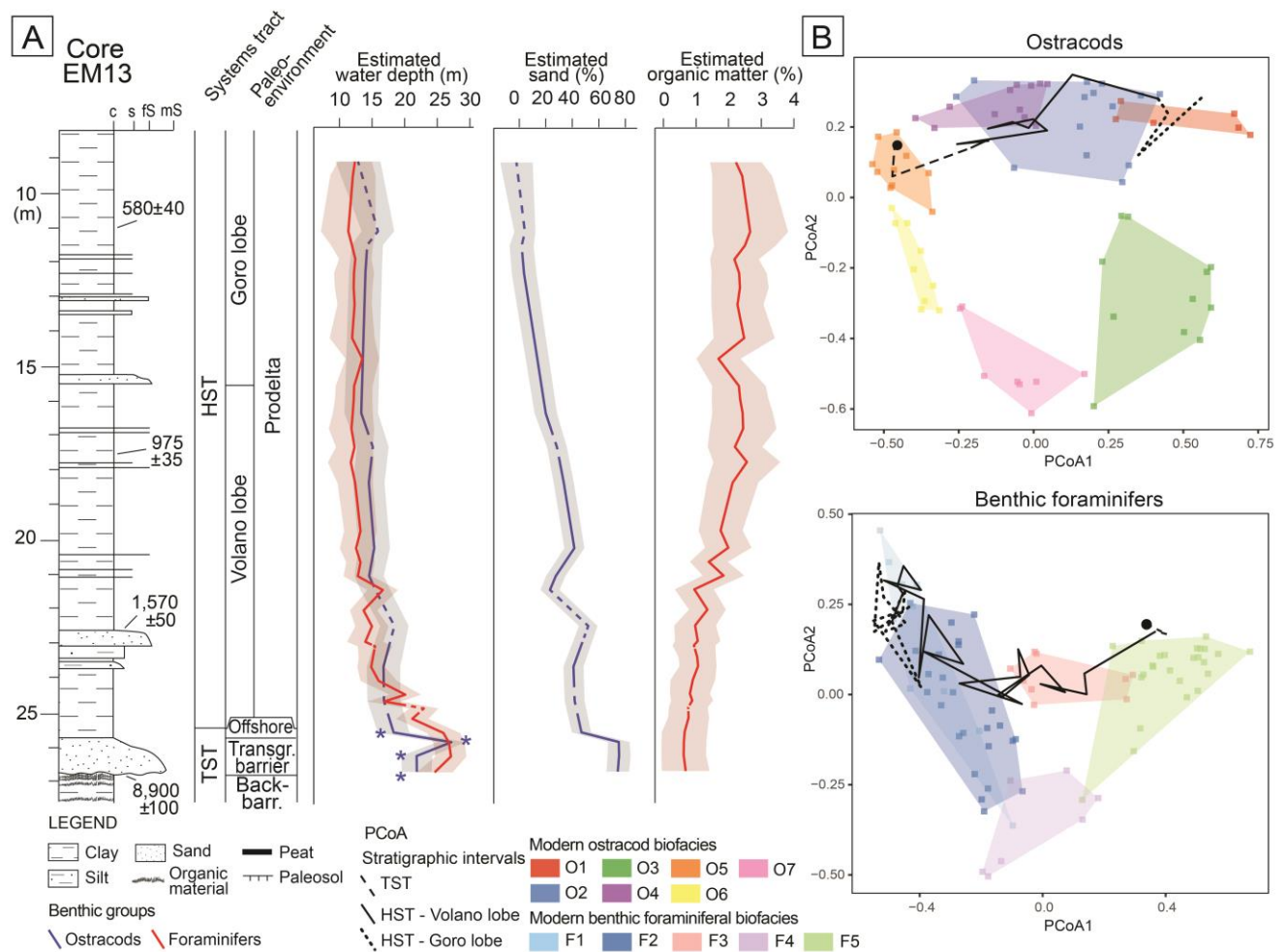


Figure 7 – (a) Estimated values of environmental drivers on the modern benthic ostracods and foraminifers (from Barbieri et al., 2019) extracted from the wPCoA of core EM13. On the right of the stratigraphic log, ages are reported as calibrated years B.P. (b) wPCoA of the core trajectory superimposed over the distribution of modern sites on the multivariate space, grouped in accordance to modern biofacies. For further explanations, refer to Figure 6.

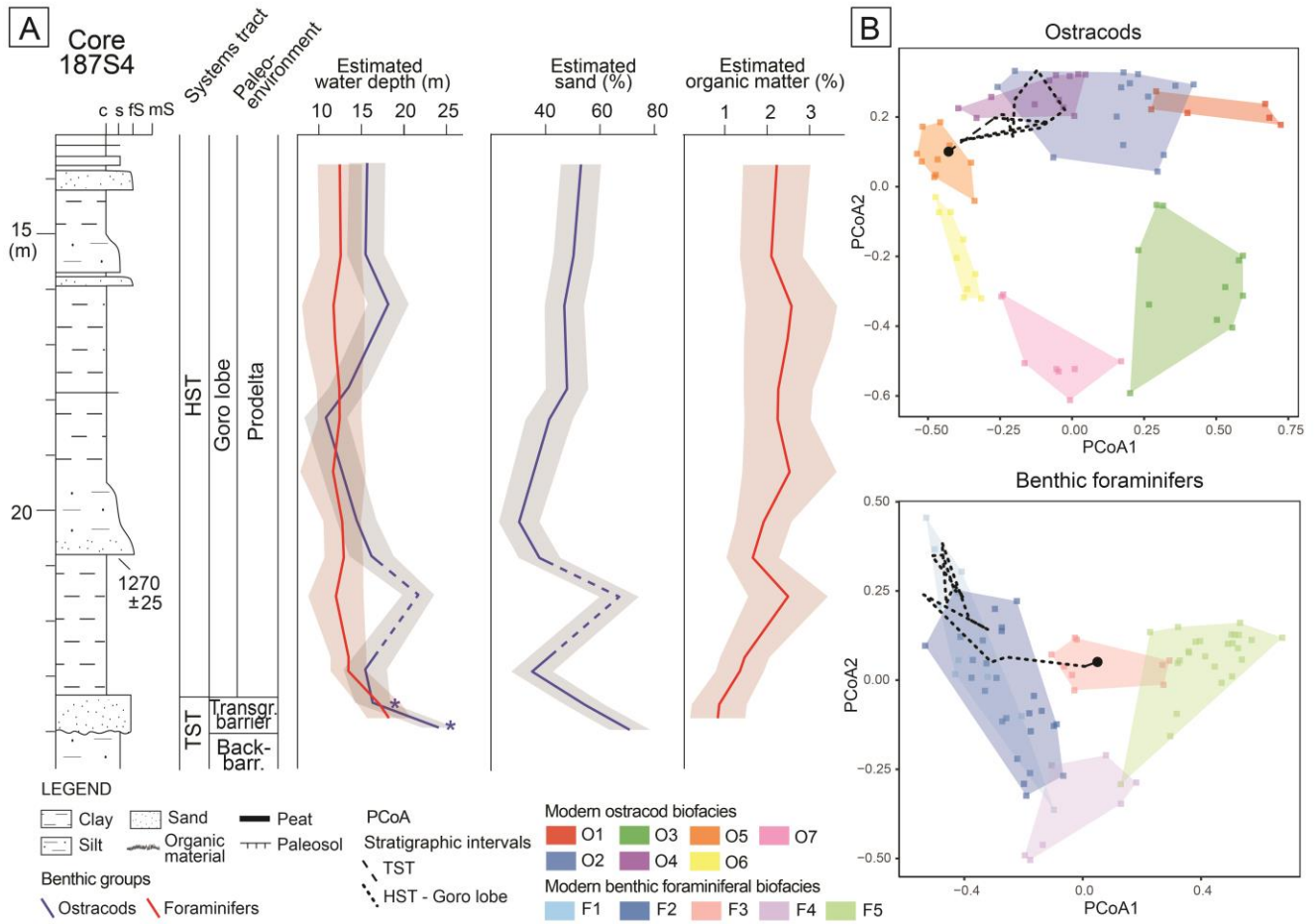


Figure 8 – (a) Estimated values of environmental drivers on the modern benthic ostracods and foraminifers (from Barbieri et al., 2019) extracted from the wPCoA of core 187S4. On the right of the stratigraphic log, ages are reported as calibrated years B.P. (b) wPCoA of the core trajectory superimposed over the distribution of modern sites on the multivariate space, grouped in accordance to modern biofacies. For further explanations, refer to Figure 6.

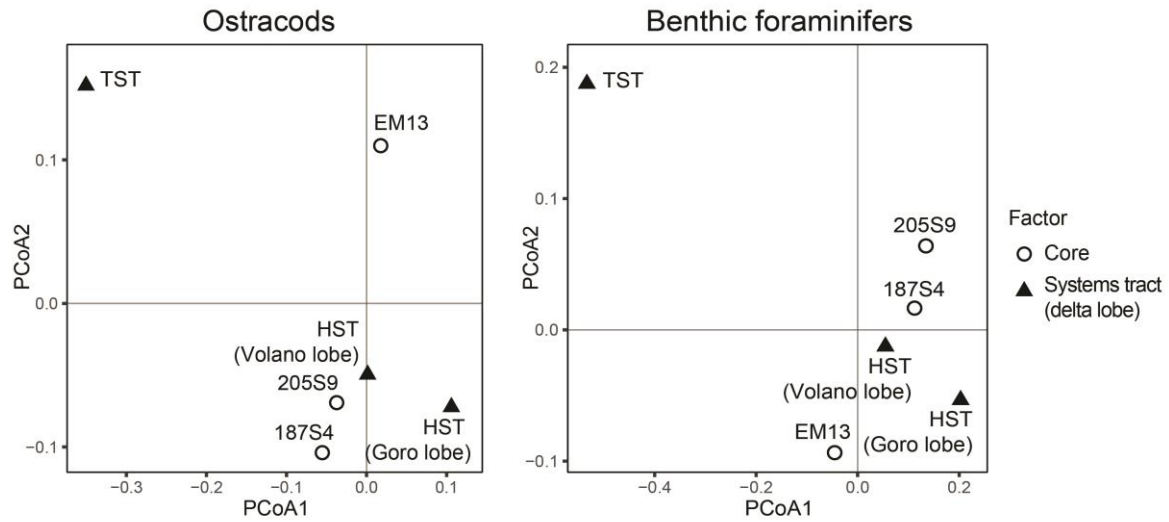


Figure 9 – PCoA ordination of distances among the centroids for individual levels of the two main effects in the benthic ostracod (a) and foraminifer (b) dataset, namely cores (205S9, EM13, 187S4) and systems tracts (transgressive and highstand Volano and Goro delta lobe deposits).