

## Dynamics of benthic marine communities across the Early-Middle Pleistocene boundary in the Mediterranean region (Valle di Manche, Southern Italy): Biotic and stratigraphic implications

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### ABSTRACT

The Valle di Manche (VdM) section (Calabria, Southern Italy) offers the opportunity to investigate the ostracod turnover along a continuous shelf succession straddling the Early-Middle Pleistocene boundary, and compare it against other paleoenvironmental (i.e., mollusks) and paleoclimatic (*Uvigerina peregrina*  $\delta^{18}\text{O}$ ) records. High-resolution (ca. 1 sample/m) ostracod fauna quantitative data, coupled with gradient analysis (Detrended Correspondence Analysis and non-Metric Multi-Dimensional Scaling), document a strong relationship between changes in faunal composition and lithofacies vertical stacking patterns. The comparison between the mollusk- and ostracod-derived ordination data demonstrates that the meio- and macro-faunal turnover is guided by a common complex gradient: bathymetry. The integrated ostracod-mollusk gradient analysis also provides a trend in water depths along the section, highlighting to what extent such multivariate approach can improve the paleoenvironmental and sequence stratigraphic interpretation of ancient shallow marine successions. When plotted stratigraphically, ordination major axis sample scores reveal two increasing-decreasing patterns in water depth that fit well with the T-R cycles previously identified. Paleobathymetric estimates combined with the vertical distribution of key ostracod groups (i.e., epiphytic taxa on sandy substrates vs. deep-sea mud related taxa) allow refining depositional trends, stratal stacking patterns and position of previously not well resolved sequence stratigraphic surfaces within each T-R cycle (e.g., Transgressive Surface-TS). Indeed, two rapid increases in water depth values mark the TSs that separate shallowing-upward, progradational (RST) from deepening upward, retrogradational (TST) stratal stacking patterns of shelf deposits. The TSs, which underline fine-grained successions dominated by deep-sea mud-lover taxa, are invariably constrained to the inception of interglacials Marine Isotope Stages (MIS) 21 and 19, identified within the VdM section by benthic foraminifera  $\delta^{18}\text{O}$  values. Within both the VdM T-R cycles, the deepest conditions (ca. 140 m of water depth) are invariably identified within the *Neopycnodonte* unit, slightly above the lightest  $\delta^{18}\text{O}$  intervals. The overlying decreasing bathymetric trend, coupled with shifts in ostracod ecological groups, allows to identify in the bryozoans lithofacies the stillstand + falling of the relative sea-level, also tracked by a progressively heavier  $\delta^{18}\text{O}$  record. More stable paleobathymetric conditions (around 40–45 m of water depth) characterize the overlying silt-sand deposits dominated by epiphytic species and showing the heaviest  $\delta^{18}\text{O}$  values.

### 1. Introduction

During the last decades, the value of marine benthic fauna and related traces as paleoenvironmental and paleoclimatic proxy has been exploited in several Quaternary and pre-Quaternary successions (e.g.

Murray, 2006; Baucon et al., 2012; Horne et al., 2012; Horton et al., 2013; Ávila et al., 2015; Gliozzi et al., 2015; Huntley and Scarponi, 2015; Bruno et al., 2017). Specifically, the distribution of ostracods in almost every aquatic depositional settings and their good ecological sensitivity to changing environmental conditions make these small

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crustaceans (0.4 to 2.0 mm on average) a routinely employed tool in paleoenvironmental reconstructions from continental to marine settings (e.g., Bonaduce et al., 1975; Henderson, 1990; Montenegro and Pugliese, 1996; Faranda et al., 2007; Pascual et al., 2008; Marriner and Morhange, 2007; Bini et al., 2012; Marco-Barba et al., 2013a, 2013b; Grossi et al., 2015; Martinez-Garcia et al., 2015; Mazzini et al., 2015, 2017; Pint et al., 2015). Recent studies have also documented the ostracod capability to track high-frequency and high-energy depositional events (paleofloods) in the marine realm (Angue Minto'o et al., 2015; Barbieri and Vaiani, 2018; Fanget et al., 2016). In contrast, minor attention has been paid on the relevance of marine ostracods in identifying stratal stacking patterns and depositional trends in a sequence stratigraphic perspective, also with respect to other biological proxies (e.g., Yasuhara et al., 2012; Amorosi et al., 2014a).

Through time, a series of Plio-Pleistocene open marine sections outcropping in Southern Italy and considered of great significance for the chronostratigraphy of the Quaternary period (i.e., Monte San Nicola, Vrica, Montalbano Jonico and Fronte sections), were analyzed for the ostracod fauna to improve paleoenvironmental reconstructions (Colalongo and Pasini, 1980; Aiello et al., 2000, 2015; Amorosi et al., 2014b). Changes in paleobathymetry and dissolved oxygen/food availability are likely to represent the main drivers of the ostracod turnover in these sections (e.g., Aiello et al., 2015; Marino et al., 2015; Negri et al., 2015). The on-land marine Valle di Manche section (Calabria, Southern Italy; Fig. 1A–B) preserves a detailed and time-constrained history of climate evolution and sea-level variability across the Early-Middle Pleistocene transition based on a multi-proxy reconstruction (Scarponi et al., 2014; Head and Gibbard, 2015; Capraro et al., 2017). However a detailed ostracod investigation is currently lacking, notwithstanding the section has high potential for paleoenvironmental studies.

The Valle di Manche (VdM) section represents an ideal venue where to investigate the main driver(s) of ostracod turnover and test ostracods capacity of tracking environmental changes, as its tens m-thick succession of marine deposits is firmly constrained in time (Early-Middle Pleistocene transition; Rio et al., 1996; Fig. 1B). In addition, a quasi-continuous, high resolution record of benthic foraminifera  $\delta^{18}\text{O}$  values ( $\delta^{18}\text{O}$  *Uvigerina peregrina*) offers a well-defined framework of Milankovitch climate-eustatic variability (from late MIS 22 to early MIS 18 Fig. 2, Capraro et al., 2005, 2017). Lastly the reconstruction of macrobenthic turnover and derived paleobathymetric quantitative estimates (Scarponi et al., 2014), from the same stratigraphic profile, furnish the rare opportunity to compare ostracod dynamics against a different paleoecological proxy into a shelf setting. In this respect, distinct benthic groups (i.e., mollusks and ostracods) may show

differential response to the drivers of environmental change, because of differences in their ecological requirements.

The main purpose of this study is to describe the vertical distribution patterns of ostracods across the middle portion of the VdM section (Fig. 2) to (i) evaluate if ecologically different and widely used proxies as ostracods and mollusks show comparable turnover along the same sedimentary record or if they respond to different driver(s) of environmental change and (ii) highlight to what extent ostracod quantitative analyses can improve and refine the VdM stratigraphic and paleoenvironmental framework (e.g., biofacies characterization and stratal stacking patterns). Indeed, integrated investigations involving multiple environmental proxies have the greatest potential to increase our understanding of biotic responses to environmental changes, meanwhile allowing for a clearer reconstruction of the stratigraphic architecture of sedimentary successions (e.g., Amorosi et al., 2014a; Rossi et al., 2017).

## 2. Geological setting

### 2.1. The Crotona Basin

The Crotona Basin (CB hereafter, Calabria, Southern Italy; Fig. 1A) is located above the internal part of the Calabrian accretionary wedge (Rossi and Sartori, 1981) and hosts a remarkably thick, well-exposed and highly fossiliferous succession, upper Miocene to Pleistocene in age. As the San Mauro Marchesato confined sub-basin, within the central sector of the CB (Fig. 1A), has been affected by high subsidence related to tectonic activity (see Van Dijk, 1994; Speranza et al., 2011; Macri et al., 2014), marine sedimentation lasted till the Middle Pleistocene (Capraro et al., 2006; Massari et al., 2010). Within the investigated sub-basin, the upper tectono-stratigraphic unit (San Mauro Sandstone unit of Roda, 1964) was further subdivided (Rio et al., 1996) into three sub-units (SM1 to SM3) that can be conveniently traced across the San Mauro sub-basin and in part across the VdM section (Fig. 1B).

The SM2 unit, ca. 5 to 40 m thick, spans from the uppermost MIS 22 to the full MIS 18.4 glacial (Capraro et al., 2005, 2017; Fig. 1B). It consists of grayish, prominent packages of marine deposits ranging from muds to sandy silts, which reflect a series of deepening and shallowing trends between “fully glacial sand-packages” pertaining to MIS 24/22 and MIS 18. Indeed, stratal geometries of the SM2 point to a major increase in tectonic subsidence rates, which emphasized the glacioeustatic sea-level rise after the MIS 24/22 glaciation (Capraro et al., 2005). The overlying unit (SM3, Middle Pleistocene) is characterized by thick sandstone/conglomerate bodies showing a distinct shallowing-upward trend, predating the definitive uplift of the sub-

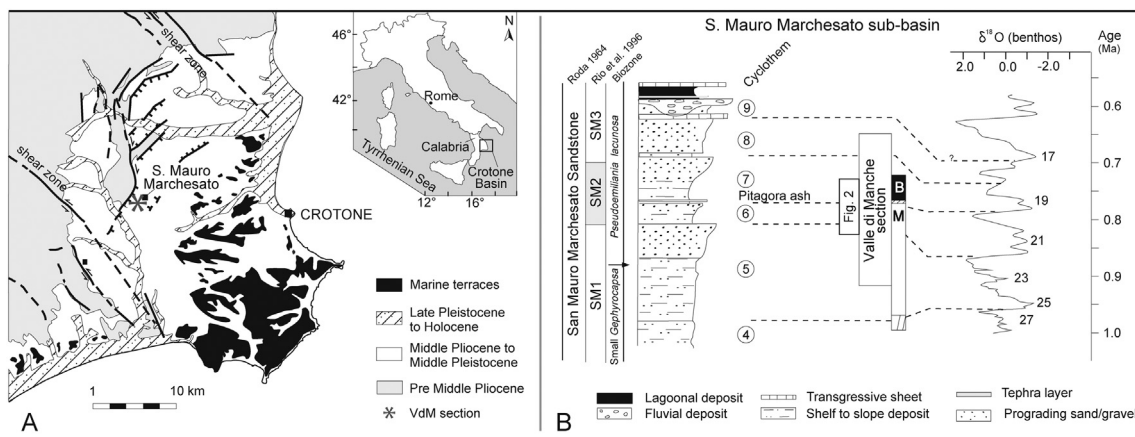


Fig. 1. Geological and stratigraphic framework of the VdM section (slightly modified from Scarponi et al., 2014). (A) Location and geological sketch map of the Crotona Basin and the S. Mauro Marchesato (SMM) sub-basin. Location of the VdM section, south of the S. Mauro Marchesato town, is also reported. (B) The SMM cyclothem succession and correlation to Marine Isotope Stages (after Massari et al., 2002). Biostratigraphic data (biozone) and subdivision in component units (SM1–3) of the SMM Sandstone are also reported. Note the connection between the Matuyama–Brunhes geomagnetic reversal (mid MIS 19) and the Pitagora ash layer. B: Brunhes chron; M: Matuyama chron.

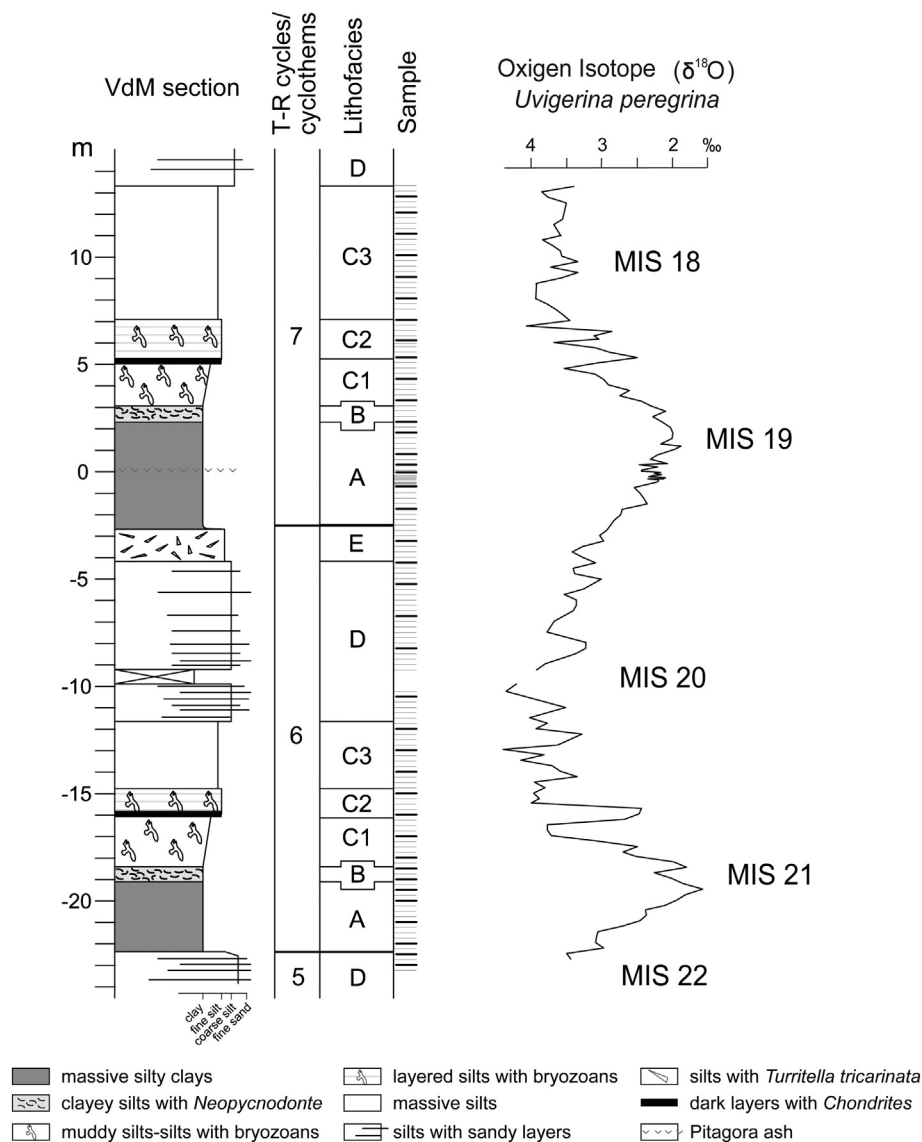


Fig. 2. Stratigraphy of the middle portion of the VdM section, straddling the Early-Middle Pleistocene transition. Lithofacies codes (see text in Sub-section 2.2), T-R cycles (after Scarponi et al., 2014) and  $\delta^{18}\text{O}$  stratigraphy for the benthic foraminifer *Uvigerina peregrina* are shown (after Capraro et al., 2017). The samples selected for ostracod fauna analysis are also highlighted by a thick horizontal bar. MIS: Marine Isotope Stage.

basin, possibly occurred in the Middle Pleistocene (Capraro et al., 2011; Fig. 1B).

Hence, the San Mauro sub-basin is represented by a syndimentary growth syncline that developed since the late Calabrian (Rio et al., 1996; Massari et al., 1999), where continuous creation of accommodation space allowed the deposition of a cyclothem, shallowing-upward marine to continental succession, and the Valle di Manche section represents one of the best-preserved locations (Fig. 1B).

## 2.2. The Valle di Manche section

The investigated portion of the Valle di Manche (VdM) section straddles the Early-Middle Pleistocene transition (MIS 21 to early MIS 18) and is ca. 35 m-thick. Bio-, magnetostratigraphic proxies and  $\delta^{18}\text{O}$  records invariably constrain the VdM muddy deposits to the interglacial periods (MIS 21 and MIS 19 in Fig. 2), whereas the coarser-grained successions developed under glacial (MIS 20 and MIS 18) conditions (Figs. 1B, 2). A prominent ash layer (“Pitagora Ash”), which approximates the Matuyama–Brunhes geomagnetic reversal (mid MIS 19), is recorded within the upper portion of VdM section (Figs. 1B, 2; Capraro

et al., 2017). The sequence stratigraphic framework of VdM section can be roughly outlined on the basis of the sole sedimentary features and contains two depositional units (cyclothem 6 and 7 in Massari et al., 2002; Figs. 1B, 2) interpreted as two transgressive-regressive (T-R) cycles (Capraro et al., 2017 and references therein). Indeed, each depositional cycle is composed of several lithofacies (Fig. 2), here briefly described (further details are available in Massari et al., 2007 and Capraro et al., 2017).

Lithofacies A up to 4.5 m-thick, is represented by dark, massive muds (mainly silty clays) that contain in the lower portion large dispersed burrows, vegetal remains and sulphide nodules. The macrofossils are very scarce but increase upwards, and are mainly represented by assemblages dominated by *Corbula gibba*.

Lithofacies B < 1 m-thick, is composed of loosely packed macrofossil remains embedded in a matrix of mud (clayey silts). Clumps of the gregarious deep-sea ostreid *Neopycnodonte* along with unsorted, variable preserved shelly material are the most striking features of this lithofacies.

Lithofacies C several meters thick, is mainly represented by fine to coarse silts grouping a series of macrofossil rich units. It has been

subdivided in three sub-lithofacies based on macrofossil remains and lithologic features (Capraro et al., 2017). C1: ca. 2.5 m-thick, is composed of amalgamated clayey-silts rich in bryozoans and others unsorted macrofossils (mainly small-sized mollusks). C2: up to 1.5 m-thick, consists of silts rich in bryozoans alternating to poorly fossiliferous clayey strata characterized by *Chondrites* (disaerobic fossil traces, Bromley and Ekdale, 1984). C3: up to 6 m-thick, massive silts containing dispersed skeletal material (mainly mollusks and bryozoans), sparse vegetal remains and strings of the polychaeta *Ditrupea* that increase in abundance upwards.

Lithofacies D is made up of meters thick successions of silts with sparse macrofaunal content, embedding cm-to-dm thick sharp based, densely laminated fine sands with abundant strings of plant debris. Coarser layers are locally interbedded with physical concentrations of disarticulated and oriented shells (mainly pectinids and polychaetes).

Lithofacies E is ca. 1 m-thick of loosely packed shells of the semi-infaunal filter feeder *Turritella tricarinata*, within a silt matrix, retrieved only in the middle portion of the investigated section.

### 3. Material and methods

#### 3.1. Ostracod data collection

Recently, a high-resolution sampling campaign (ca. 20 cm/sample) has been performed for fossil and geochemical analyses taking the 'Pitagora Ash' as the reference zero level (Capraro et al., 2015; Fig. 2). Following stratigraphic criteria, 39 samples have been chosen to undertake a high-resolution study of the ostracod fauna across the VdM section and within each depositional sequence. Selected samples are 1 m or less spaced apart from each other (Fig. 2). Special attention (higher sampling resolution) is paid to the muddy and silty units (lithofacies A-C, E; Fig. 2), where a rich ostracod fauna is expected, while the sampling density becomes lower within sandy deposits (lithofacies D). The topmost sandy interval has been not analyzed (Fig. 2).

Samples (ca. 50–55 g dry weight each) were soaked overnight in hydrogen peroxide solution (4% H<sub>2</sub>O<sub>2</sub>), gently water-screened with a 63 µm-mesh sieve and dried in an oven at 40 °C for 8 h. Each sample residue was qualitatively observed under a binocular microscope, described and split into small portions. If possible at least 100–150 well-preserved ostracod valves were counted for each sample in the size fraction > 125 µm (carapace was counted as two valves), otherwise all valves retrieved were counted. The presence of juveniles/young instars was noted, being a useful indicator of the autochthony along with the state of preservation of valves (Boomer and Eisenhauer, 2002), but not considered for counting. Ostracod specimens were mostly identified and counted at species level under a binocular microscope. Species/taxa relative abundances (%) were also calculated for each sample, as well as the species diversity (fisher alpha index on samples with  $n > 10$  valves; Bassetti et al., 2010).

The VdM dataset includes ~3650 valves, belonging to ca. 90 species, 38 genera and 3 groups (*Krithe* spp., *Parakrithe* spp. and *Callistocythere* spp.). Fossil counts and relevant literature used for taxonomic identification are reported in Azzarone et al. (submitted) and Supplementary Material (SOM-Table S1), respectively. Less than 10% of the encountered species are considered extinct. Furthermore, variable amounts of clearly allochthonous specimens, showing evidences of transport (i.e., blackish colors, traces of abrasion and/or shell damages), are found. All the allochthonous specimens (mainly belonging to genera *Aurila*; *Callistocythere*; *Carinocythereis*; *Costa*; *Loxococoncha*; *Limnocythere*; *Pontocythere*; *Pseudocandona*; *Urocythereis*; *Semicytherura*; *Krithe* and *Henryhowella*) were not inserted in the VdM ostracod dataset.

The relative abundances of a selection of taxa (i.e. the most common and/or informative in terms of paleoenvironments) were stratigraphically plotted against the studied section. The structure and composition of this representative portion of the ostracod fauna were

described and interpreted with respect to each lithofacies (Sub-section 2.2), to define ostracod-lithofacies relationship and possibly refine facies paleoenvironmental characterization. The taxon relative abundance vs. stratigraphic depth includes a total of 4 groups and 14 species one of which, i.e. *Cimbourila cimbaeformis*, is considered extinct in the Calabrian (Faranda and Gliozi, 2008). Groups include species belonging to the same genus and sharing common ecological features.

#### 3.2. Gradient analysis

Multivariate ordination techniques are applied to investigate ostracod faunal turnover and main controlling driver(s) in shelf depositional settings at the Early-Middle Pleistocene transition. Specifically, Detrended Correspondence Analysis (DCA) and non-Metric Multi-Dimensional Scaling (nMDS) are both used. These unconstrained posteriori ordination approaches are commonly employed with compositional data to identify major gradients in faunal composition (e.g., Scarponi and Kowalewski, 2004; Dominici et al., 2008; Gliozi and Grossi, 2008; Ligios et al., 2008; Pascual et al., 2008; Ritter and Erthal, 2013; Belanger and Garcia, 2014; Kowalewski et al., 2015; Laut et al., 2016; Scarponi et al., 2017). Here, only DCA results are reported (nMDS outputs in Azzarone et al., submitted). Despite DCA multiple drawbacks (e.g., Beals, 1984; Jackson and Somers, 1991; McCune et al., 2002) and difficulties in interpreting higher order gradients (axis > 1; Bush and Brame, 2010), DCA has proved to be effective when distribution of taxa relates to strong variations in controlling environmental variables (e.g., Wittmer et al., 2014), which is likely the case here at least for mollusk samples previously investigated (Scarponi et al., 2014).

For ordination analyses, the species-level data-matrix includes only samples showing > 20 specimens (34 samples) and species recorded in more than one sample (51 species). As for DCA, faunal counts were log-transformed to prevent most abundant species dominating the gradient. Whereas, nMDS analysis is performed on Bray-Curtis distance on a set of culled matrices (Azzarone et al., submitted). However, varying the taxon and sample thresholds in both ordinations yielded comparable results (Fig. 2A–F and Table 1A in Azzarone et al., submitted).

In addition, DCA and nMDS inferred ostracod faunal turnover was compared with that derived by DCA analyses of mollusk assemblages (see Scarponi et al., 2014) sampled from the same record by means of linear correlation (DCA mollusk vs. ostracod DCA/nMDS axis 1 sample scores; Table 1B in Azzarone et al., submitted). To avoid that environmental variables driving changes in molluscan and ostracod faunas could reflect mainly differences in the number of samples and their sampling resolution (i.e., samples 17 vs. 34 and average sampling resolution 2.2 vs. 1 m/sample, respectively), a reduced ostracod dataset comparable to the mollusk one (in sample size and sampling resolution), was compiled and DCA and nMDS run (results reported in Azzarone et al., submitted). Then, the ordination axis 1 ostracod sample scores were correlated with the mollusk-derived DCA axis 1 output of Scarponi et al. (2014; Table 1B in Azzarone et al., submitted). It is important to note that both mollusk- and ostracod-derived DCA scores are based on samples taken in the same stratigraphic interval (average offset 0.2 m, Table 1A in Azzarone et al., submitted).

As substrate consistency is one of the main drivers of ostracod turnover (and also could be related to water depth changes), we also employed a correlation model to evaluate if grain size (% of sand in a sample) is a linear function of DCA sample scores (see Table 2A in Azzarone et al., submitted).

#### 3.3. Environmental interpretation of the ostracod data

The ostracod environmental characterization of VdM lithofacies, and an approximate interpretation of the main driver(s) of faunal turnover along the section (DCA axis 1), relied upon the auto-ecological characteristics and the present-day spatial distribution patterns of marine ostracods in the Mediterranean Sea and North Atlantic areas

(e.g., Bonaduce et al., 1975; Breman, 1975; Athersuch et al., 1989; Sciuto and Rosso, 2008; Angue Mint'oo et al., 2013; Cabral and Loureiro, 2013; Frezza and Di Bella, 2015; Sciuto et al., 2015).

All the extant retrieved species have, to a good approximation, well-to fairly-known ecological features. However, the relationship existing between abundances of extant ostracod species and the major abiotic marine parameters, such as bathymetry, substrate granulometry, percentage of organic matter and dissolved oxygen, is far to be quantified or, especially for extinct species, poorly investigated. For the latter species (e.g., *A. cimbaeformis*, *Cytherella gibba* and *Cytherella robusta* among the most common in the VdM dataset) only indirect ecological inferences can be employed (Aiello et al., 2015). Hence, further paleoenvironmental information were provided by comparing our data with those recorded within other Mediterranean shelf successions of late Quaternary age (Barra, 1991; Faranda et al., 2007; Aiello et al., 2012, 2015; Sciuto and Meli, 2015) and those obtained from macrobenthic samples previously collected along VdM section (Scarponi et al., 2014).

## 4. Results

### 4.1. The ostracod content of VdM lithofacies

The structure and composition of the autochthonous ostracod fauna are here analyzed for the first time and framed in the context of the lithostratigraphic framework recently defined by Capraro et al. (2017; Figs. 2, 4). Recurring vertical stacking patterns of lithofacies (except for facies E), developed during consecutive interglacial-glacial periods (e.g., MIS 21–20 and MIS 19–18 in Fig. 2), are a characteristic trait of VdM section.

For each of the retrieved lithofacies (see Sub-section 2.2), a description of the most representative/abundant ostracod taxa is reported

below along with the paleoenvironmental interpretation. Selected species are also illustrated (see Fig. 3).

#### 4.1.1. Lithofacies A

Within this lithofacies (ca. –22.5 to –19 m and –2.5 to 2.25 m; Fig. 4) the ostracod fauna is variable in terms of species richness and abundance, reaching a minimum close to the tephra layer (< 10 valves). *Henryhowella sarsii*, *Kriihe*-group and *Cytheropteron* species, mainly *C. monoceros* and *C. ruggierii*, are the dominant taxa with abundances up to > 30%. Highly variable percentages of *Palmoconcha subrugosa* (0–20%), *Bosquetina tarentina* (0–25%) occur. Rare and scattered valves of *Paracytherois mediterranea*, *Bairdia conformis* and *Cytherella vulgatella* (< 10%) are also recorded. High percentages of *Argilloecia*-group or *Pterygocythereis coronata* (up to ca. 20%) occur within the middle-upper portion of the lithofacies of both 6 and 7 T-R cycles. Taxa presently recorded in infralittoral environments are scarcely represented, except at the basal portion of both cycles where not negligible percentages (up to 14%) of *Aurila convexa*, *Semicytherura ruggierii*, *Leptocythere multipunctata* and *Callistocythere* species are recorded.

The occurrence of lower circalittoral-epibathyal species (e.g., *H. sarsii*, *C. monoceros*, *B. tarentina*, *P. coronata*, Fig. 3), exclusively recorded at water depths > 60–70 m in the Adriatic Sea (Bonaduce et al., 1975), indicates a bathymetry compatible with an outer shelf (e.g., between ca. 80–150 m). Variable amounts of *H. sarsii*, a species preferring abundant and newly produced food resources (Fig. 3; Sciuto and Rosso, 2008), reflect changeable conditions of food quality and availability. In particular, *H. sarsii* seems to be locally replaced by species of the opportunistic genus *Cytheropteron* that is able to tolerate elevated fluxes of old organic matter (Sciuto and Rosso, 2008). Moreover, in the middle-upper part, high values of the infaunal (*Kriihe*)/epifaunal (*H. sarsii* + *Cytheropteron*) ratio concomitant with the occurrence or increase in relative abundances of taxa tolerant to xenoxic conditions

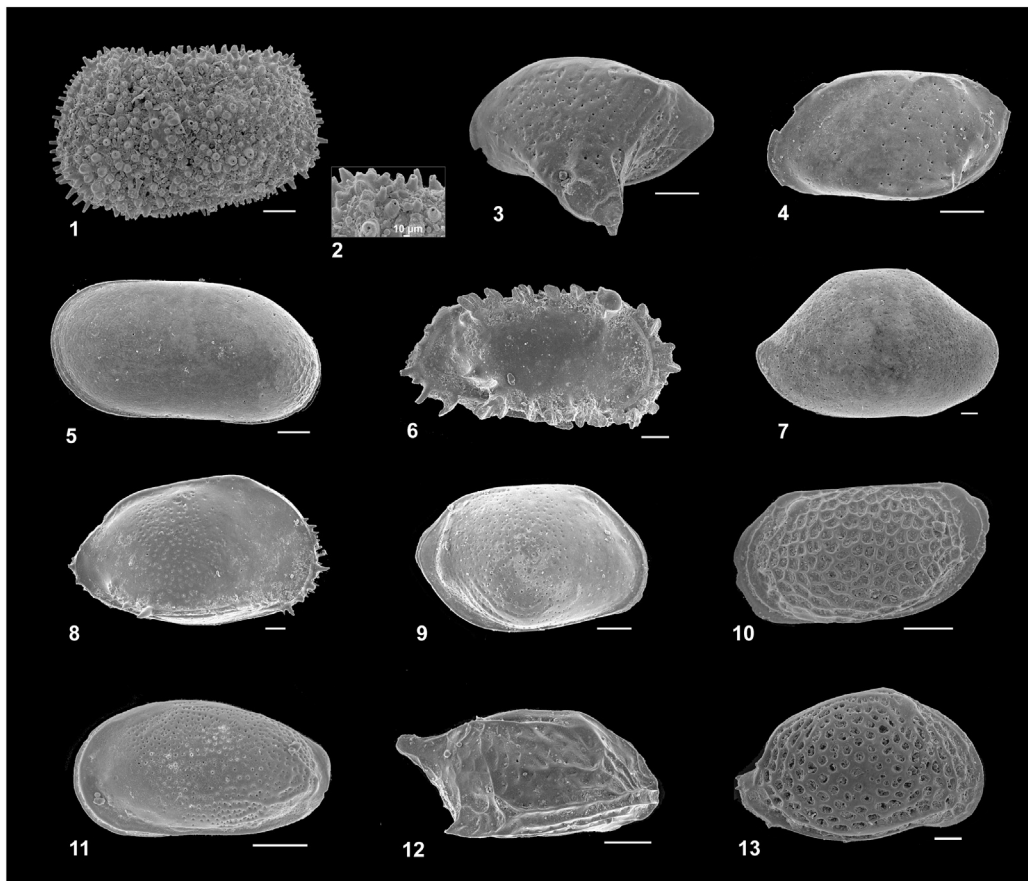


Fig. 3. Plate showing the SEM images of the key/most abundant ostracod species encountered within the VdM section. Scale bar = 100  $\mu$ m. All lateral external views. Key: RV = right valve; LV = left valve. 1: *Henryhowella sarsii* (G.W. Muller, 1894); LV. 2: Close up of *H. sarsii* surface ornamentation (valve showed in 1). 3: *Cytheropteron monoceros* (Bonaduce et al., 1975); LV. 4: *Cytheropteron ruggierii* (Pucci 1955); LV. 5: *Cytherella vulgatella* (Aiello, Barra, Bonaduce & Russo, 1996); LV. 6: *Pterygocythereis coronata* (Roemer, 1838); RV. 7: *Bairdia conformis* (Terquem, 1878); RV. 8: *Bosquetina tarentina* (Baird, 1850); RV. 9: *Palmoconcha subrugosa* (Ruggieri 1967); RV. 10: *Sagmocythere versicolor* (G.W. Muller, 1894); LV. 11: *Leptocythere multipunctata* (Seguenza 1883); LV. 12: *Semicytherura ruggierii* (Pucci, 1955); RV. 13: *Aurila convexa* (Baird, 1850); RV.

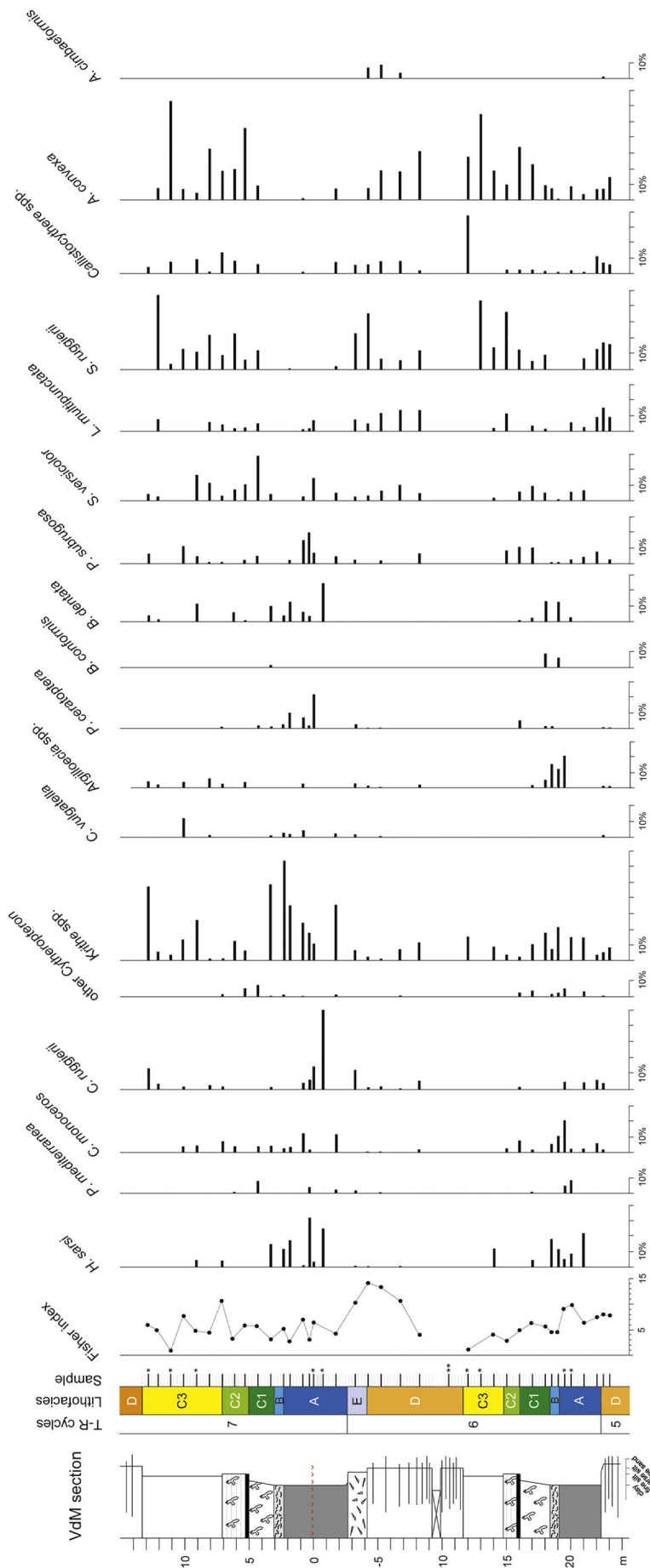


Fig. 4. Relative abundances of selected ostracod taxa from the VdM section with respect to the lithofacies and the T-R cycles. Samples containing  $< 50$  valves are highlighted by an asterisk. Species diversity (Fisher index) values are stratigraphically plotted. Two asterisks indicate the sample barren of ostracods. Lithological legend is reported in Fig. 2.

(i.e., *Argilloecia*-group or *C. vulgatella*; Fig. 3), suggest lower levels of oxygenation (Whatley, 1990; Aiello et al., 2015). In contrast, the remarkable amounts of infralittoral/upper circalittoral taxa (i.e., *A. convexa*, *Callistocythere* spp., *L. multipunctata*; Fig. 3) recorded in the lowermost portion of lithofacies A are interpreted to reflect a gradual increase in water depth.

#### 4.1.2. Lithofacies B

The thin lithofacies B (ca. –19 to –18.5 m and 2.25 to 3 m; Fig. 4) shows a low-diversified ostracod fauna dominated by *Krithe*-group (ca. 7–64%) and *H. sarsii* (ca. 12–18%), accompanied by lower amounts of *B. tarentina* (up to ca. 12%) and *C. monoceros* (<10%). Notable percentages of *Argilloecia* species (ca. 15%) and *B. conformis* (up to 10%) are found only within the lower T-R cycle (cycle 6). Rare valve of *P. coronata* (<3%) also occur. Taxa commonly reported from the infralittoral/upper circalittoral settings (i.e., *Aurila*, *Callistocythere* and *Leptocythere* species) are almost absent, except for the sporadic occurrence of *A. convexa* (abundances 0–7%).

The dominance of species preferring water depths > 60 m (*H. sarsii*, *C. monoceros*, *B. tarentina*, *B. conformis*; Fig. 3), and the absence or low percentages of infralittoral/upper circalittoral genera indicate deposition in an outer shelf environment. Despite the good preservation state of *A. convexa* shells, the local occurrence of this infralittoral-upper circalittoral species can be related to sea bottom currents displacing ostracods from shallower water depths.

#### 4.1.3. Lithofacies C1

Within this lithofacies (ca. –18.5 to –16 m and 3 to 5 m; Fig. 4) the ostracod fauna is quite diversified and shows the occurrence of lower circalittoral-epibathyal taxa (i.e., *H. sarsii*, *C. monoceros*, *B. tarentina*, *B. conformis* and *Argilloecia* species), mainly concentrated in correspondence of the lower portion of this unit. However, species preferring infralittoral-upper circalittoral settings (i.e., *A. convexa*, *S. ruggierii* and *Leptocythere multipunctata*; Fig. 3), here constitute a remarkable component of the ostracod fauna. In particular, these species show in both T-R cycles an upward increasing trend paralleled by a strong decrease in relative abundances of *Krithe*-group. *Palmoconcha subrugosa* and *S. ruggierii* occur as secondary taxa (<13%), while minor amounts of *Callistocythere* spp. (0–6.4%) are found.

The composition of the ostracod fauna points to an upper circalittoral setting, as a mid-shelf (ca. 50–80 m water-depth range), with a granular-cohesive (silt-clay) bottom according to the high amounts of species preferring mixed substrates (*A. convexa*, *S. versicolor* in Fig. 3, and *S. ruggierii*). The upward increase trend in infralittoral-upper circalittoral species, which progressively replaces *Krithe*-group as dominant taxa, is interpreted to reflect a decrease in paleobathymetry and, possibly, a concomitant increase in vegetation cover at the sea floor.

#### 4.1.4. Lithofacies C2

Lithofacies C2 (ca. –16 to –15 m and 5 to 7 m; Fig. 4) shows an ostracod fauna dominated by *S. ruggierii* (ca. 9.8–37%) and *A. convexa* (ca. 9.8–20%), with the secondary occurrence of *L. multipunctata* (ca. 2–11.7%), *Callistocythere* (ca. 3–14%) and *Krithe* (ca. 1.7–12.7%) groups, and *C. monoceros* (3–7.5%). Variable percentages of *B. tarentina* (0–6.4%), *P. subrugosa* (0–8.8%) and *S. versicolor* (0–7.4%) are also found.

The dominance of species typical of upper circalittoral-infralittoral environments (i.e., *S. ruggierii*, *A. convexa*, *L. multipunctata* and *Callistocythere* spp.) along with the not negligible occurrence of taxa preferring water depths from the upper circalittoral zone downward (mainly *C. monoceros* and *B. tarentina*; Fig. 3) suggests a mid-shelf depositional setting. High percentages of epiphytic taxa, mainly *A. convexa* and *Callistocythere* species, indicate a dense vegetation cover at the bottom.

#### 4.1.5. Lithofacies C3

Along this lithofacies (ca. –15 to –11.5 m and 7 to 13.5 m; Fig. 4) ostracods are generally scarce (<10 valves) and characterized by a variable species diversity. *Aurila convexa*, *S. ruggierii* and *Callistocythere* spp. are well-represented, with the secondary occurrence of *Krithe*-group that locally peaks (up to ca. 48%) within the T-R cycle 7, in concomitance of a slight increase of *B. tarentina*, *H. sarsii* and/or *Cytheropteron* species (relative abundances >4%). Generally, scattered valves of *P. subrugosa*, *C. vulgatella* and *Argilloecia* species occur in the investigated interval, reaching in one sample from the uppermost portion a total amount of ca. 38% (T-R cycle 7; Fig. 4).

The dominance of *S. ruggierii* and epiphytic taxa as *A. convexa* and *Callistocythere* spp., along with the secondary occurrence of ostracods commonly recorded at water depths > 60–70 m (above all the *Krithe*-group; Bonaduce et al., 1975), points to a vegetated mid shelf setting. However, the low abundance values and the highly variable species diversity of the ostracod fauna suggest unstable environmental conditions. Specifically, the high-frequency turnover involving *A. convexa* + *S. ruggierii* and *Krithe*-group + other circalittoral-bathyal species (mainly *B. tarentina*), recorded within the uppermost T-R cycle, possibly reflects abrupt shifts in water depths sometimes paralleled by changes in bottom conditions. In this regard, the temporary establishment of a more pelitic substrate and lower levels of oxygenation is locally tracked by the high amounts of the opportunistic species *P. subrugosa* (Fig. 3), that prefers muddy substrate, and taxa tolerant to xenoxic conditions (*C. vulgatella* and *Argilloecia*-group).

#### 4.1.6. Lithofacies D

This lithofacies (ca. –24 to –22.5 m; –11.5 to –4 m and 13 to 15; Fig. 4) commonly contains a rich ostracod fauna showing a marked upward increase in abundance (from ~20 to ~100 valves) and species richness. The ostracod fauna is almost exclusively composed of typical infralittoral-upper circalittoral genera (i.e., *Aurila*, *Callistocythere*, *Semicytherura* and *Leptocythere*) with the dominance of *Aurila-Cimbarila* species (up to 33%), mainly represented by *A. convexa* and *C. cimbaeformis*. The latter is an extinct species (Early Pliocene-Calabrian; Faranda and Gliozzi, 2008). Within the T-R cycle 6, *Leptocythere multipunctata* displays an upward decreasing trend. A similar trend is also showed by *P. subrugosa*, *C. ruggierii* and *Krithe*-group that are encountered with low percentages (commonly <8%). Rare displaced valves of freshwater-low brackish ostracods belonging to genera *Limnocythere* and *Pseudocandona* are locally found.

The ostracod fauna structure (high species diversity) and composition (i.e., dominance of infralittoral species along with absence/scarcity of species typical of lower circalittoral or deeper water species) indicate an inner-mid shelf environment with silty-sandy bottoms covered by vegetation. The upward decreasing trend of opportunistic taxa preferring muddy substrates (mainly *L. multipunctata*, *P. subrugosa* and *Krithe*-group) reasonably reflects the progressive establishment of coarser bottoms and shallower and more stable environmental conditions according to the increase in species diversity. The local occurrence of few freshwater-low brackish ostracods fits with a shallow marine environment occasionally influenced by river fluxes.

#### 4.1.7. Lithofacies E

Only one sample was analyzed for this lithofacies (–4 to –2.5 m; Fig. 4). It contains an ostracod fauna characterized by high amounts of *S. ruggierii* (ca. 23.5%) and *C. ruggierii* (ca. 12.5%), that is the only *Cytheropteron* species found. *Callistocythere* and *Krithe* groups occur with percentages <10%. Rare to very rare valves of *C. vulgatella*, *P. coronata*, *S. versicolor*, *P. subrugosa*, *P. mediterranea*, *H. sarsii* and *Argilloecia* spp. are also found. *Aurila* species are not recorded.

The occurrence of one species of *Cytheropteron* (*C. ruggierii*; Fig. 3), the only not rare in the Mediterranean infralittoral zone (Bonaduce et al., 1975; Aiello et al., 2015), and the very low amounts of taxa presently recorded at water depths deeper than 60–70 m (i.e., *H. sarsii*





supposition that both mollusk and ostracod faunas could be associable to the same drivers of community composition, especially when analyzed along a substantial portion of the marine gradient (i.e., entire shelf). However, to our knowledge, our reconstruction at VdM is one of the few studies specifically dealing with macro- and meiofaunal response to environmental drivers in open marine settings.

This redundancy should not be viewed as unfavorable to integrated analyses of ostracods and mollusks. On the contrary, the VdM results strengthen the high value of these faunal groups as paleoenvironmental tools, which may substitute each other or/and balance each other's weaknesses, especially considering that paleobiological data are strongly influenced by the stratigraphic framework. Indeed, the distribution of taxa along sedimentary successions is controlled not only by ecological processes (e.g., taxa environmental niches), but also (and equally important) by the sedimentary processes that govern whether fossil-containing sediments are deposited and preserved (Patzkowsky and Holland, 2012).

### 5.2. Drivers of macro and meiofaunal composition

The joint consideration of macro- and meiofaunal associations from the VdM section highlighted a common cause driving faunal turnover along the section. Furthermore, the available ecological information on ostracods coupled with the already investigated molluscan main drivers of faunal turnover, explored in a companion paper (Scarponi et al., 2014), suggest that most of environmental variation could be attributed to bathymetry (Fig. 5 and Section 4.2), and correlated environmental parameters (see also Fig. 3 in Azzarone et al., submitted).

In marine depositional contexts, bathymetry is a well-known indirect driver of macrofaunal turnover (e.g., Tyler and Kowalewski, 2014) and in the fossil record bathymetry commonly shows the highest correlation with faunal turnover (Patzkowsky and Holland, 2012; Wittmer et al., 2014; Scarponi et al., 2017). This is especially evident when, as in this case, the sedimentary succession records glacial/interglacial cycles developed along the entire shelf (Rio et al., 1996; Capraro et al., 2017). Concerning ostracods, a strong influence of bathymetric variations linked to glacio-eustatic phases has been clearly documented from the Montalbano Jonico shallow-marine (< 200 m of inferred water depth) section (Aiello et al., 2015).

On the other hand, the assessment and evaluation of the relative weights of the environmental variables linked to the shelf bathymetric gradient, and potentially driving biotic response to environmental change should require a wide set of measurements not yet available. Nevertheless, such highly interrelated variations are here hinted by ecology information of ostracod taxa (Figs. 4, 6).

Given the coarse bathymetric information on ostracods taxa here recovered, water-depth calibrations of unconstrained ordinations of ostracod samples (DCA1) rely on the rich amount of quantitative information on bathymetry preference available for the majority of the mollusk species retrieved in concomitance or proximity of sampled horizons. Given the non-perfect concordance between the two sets of sampling schemes (i.e. mollusks vs. ostracods), reduced major axis regression of mollusk-derived bathymetric estimates of samples vs. ostracods DCA 1 sample scores, allowed a rough calibration of bathymetric ostracod samples and, more importantly, derived trends along the section (Fig. 6; Azzarone et al., submitted).

### 5.3. Paleoenvironmental and sequence stratigraphic implications of the VdM faunal patterns

The ostracod-mollusk faunal turnover recorded by DC1 sample scores (Fig. 6) outlines two similar v-shaped patterns of variation that reflects two increasing-decreasing trends in water depth. The latter mimic very closely the glacial-interglacial  $\delta^{18}\text{O}$  cycles that have been interpreted as correlative to the MIS 21-MIS 20 and MIS 19-MIS 18 intervals, respectively (Fig. 6; Capraro et al., 2005, 2017; Azzarone

et al., submitted). For both cycles, the internal organization of facies is virtually identical, especially in the fine-grained intervals (Fig. 2), confirming that the main traits of the VdM succession were primarily shaped by glacioeustasy (Rio et al., 1996). Nonetheless, superimposed is a strong local subsidence that, in spite of the massive sediment supply, promoted the continuous creation of accommodation space, thus ensuring the persistence of open marine conditions also in the course of eustatic sea-level minima (Massari et al., 2007).

Ecology information on key taxa shows also how changes in substrate conditions (lithology, vegetation cover and oxygen/food type availability) are relatable to water depth inferences. Indeed, open marine ostracods preferring muddy substrates (i.e., *H. sarsii*, *C. monaceros* and *Paracytherois mediterranea*) and species commonly recorded on vegetated sandy bottoms (i.e. *Aurila* and *Callistocythere* species) show, respectively, concordant and specular stratigraphic variation respect to DC1 sample score (Fig. 6; Azzarone et al., submitted). Thus, changes in substrate conditions (i.e. lithology and vegetation cover) tracked by the ostracod fauna are strictly connected to water depth inferences. In contrast, the temporary establishment of a stressed environment recorded by peaks in opportunistic species, tolerant to low oxygen levels (i.e. *Palmoconcha subrugosa*, *Palmoconcha turbida*, *Cytherella vulgatella* and *Argilloecia*-group), appears less clearly predictable in respect to water depth variations.

In the lowermost portion of the VdM section (ca. 24–19 m below the Pitagora Ash; Fig. 6), at the transition between lithofacies D-A, the abrupt upward increase in DC1 scores is paralleled by a marked shift toward lighter oxygen isotopic ratio, testifying the occurrence of a distinct bathymetric change during the interglacial MIS 21 (Fig. 6). Specifically, within the 3-m-thick interval of muddy deposits (lithofacies A) the ostracod water-depth estimates record a steady deepening (from ca. 60 m to ca. 120 m; Fig. 6). The onset of this fast deepening upward trend, retrieved in proximity of decimetric thick sandy beds containing the boreal guest *A. islandica* (Scarponi et al., 2014), is retained to represent the transgressive surface (TS) separating the forced regressive/lowstand coarse deposits attributed to MIS 22 (estimated paleodepth ca. 50 m in the lower portion of the studied section, which possibly does not record the full glacial conditions but the following glacial termination; Fig. 6), from the overlying increasingly finer succession of MIS 21 (Fig. 6). The retrogradational stacking pattern of facies, commonly characterizing transgressive successions (TST in Fig. 6), is also highlighted by the dominance of deep-sea (> 70 m) mud-lover species, which depicts a coupled change in water depth and substrate lithology in respect to the underlying inner-middle shelf setting with vegetated coarser grained bottoms (lithofacies D; Section 4.1.6). Moreover, changeable conditions in terms of oxygen availability likely occur (lithofacies A; Section 4.1.1.) as testified by local peaks in opportunistic taxa and the mollusk *Corbula gibba*. The latter is here indicative of stressed conditions (see also Ceregato et al., 2007; Tomašovýtch et al., 2017).

Up section, the turnaround point of DC1 scores is recorded in correspondence of the *Neopycnodonte* unit (lithofacies B), where the maximum estimates of water depth are obtained (i.e. ca. 140 m) slightly above the lightest oxygen isotopic ratios (Fig. 6). Thus, based on coupled macro- and meiobenthic inferences, lithofacies B is considered an ecological condensed interval (see also Scarponi et al., 2014, 2017), representative of the maximum flooding zone (MFZ) developed during the MIS 21 interglacial peak (Fig. 6). Although no distinctive sedimentological features of the maximum flooding surface (MFS) can be identified within unit B, an evident seaward shift of facies is here highlighted by the initially gradual and then abrupt drop in DC1 scores recorded at the onset of the bryozoans-rich silt deposits (lithofacies C1). The decreasing trend in DCA sample score reflects a rapid and continuous decrease in bathymetry (from ca. 120 m to ca. 30 m; Fig. 6, Azzarone et al., submitted) occurred during the glacial period MIS 20. The upward increment of sparse vegetal remains and strings of the polychaeta *Ditrupa*, indicative of high sedimentation/turbidity and

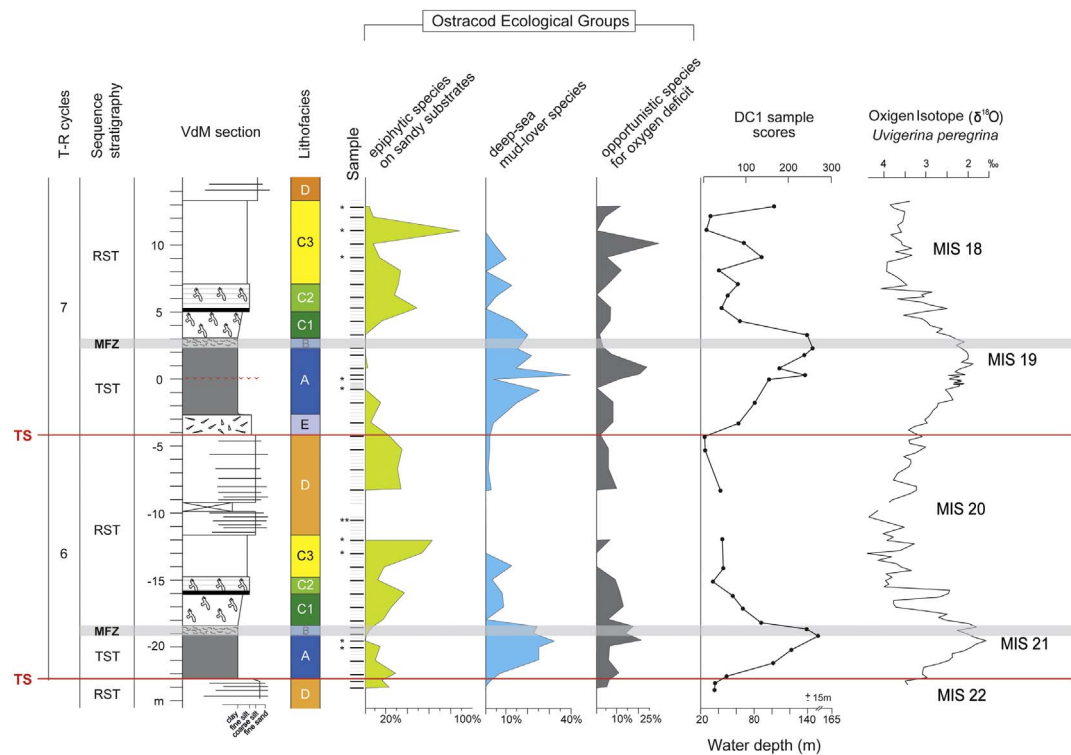


Fig. 6. Distribution trend of ostracod ecological groups along the VdM section and vertical patterns in DC1 scores/paleobathymetric estimations based on an integrated ostracod-mollusk gradient analysis. VdM  $\delta^{18}\text{O}$  stratigraphy and lithofacies are also reported (lithological legend is reported in Fig. 2). Samples containing < 50 valves are highlighted by an asterisk, two asterisks indicate the sample barren of ostracods. The sequence stratigraphic interpretation of the multi-proxy paleoenvironmental data is plotted along with the refined identification of the T-R cycles. TST: transgressive system tract; RST: regressive systems tract; TS: transgressive surface and MFZ: maximum flooding zone, MIS: Marine Isotope Stage.

unstable mixed substrates along inner-shelf (Cosentino and Giacobbe, 2006), and concomitant shift toward heavier values of  $\delta^{18}\text{O}$  (Fig. 6) support the interpretation. The re-establishment of progressively shallower inner-shelf conditions during the MIS 20 sea level fall is clearly tracked also by the abrupt diffusion of epiphytic taxa preferring sandy substrates to the detriment of deep-sea mud-lover species (Fig. 6). According to the development of a shelf vegetated sandy bottom, opportunist species show an overall upward decreasing trend (Fig. 6).

Although the presence of a scarce ostracod fauna prevents a continuous record of DC1 scores across the overlying silty-sandy deposits (lithofacies C3 and D), a relatively stable lowstand paleobathymetry can be identified during fully glacial conditions of MIS 20 (heaviest values of  $\delta^{18}\text{O}$  in Fig. 6). A minimum of water paleodepth is reached close to the upper boundary of lithofacies D (Fig. 6), where mud-lover species are almost absent and concentrations of disarticulated and oriented shells are indicative of high-energy events, such as river floods and/or storm-induced flows within shelf settings (Massari et al., 1999).

The overlying finer deposits/lithofacies E is indicative of a deeper environment, subject to influence of riverine waters, as testified by high abundance of *T. tricarinata* (Dominici, 2001). This renewed sea-level rise is accompanied by a slightly increase in deep-sea species, paralleled by a sudden fall of epiphytic taxa (Fig. 6). This turnover in ostracod fauna composition is clearly revealed by an abrupt increase in DC1 score values and tracks a rapid water-depth shift (~50 m to ~80 m within 0.5 m of stratigraphic thickness), attributed to the MIS 19 transgression (upward lighter trend in oxygen isotopic ratios; Fig. 6). This rapid and steady deepening trend is responsible for the subsequent re-establishment of an outer shelf environment with muddy substrates (high amounts of mud-lover taxa) and changeable oxygen conditions suggested by peaks in opportunistic species in the middle portion of lithofacies A (Fig. 6). Hence, the lithofacies E lower boundary is marked by a shift from coarsening- and shallowing-upward trend (i.e., coupled litho- and bio-facies C1-D) to a fining-and deepening-upward succession

(i.e., lithofacies E–A; Fig. 6). This shift from shallowing to deepening trend is interpreted to mark the transgressive surface (TS linked to MIS 19 interglacial; Fig. 6).

Thus, with respect to previously defined sequence stratigraphic interpretation (Fig. 2; Scarponi et al., 2014), the transgressive surface separating sequence 6 to 7, is here positioned at ca. –4 m (Fig. 6), thanks to a higher resolution sampling scheme. As for the precedent depositional cycle attributed to MIS 21–MIS 20, ostracod fauna variations clearly trace an increasing-decreasing bathymetric trend with the turnaround point recorded within the upper portion of the *Neopycnodonte* unit, containing the MFS (water-depth estimate of ca. 140 m), to the overlying bryozoans deposits (lithofacies C1 and C2). The latter are constrained to the glacial inception of MIS 18 by the increasing  $\delta^{18}\text{O}$  values (Fig. 6).

Integrated standard and ordination analyses of ostracod fauna also highlight the superposition of higher frequency changes on the overall shallowing-upward trend recorded within the lithofacies C3 of MIS 18 (Fig. 6). One out of two main peaks in DC1 scores (at ca. 9 m and 13 m) matches with an increase in deep-sea mud-lover species reinforcing the hypothesis of small-scale deepening pulsations (in the range of tens meters). However, at this resolution scale, we cannot totally exclude the influence of other factors, as upwelling currents. Comparable conditions have been identified by ostracods within coeval (MIS 18) shelf deposits belonging to the Montalbano Jonico-MJ section (Aiello et al., 2015), and interpreted as the consequence of upwelling episodes, leading to the sporadic co-occurrence of “deep” and “shallow” autochthonous ostracod taxa. The development of unstable paleoenvironmental conditions during the glacial MIS 18 is also supported by the local occurrence within lithofacies C3 of peaks in opportunistic taxa tolerant to oxygen deficit (Fig. 6). High amounts of these taxa (> 10–15% of relative abundance) also characterize some portions of the muddy intervals (lithofacies A and B), suggesting the sporadic occurrence of relatively low-oxygen conditions during interglacial periods

(i.e. MIS 21 and MIS 19; Fig. 6). Coeval kenoxic events have been recognized by Aiello et al. (2015) at the Montalbano Jonico section within intervals containing the deepest ostracod assemblages.

## 6. Conclusions

The combined use of a high-resolution, multi-proxy (ostracods and mollusks) dataset and multivariate ordination techniques (DCA and nMDS) on the VdM section (Calabria, Southern Italy) has proved to be a powerful tool for investigating the main controlling driver on meio- and macro-faunal turnover in past shelf settings. Pairwise, quantitative ostracod analyses have demonstrated to be able to identify, within a shelf succession deposited during two consecutive glacial-interglacial cycles, specific stratal stacking patterns and a refined paleoenvironmental and sequence stratigraphic interpretation of the section.

The major outcomes of this study can be summarized as follows:

- Ordination analysis performed on the VdM ostracod dataset shows a distinct environmental gradient underlying the faunal turnover. This complex gradient corresponds to bathymetry and associated parameters (e.g. vegetation cover), as documented by the ecological information available for key extant species. Ostracod and mollusk communities respond in a synchronized and similar manner to the environmental changes occurred on the shelf during two consecutive glacial-interglacial cycles, from MIS 21 to 18.
- The integrated, multivariate analysis of ostracods and mollusks furnishes a high-resolution, reliable estimation of the paleobathymetric trends recorded within the VdM section, allowing an improved differentiation between system tracts and identification of sequence stratigraphic surfaces. Respect to previous studies, here the two TSs which represent the cycle boundaries are precisely constrained by a high-resolution sampling that depict two rapid increases in water depth values at the inception of interglacials MIS 21 and MIS 19 identified within the VdM section by benthic foraminifera  $\delta^{18}\text{O}$  values.
- The joint consideration of macro- and meiofaunal associations proves to have the greatest potential for interpreting ancient shallow marine successions in a paleoenvironmental-sequence stratigraphic perspective, meanwhile examining the biological and sedimentary response of shelf settings to glacio-eustatic oscillations.

Source Data along with any additional Extended Data display items are available in Azzarone et al. (submitted). Supplementary data associated with this article can be found in the online version, at <https://doi.org/10.1016/j.palaeo.2017.12.042>.

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