

Cyclic changes in oxygenation based on foraminiferal microhabitats: Early–Middle Pleistocene, Lucania Basin (southern Italy)

SIMONA STEFANELLI

Geology and Geophysics Department, University of Bari, Via Orabona 4, 70125 Bari, Italy (e-mail: stefanelli@geo.uniba.it).

ABSTRACT – In the Pleistocene Montalbano Jonico composite section (southern Italy) the microhabitat preferences of the benthic foraminifera have been determined by comparison with data on living forms. The stratigraphic distribution of the different living positions seems to be related to the cyclic oxygen fluctuations recorded in the succession. In the high-oxygenated phases, when the oxygenated zone within the sediment column is wide, the assemblages show a distinct vertical microhabitat distribution. In the low-oxygenated phases, when the minor oxygen availability at the bottom–water interface reduces the oxygen penetration within the sediment, infaunal microhabitat is the preferred living depth.

In order to quantify the oxygen fluctuations recorded in the succession, a palaeo-oxygen curve is reconstructed testing Kaiho's benthic foraminiferal oxygen index (BFOI) in the equation: $y = 1.686 + 0.033337x$. In general, good correlations are observed between the dissolved oxygen regimes and the benthic assemblage composition. The low-oxygenated phases are identified with the low-medium oxic regime and the high-oxygenated phases with the high oxic regime.

In the deeper part of the composite section, oxygen has played an important role on the foraminiferal assemblage composition. In contrast, in the shallower part, a combination of oxygen and sea-level changes regulates the distribution and composition of the assemblages. *J. Micropalaeontol.* 23(1): 81–95, May 2004.

INTRODUCTION

The microhabitat category of benthic foraminifera depends on their living depth in the sediment. If the fauna lives on the top of the sediment, the microhabitat is defined as epifaunal; if the fauna lives in the sediment, the microhabitat is defined as shallow infaunal (depths of 0.5–2 cm) or deep infaunal (at depths greater than 2 cm) (Murray, 1991; Barmawidjaja *et al.*, 1992; Linke & Lutze, 1993; Buzas *et al.*, 1993; Jorissen *et al.*, 1995). Most benthic foraminifera seem to prefer the sediment–water interface where the most abundant resources are available (van der Zwaan *et al.*, 1999). Many factors have been proposed to explain benthic foraminiferal microhabitat distribution. Two of them, oxygen concentration and organic matter flux (food availability), seem to play an important role (van der Zwaan *et al.*, 1999). In most cases, these factors cannot be separated and the combination of their effects is considered to be the real regulator of benthic foraminifera microhabitat position (Jorissen *et al.*, 1992; Linke & Lutze, 1993; Jorissen *et al.*, 1995; Jorissen, 1999).

Jorissen *et al.* (1995) and Loubere (1997) demonstrated that the redox zone depth, which depends on organic flux and oxygen, regulates the microhabitat position. When the redox zone is deep, the oxygen content is high and organic flux is low or moderate. The first centimetres of sediments are rich in epifaunal and shallow infaunal taxa, whereas deeper layers contain intermediate and deep infaunal species. As the oxygen demand increases, the redox zone rises, reducing the oxygenated levels and, thus, determining an important change in benthic faunal compositions. In this ecological regime, taxa having infaunal microhabitats dominate the assemblages. With further loss of oxygenation the infaunal taxa that are less tolerant to low oxygen conditions will be gradually replaced by infaunal taxa with greater resistance to lower oxygen conditions (van der Zwaan & Jorissen, 1991; Barmawidjaja *et al.*, 1992).

Some investigations have demonstrated, however, that foraminiferal microhabitats should not be classified according to a static concept but according to a dynamic process, since some species are able to change their life position (Jorissen, 1988; Buzas *et al.*, 1993; Linke & Lutze, 1993). The ability to change microhabitats is limited to some taxa, termed 'potentially infaunal taxa'. These are able to track seasonal fluctuations of critical oxygen levels within the sediment (Barmawidjaja *et al.*, 1992).

Recently, Murray (2001) argued that oxygen levels and food supply largely control the benthic foraminiferal distribution only in the deep marine environments. On the contrary, in shallow marine environment, he considers that it would be too simplistic to attempt to define their distribution only in terms of oxygen and food supply, because other factors have been shown to play a major role.

In southern Italy, attention has been focused on the Montalbano Jonico composite section, which is more than 400 m thick. Two principal marine domains, deep and shallow, were recognized on the basis of benthic fossil assemblages (Ciaranfi *et al.*, 1997, 2001). Since cyclic oxygen fluctuations were evident, the microhabitat preference distribution of the benthic foraminifera in the composite section was presented. The aim of this paper is to interpret the microhabitats of the Pleistocene foraminifera with reference to modern data and to use that information to infer past oxygen conditions.

AREA OF STUDY

The Montalbano Jonico composite section crops out in the Lucania basin, one of the minor basins of the Bradano Trough (Casnedi, 1988). This basin is limited westward by the external Apennines thrust belt and eastwards by the foreland carbonate units (Fig. 1a). Along the internal border, the Pliocene and Early

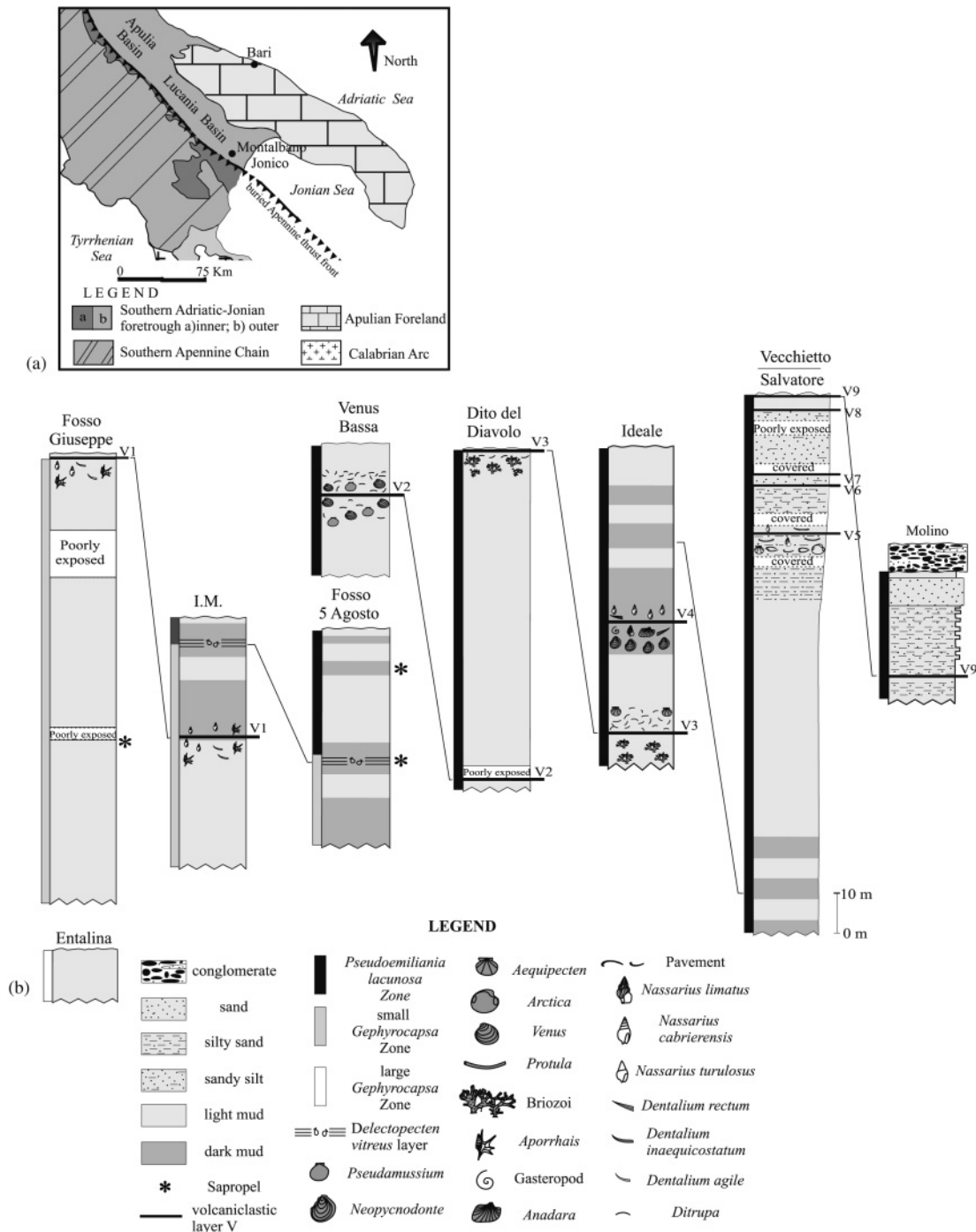


Fig. 1. (a) Location of the Lucania basin, southern Italy; (b) the selected stratigraphic sections that crop out in the area of Montalbano Jonico town. (Modified from Ciaranfi *et al.*, 2001).

Pleistocene siliciclastic sediments were affected by strong uplift, while moderate subsidence characterized the external border (Ciaranfi *et al.*, 1997, 2001). During the late Early Pleistocene, the more internal portion of the Lucania basin evolved due to a relative sea-level fall caused by the uplifting of the Apennine chain. Consequently, erosional truncation of land areas occurred, up to almost complete removal of Pleistocene sediments. By contrast, the depocentral areas of the Lucania

basin were affected by strong subsidence that caused a relative sea-level rise. Consequently, a narrow and deep trough was formed, in which the deposition of hemipelagic sediments took place. During the Early Pleistocene, the depocentral areas and the foreland border of the Lucania basin were involved progressively in the Bradano Trough evolution caused by the moving eastward of the uplifting Apennines border. During the Middle Pleistocene, a generalized shallowing phase took place,

causing the subaerial exposure of silty-clayey and silty-sand successions.

Montalbano Jonico composite section

In the area of Montalbano Jonico town, correlation of several exposed successions allows the reconstruction of a continuous marine succession, about 450 m thick, belonging to the 'Argille subapennine' Formation (Fig. 1b). The section consists of coarsening-upward deposits, from muddy clays to muddy sands, and represents one of the more recent onland marine Pleistocene successions (Ciaranfi *et al.*, 1997, 2001). The vertical distribution of macro and micro invertebrate fossil assemblages (Ciaranfi *et al.*, 1997; D'Alessandro *et al.*, 2003; Stefanelli, 2003) indicates changes of the primary environmental parameters, particularly, bathymetry, sedimentation rate and oxygen content at the bottom–water interface and in sediment pore water.

The Montalbano Jonico composite section is interrupted by a gap. A lower part termed 'Interval A' and an upper part termed 'Interval B' can be identified (Fig. 2).

Interval A is about 168 m thick and is characterized by hemipelagic muds. The foraminiferal assemblages are composed of *Globocassidulina subglobosa*, *Globobulimina affinis*, *Bulimina marginata*, *Cibicidoides* sp., *Hyalinea balthica*, *Uvigerina* group 'costate forms' and *Sphaeroidina bulloides* (Stefanelli, 2003) and indicate the deposition of this interval in a deep sedimentary basin, consistent with the upper bathyal–lower circalittoral zone (from 500 m to 110 m, *vide* Sgarrella & Moncharmont Zei, 1993). A regressive trend seems to begin around the volcanoclastic layer V1 at about 115 m above the base. The very low diversity benthic species detected in intervals at different heights, precisely, at 40 m, 68.5 m, 70 m, from 135 m to 141 m, and 160 m, allows the recognition of five episodes of strong oxygen deficiency. The high dominance of *Globobulimina affinis*, *Bolivina alata*, *Bolivina dilatata* and *Brizalina spathulata* in the assemblages associated with three of these episodes suggests they are sapropels, in agreement with the criteria of Cita & Podenzani (1980), Nolet & Corliss (1990), Sen Gupta & Machain-Castillo (1993) and Jorissen (1999). In addition, in these intervals, *Delectopecten vitreus* discontinuous pavements are recognized, which are considered to be marker beds of hypoxic episodes (D'Alessandro *et al.*, 2003).

Within the uppermost two sapropels, oxygen isotope stages 25 and 23 (Ciaranfi *et al.*, 2001), the first occurrence of *Gephyrocapsa* sp. 3 and the last common occurrence of *Reticulofenestra asanoi* were found (Maiorano *et al.*, 2004). Based on these data, the two sapropels correspond well to the sapropels associated with insolation-cycles 90 and 86. The other interval is simply marked as S because of the absence, at the moment, of specific chrono-biostratigraphic references. Oxygen declines observed in the other intervals, i.e. SI and SII, may also be linked to rapid burial events (D'Alessandro, pers. comm).

Interval B is about 280 m thick and consists of muds, and silty muds and silty sands in its topmost part. The occurrence in the shallow foraminiferal assemblage, which includes individuals belonging, above all, to Elphidiidae, Miliolidae and Discorbidae (Stefanelli, 2003), indicates the deposition of this interval in a shallow sedimentary basin, consistent with the upper circalittoral–lower infralittoral zone (from about 110 m to 40–30 m, *vide* Sgarrella & Moncharmont Zei, 1993). Interval B

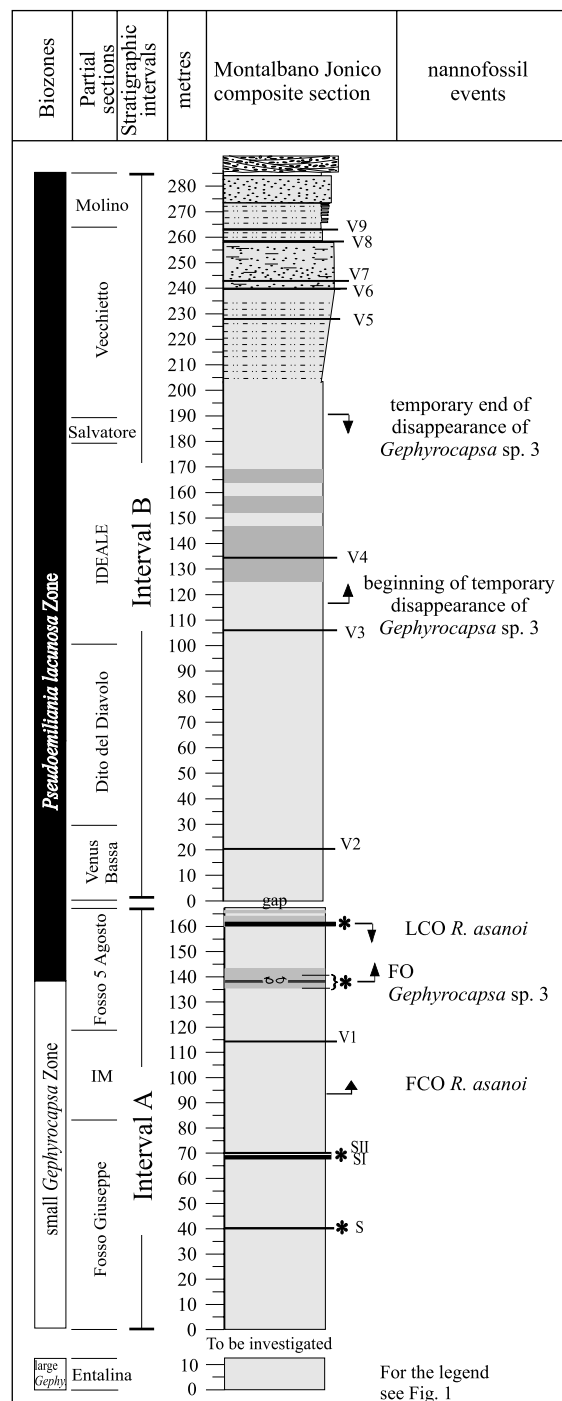


Fig. 2. The Early–Middle Pleistocene Montalbano Jonico composite section, over 400 m thick, plotted against the nannofossil events and biozones. (Modified from Maiorano *et al.*, in press). The section is interrupted by a gap. A lower part (Interval A) and an upper part (Interval B) can be identified. The presence of macrofossil remains close to the volcanoclastic layers provided the precise identification of these layers, thus, allowing their use as marker beds for the reconstruction of the succession (Ciaranfi *et al.*, 1997, 2001).

includes eight volcanoclastic horizons (V2 to V9), respectively, at 20 m, 105 m, 134 m, 228 m, 240 m, 243 m, 257 m and 263 m. The volcanoclastic layers, made of ash, sands rich in volcanic

minerals and pumice clasts, have been referred to alkaline undersaturated volcanism, probably coming from a southern Italy volcanic source (Ciaranfi *et al.*, 1996). About 10 m above the layer V3 and about 50 m above the layer V4, the beginning of the temporary disappearance of *Gephyrocapsa* sp. 3 and the end of its temporary disappearance, respectively, were found (Maiorano *et al.*, 2004).

MATERIAL AND METHODS

Approximately 470 samples were analysed for their benthic foraminiferal content. The samples were collected every 70 cm in Interval A, every 40 cm around the sapropel associated with I-cycle 90 and every 1.30 m in Interval B. The fraction >63 µm was examined in order to allow direct comparison with data from the literature. About 300 individuals were counted for every fraction, re-calculated as percentage values and plotted in curves to display the vertical distribution of each taxon. Species with relative frequencies above 1% were divided into three groups, according to Murray (1991), Jorissen *et al.* (1992), Barmawidjaja *et al.* (1992), Jorissen (1999) and Jorissen & Wittling (1999): i.e. epifaunal, shallow infaunal and deep infaunal (Appendix A). Frequencies of species were then plotted in curves for each group.

As the decline in oxygen gradient principally causes a decrease in the benthic faunal diversity, the Shannon Index $H(S)$, following the Shannon–Wiener information equation (Buzas & Gibson, 1969), was also calculated, in order to trace the changes in the faunal diversity.

In order to extract an empirical curve of oxygen concentration from the Early–Middle Pleistocene benthic foraminiferal assemblages, the equation of Baas *et al.* (1998): $y = 1.686 + 0.03337x$ is used, where y is the oxygen concentration in ml l⁻¹ and x is the Benthic Foraminiferal Oxygen Index (BFOI) value. The BFOI is calculated following the equations of Kaiho (1994):

$$[O/(O + D)] \times 100, \quad (1)$$

where O and D are the numbers of specimens of oxic and dysoxic indicators, respectively;

$$\{[S/(S + D)] - 1\} \times 50 \text{ when } O = 0, \quad (2)$$

where S is the number of specimens of suboxic indicators of group B.

It must be emphasized, however, that in order to enable the application of Kaiho's model to the investigated succession, some limitations are encountered. First, the number of dysoxic indicators encountered by Kaiho is much higher than the number of dysoxic indicators found in this study (Appendix B). The discrepancy is certainly related to the different water depth of the investigated section. The Montalbano Jonico composite section was deposited in a shallower sedimentary basin when compared to the sites investigated by Kaiho. Secondly, the small specimens of oxic indicators are classified as oxic rather than suboxic indicators because, in the Montalbano Jonico composite section, these species are strictly related to well-oxygenated sediments (Stefanelli, 2003). Moreover, the species *Cibicidoides ungerianus* and *Cibicidoides pachydermus*, listed in the studied assemblages, are species not specifically identified by Kaiho.

This may denote important differences in the linkages of benthic foraminiferal communities to ambient bottom-water oxygenation.

RESULTS

Benthic foraminiferal trends

In Figure 3 the stratigraphic distributional patterns of the major epifaunal and infaunal species are displayed for Interval A. Among the epifaunal taxa, *Cibicidoides* spp. and *Hyalinea balthica* are present with significant frequencies. Yet, they are rarely present in the same intervals since they present an opposite cyclic trend. *Bigenerina nodosaria* and *Quinqueloculina* group are present at low frequency. Among the shallow infaunal taxa, the most abundant species are *Bulimina marginata*, *Cassidulina carinata* and the *Uvigerina* group 'costate forms'. *B. marginata* increases in frequency in the lowermost part of the stratigraphic interval and between the layers S and SI. Then, it shows a decreasing trend in abundance towards the top. *C. carinata* is constantly present; its maximum frequency is recorded immediately below the sapropels associated with I-cycles 90 and 86. The species decreases in abundance and disappears in the layers of oxygen deficiency. The *Uvigerina* group 'costate forms' shows an opposite trend to *C. carinata* and *B. marginata*, with its maximum frequency recorded around the volcanoclastic layer V1. *Sphaeroidina bulloides* is frequent immediately below the interval S and shows a general increasing trend in abundance towards the top of Interval A. The *Bolivina* group (including the species *B. alata* and *B. dilatata*) and *Brizalina spathulata* are always present with frequencies less than 20%, except in the intervals marked as SI, SII and in sapropels associated with I-cycles 90 and 86. In these levels they show the maximum frequency and are dominant. *Gyroidina* sp. is less frequent and shows a decreasing trend in abundance towards the top. The mostly significant deep infaunal taxon is *G. affinis*. It is more abundant in the stratigraphic portion below V1 and decreases in abundance towards the top. The peaks of maximum frequency are recorded in S, SI, SII and in the sapropel associated with I-cycle 90. Also frequent are *G. subglobosa*, *Melonis* sp. and *Textularia* sp. The former taxa decrease in abundance towards the top and show an opposite trend to *Textularia* sp. These taxa, however, disappear in the layers of oxygen depletion.

In Figure 4, the distribution of the microhabitat groups immediately below, across and above the sapropel layers and the intervals SI and SII is plotted together with the $H(S)$ values. In these layers, the epifaunal group disappears and the $H(S)$ values strongly decrease. The assemblages are characterized by a great number of individuals, belonging to the shallow infaunal species *B. alata*, *B. dilatata* and *B. spathulata* and to the deep infaunal species *G. affinis*.

Focusing on the distributional patterns within the intervals S, SII and the sapropel unit associated with I-cycle 90, *G. affinis* and *Bolivina* group are never simultaneously present in the assemblages. *G. affinis* dominates the assemblage at the bottom layers and the *Bolivina* group the assemblage at the top. In SIII the assemblage is rich in individuals of *G. affinis*. Conversely, the *Bolivina* group dominates the assemblage within the sapropel unit associated with I-cycle 86.

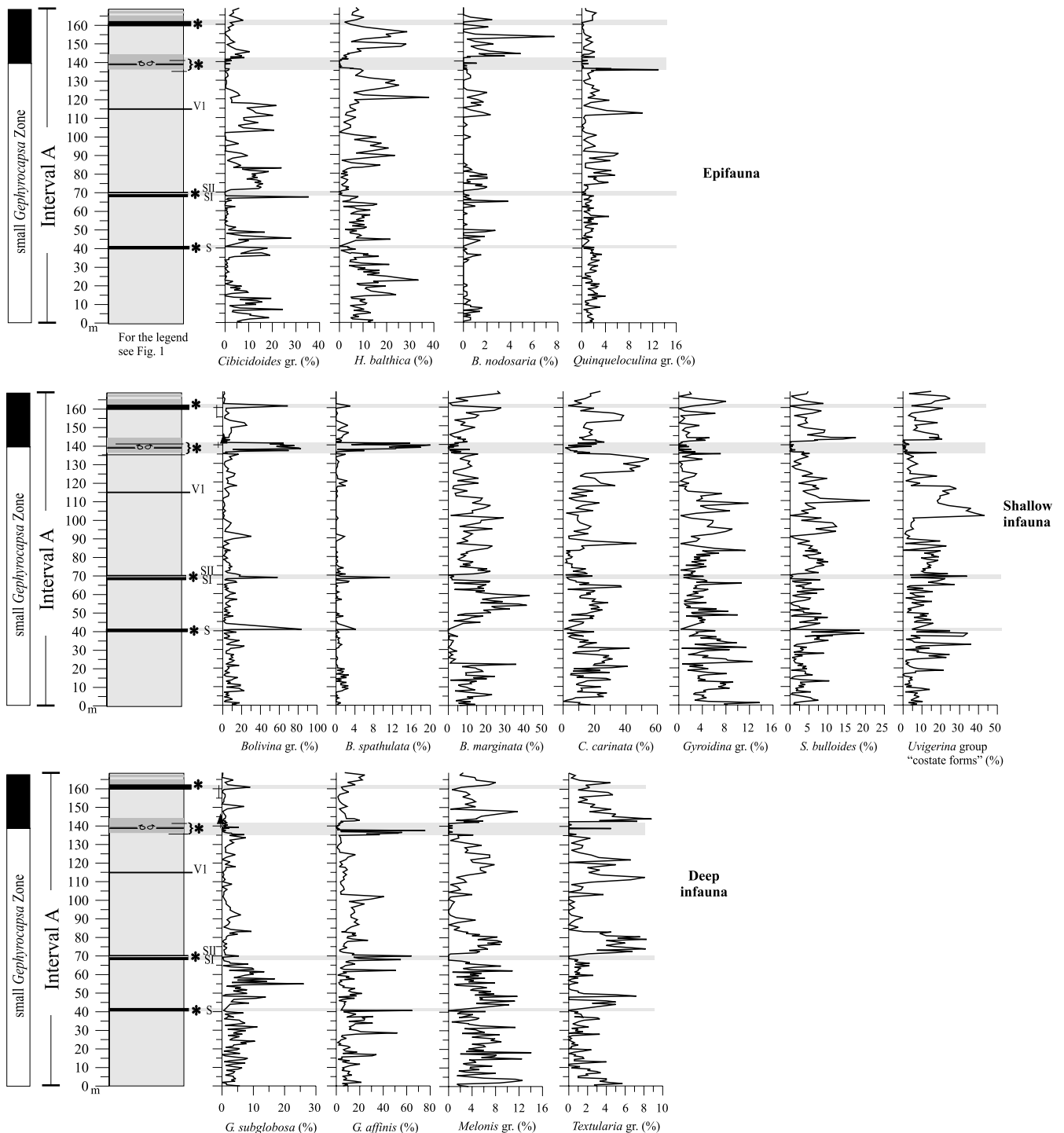


Fig. 3. Stratigraphic distribution of the most representative taxa in Interval A.

In a short interval, between SI and SII and within the sapropel associated with I-cycle 90, an increase in abundance of the shallow infaunal taxa *C. carinata* and *Uvigerina* 'costate forms' group that replace *Bolivina* and *G. affinis*, is observed also associated with the increase of *H(S)* values.

In Figure 5 the distributional patterns of the most significant epifaunal and infaunal species are displayed for Interval B.

Elphidium advenum, *Elphidium complanatum*, *Elphidium crispum* and *Quinqueloculina* spp. are the most representative epifaunal taxa that show cyclic trends of rich and poor intervals. In the shallow infaunal group, different distributional patterns are observable. *Protoelphidium granosum*, *Criboelphidium decipiens* and *Ammonia beccarii* increase in frequency in the intervals in which *C. carinata*, *B. marginata* and *Valvulineria* sp. are absent

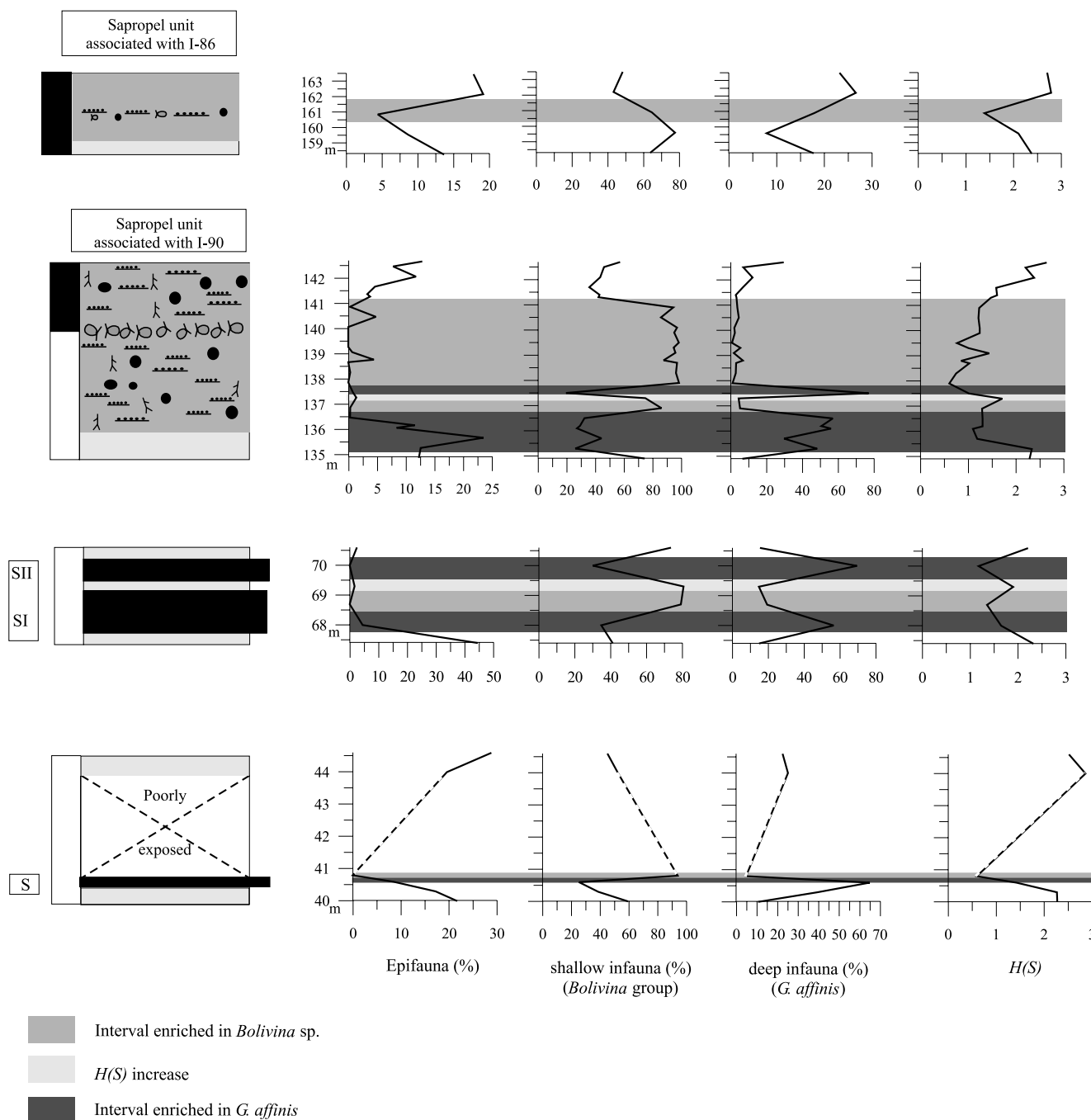


Fig. 4. Distribution patterns across the intervals of strong oxygen depletion.

or poorly represented, and vice versa. The *Uvigerina* group 'costate forms' shows an opposite cyclical trend to *C. carinata*, *B. marginata* and *Valvulineria* sp. The group has its maximum frequency in abundance in the stratigraphic interval around the volcanoclastic layer V4, from 125 m to 170 m. It decreases in abundance in the following 30 m where, simultaneously, *A. beccarii* and the unkeeled *Elphidium* increase. Deep infauna is represented only by the *Melonis* and *Textularia* groups, which occur from 125 m upwards.

Foraminiferal microhabitat distribution

In Figure 6 the distributional patterns of epifauna, shallow and deep infauna and the *H(S)* values are displayed throughout the Montalbano Jonico composite section. Epifauna is constantly present in the composite section. It disappears in the intervals documented as sapropels, where, conversely, the deep infauna component recorded its maximum frequency. The shallow infaunal position appears to be the most preferred by the Early–Middle Pleistocene foraminifera. Faunal diversities are

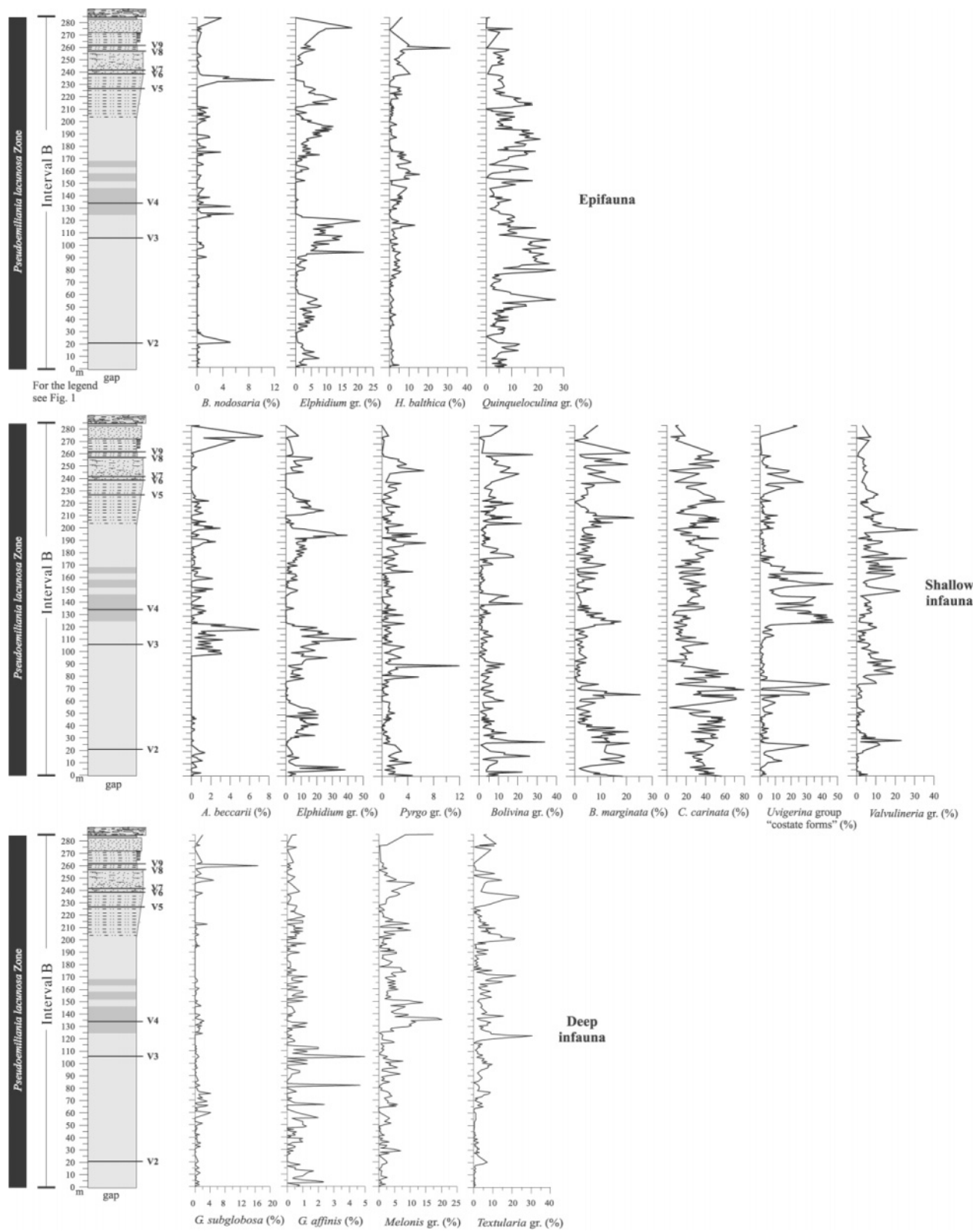


Fig. 5. Stratigraphic distribution of the most representative taxa in Interval B.

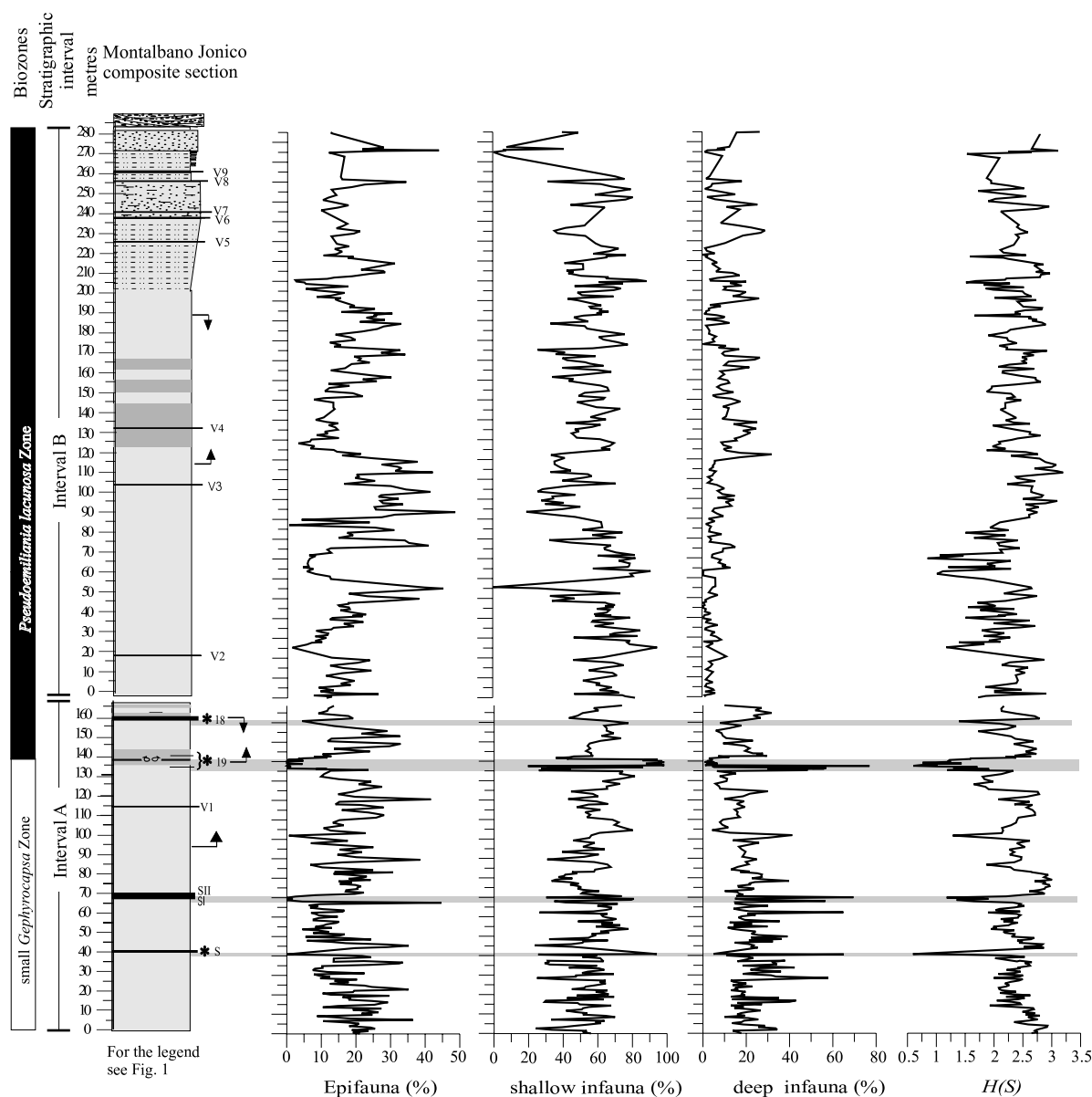


Fig. 6. Distribution patterns of the microhabitat preferences in the succession plotted with the Shannon Index. $H(S)$ is calculated using the program 'Past' (Hammer *et al.*, 2001).

variable. In Interval A and in the lowermost part of Interval B the values decrease from $H(S)=3$ to $H(S)=0.7$, on average, in the intervals of sapropel deposition. In the remaining part of Interval B, the faunas are well diversified with $H(S)$ values ranging between 3 and 2.

Palaeo-oxygen changes

In Figure 7 the sample scores of Factor 3, the principal component extracted by principal component analysis for the composite section and reflecting oxygen variation (Stefanelli, 2003), is shown. It is plotted together with the palaeo-oxygen curve reconstructed using the Baas equation. Factor 3 reflects oxygen content since it is loaded by opposing indicators of oxygen. *Cibicidoides* and *Elphidium* group, reported to prefer the well-oxygenated marine bottom (Murray, 1991), show

the highest positive loadings. *Valvulineria* sp., *C. carinata*, *B. marginata* and *Bolivina* sp., noted to prefer environments with moderate oxygen depletions in the bottom and pore-water sediments (Lutze & Coulborn, 1984; Sen Gupta & Machain-Castillo, 1993; Rathburn & Corliss, 1994), show the highest negative loadings. The graphic trend of the factor shows cyclic oxygen fluctuations, in which phases of 'good' oxygenation are alternated with phases of 'poor' oxygenation. In the generic trend, the factor is suggestive of better oxygenated conditions in Interval A when compared to Interval B.

In Interval A, the trend of the palaeo-oxygen curve is similar to the trend of Factor 3. The sole discrepancy is in the sapropel associated with I-cycle 86, where the factor indicates good oxygenation. Indeed, in this interval the sample score is distorted due to the scarcity of the benthic fauna. Only

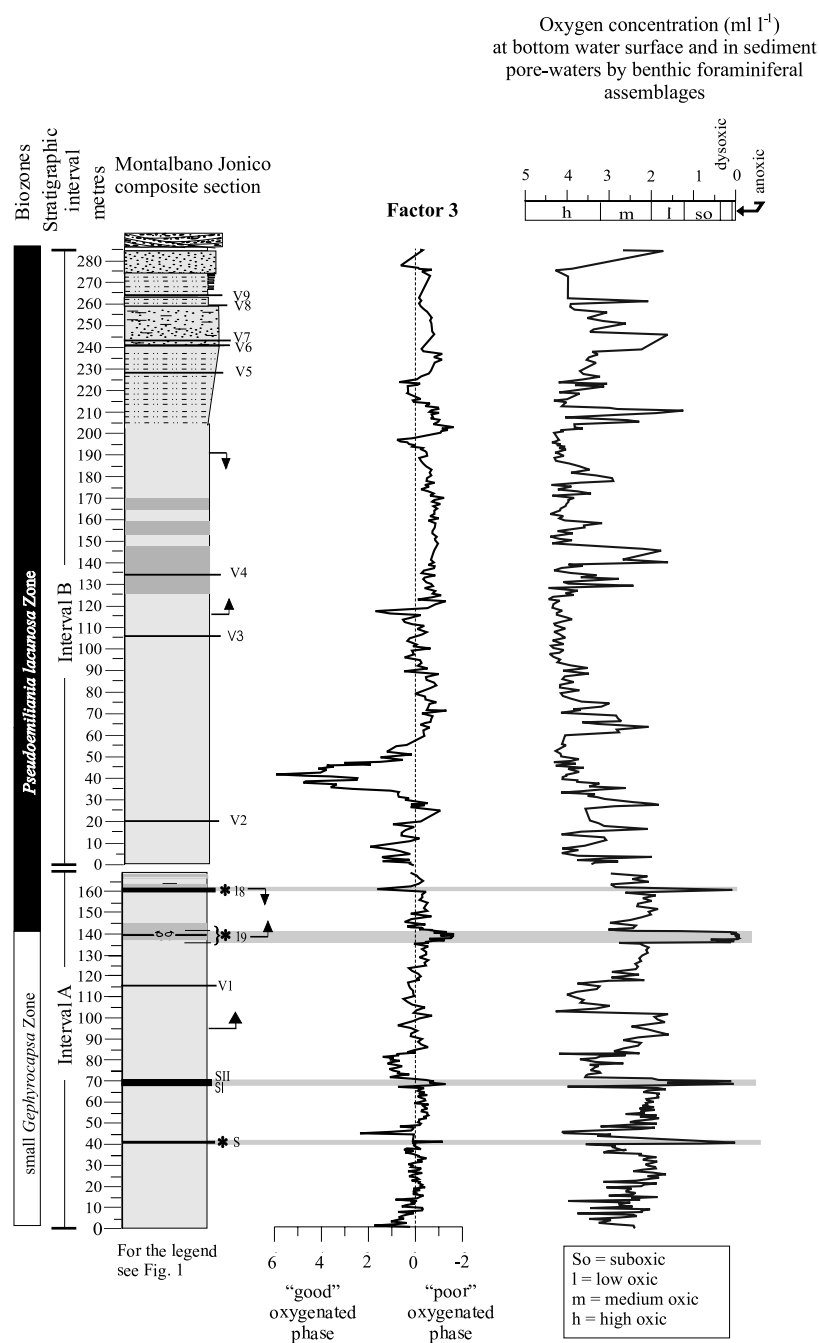


Fig. 7. Oxygen fluctuations reflected by the sample scores of Factor 3 and quantified by using Baas's equation. Factor 3 is one of the principal components extracted for the composite section performed by using PCA-analysis. The program SPSS version 9.0 was used for the Principal Component Analysis.

74 individuals were counted, 51 of which belong to the genus *Bolivina*. The palaeo-oxygen curve shows fluctuations in the high/medium oxia regime for the phases of 'good' oxygenation and low oxia condition for the phases of 'poor' oxygenation. In the intervals of sapropel deposition, the dissolved oxygen regime is interpreted as dysoxic.

In contrast, in Interval B the palaeo-oxygen curve reconstructs high/medium oxia regimes, suggesting better

oxygenated conditions when compared with Interval A. Accordingly, the results appear to be clearly discordant with the sample scores of Factor 3. However, observing the general trend of the curves, they are similar. The sole most evident discrepancy is recorded in the stratigraphic portion above the volcanoclastic V4. Between 148 m and 180 m, the palaeo-oxygen curve indicates a high oxia regime in the phase of 'poor' oxygenation.

DISCUSSION

Palaeoenvironmental implications

Interval A. In the lower part of the Montalbano Jonico composite section, the distributional patterns of *Cibicidoides* and infaunal taxa delineate trends similar to those of the oxygen fluctuations. The decreasing trend in abundance of the former taxon and the increasing trends in abundance of the latter taxa seem to reflect well the reduction in the oxygenated levels towards the top. In the phases of 'good' oxygenation, one detects well-diversified faunas characterized by the presence of the epifaunal *Cibicidoides* sp. and *H. balthica*, together with the shallow infaunal *B. marginata* and *C. carinata* and the deep infaunal *G. subglobosa*, *G. affinis* and *Melonis* group. This vertical microhabitat distribution suggests that the bottom water is highly oxygenated and that the oxygen penetration, within the sediment column, reaches several centimetres, i.e. from 2 cm to 4 cm below the sediment surface (Loubere, 1997). This means that the redox zone is deep (Fig. 8a). In the 'poorly' oxygenated intervals, important changes in benthic assemblage compositions are detected. The faunas are less diversified, the epifaunal *Cibicidoides* sp. disappears and the assemblages are enriched in the infaunal component. The predominance of taxa having infaunal microhabitat preference suggests the reduction of the oxygen levels, linked to the shallowing of the redox zone. *Cibicidoides* sp. is commonly distributed in the modern stable marine waters and relatively rich in oxygen content (Murray, 1991) and reported to be intolerant of environmental stress, in particular oxygen deficiency at the bottom (van der Zwaan, 1983). Its disappearance indicates decreased oxygen availability at the bottom water, thus reducing oxygen penetration in the sediment column.

It is interesting to observe that *Cibicidoides* sp. and *H. balthica* have opposite distributional patterns. Though having the same shallow microhabitat position, these taxa occur in different oxygenated conditions. Indeed, F. J. Jorissen (pers. comm.) suggests that their patterns may be controlled by organic flux rather than oxygen content. Schmiedl *et al.* (2003) include *H. balthica* in the group of taxa together with *B. dilatata*, *B. marginata*, *C. carinata* and *G. neosoldanii*. They report these taxa as commonly distributed in mesotrophic to eutrophic environments. Hence, the shallowing of the redox front could be linked to the increase of food availability that leads to an increased consumption of oxygen (Jorissen *et al.*, 1995) (Fig. 8b).

Also interesting is the distribution pattern of the *Uvigerina* group 'costate forms'. The group (dominated by *U. peregrina*) is commonly reported to tolerate oxygen-stressed conditions (Corliss, 1979; Verhallen, 1991). Gooday (1994) reported that the oxygen content of the overlying water masses, with $O_2 < 2 \text{ ml l}^{-1}$, seems to be the primary factor controlling its distribution. Indeed, in the Montalbano Jonico composite section, *Uvigerina* is detected with high percentages in the phases of 'good' oxygenation, thus, suggesting that it prefers oxygenated sediments. Yet, this ecological interpretation could be in good accordance with the opposite trend shown by *C. carinata* and *B. marginata*. These species are commonly found in environments with moderate oxygen depletion in the bottom and sediment pore-water (Lutze & Coulborn, 1984; Sen Gupta & Machain-Castillo, 1993; Rathburn & Corliss, 1994).

Oxygen deficiency layers. When a further loss of oxygenation takes place, i.e. sapropels, the infaunal taxa that are less tolerant to low oxygen conditions are replaced by infaunal taxa with greater resistance to lower oxygen conditions. *G. affinis*, *B. alata*, *B. dilatata* and *B. spathulata* become the dominant species of these intervals, since all the other taxa cannot survive under highly stressed oxygen conditions. In this ecological setting, the redox zone is shallow and anoxic conditions are encountered 0.5 cm below the sediment surface (Loubere, 1997) (Fig. 8c).

The genera *Globobulimina* and *Bolivina* are known to characterize the sapropel-associated assemblages (Mullins *et al.*, 1985; Nolet & Corliss, 1990; Miao & Thunell, 1993; Sen Gupta & Machain-Castillo, 1993). *G. affinis* is reported to be the species 'most closely associated' with late Quaternary anoxia in the Mediterranean, found immediately below, above and occasionally within the sapropel (Mullineaux & Lohmann, 1981; Nolet & Corliss, 1990; Sen Gupta & Machain-Castillo, 1993). Jorissen (1999) defines the species as 'especially resistant to low oxygen conditions'. *B. alata* is considered a shallow infaunal species preferring low-oxygen conditions and burrowing into sapropels (Cita & Podenzani, 1980; Sen Gupta & Machain-Castillo, 1993; Miao & Thunell, 1993). In sediments, in which dissolved oxygen is below 0.3 ml l^{-1} , *Bolivina* dominates the assemblage, exceeding 60% (Mullins *et al.*, 1985). The *Bolivina* genus, together with *B. spathulata*, is defined as a 'more opportunistic taxon, but less resistant to very low oxygen concentrations' (Jorissen, 1999). Barmawidjaja *et al.* (1992) consider the species *B. spathulata* among the taxa that increase in abundance when the total foraminiferal density decreases, probably because it is the most resistant, together with *Bolivina*, to lowered oxygen concentrations.

In the sapropel layers of the Montalbano Jonico succession, one observes the regular replacement of the deep infaunal *G. affinis* by the shallow infaunal *Bolivina*. Van der Zwaan & Jorissen (1991) and Barmawidjaja *et al.* (1992) have suggested that deep infaunal species, under decreasing oxygen content, move up to the sediment-water interface, where they gradually replace the taxa that are less tolerant of oxygen content. The replacement of *G. affinis* by *Bolivina* may be suggestive of oxygen conditions pushed to minimum extreme at the bottom of the sapropels recorded in the Montalbano Jonico composite section and a relative improvement of oxygenation at the top. This palaeoenvironmental reconstruction appears to be plausible with the different recorded planktonic foraminiferal distributions. In intervals rich in individuals of *G. affinis*, the planktonic assemblages are dominated by the *Globigerinoides ruber* group, which indicates warm conditions and low salinity in surficial water masses (Capotondi & Vigliotti, 1999). Conversely, in intervals rich in individuals of *Bolivina*, the decrease in abundance of the *G. ruber* group and the dominance of *Globigerina bulloides* and *Neogloboquadrina dutertrei* suggest cold and productive surface waters (Rohling *et al.*, 1997; Negri *et al.*, 2003).

In short intervals between SI and SII and within the sapropel associated with I-cycle 90, the decrease in abundance of *G. affinis* and *Bolivina*, simultaneously with the repopulation in the assemblage by the shallow taxa *C. carinata* and *Uvigerina* and the increase in $H(S)$ value, allows the identification of short time intervals in which sapropel deposition is interrupted (see Fig. 4).

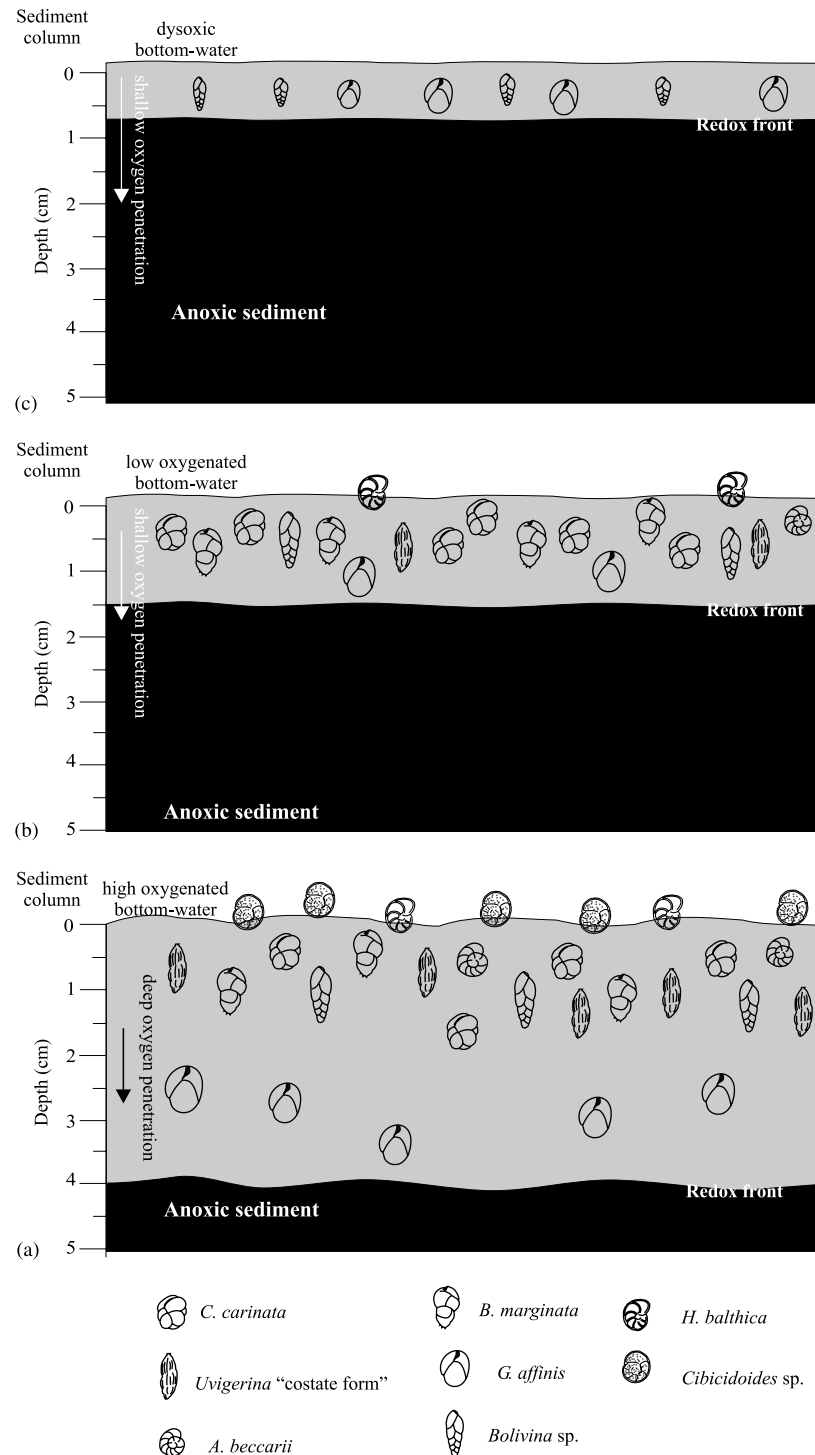


Fig. 8. Schematic reconstruction showing the microhabitat preferences with respect to the redox front position in the Montalbano Jonico composite section: (a) phases of 'good' oxygenation; (b) phases of 'poor' oxygenation; and (c) sapropel layers.

The change in the assemblage composition is suggestive of an improvement in oxygen content at the bottom water and of sediment pore-water that have caused a temporary deepening of the redox zone. The oxygen improvement is mirrored by the palaeo-oxygen curve from this study, which indicates a suboxic regime.

Interval B. In the shallow domain, the deep infaunal microhabitat is poorly represented. The low frequency of deep infaunal species is likely to be linked to the regressive trend of the sedimentary basin. *G. affinis* and *G. subglobosa* are commonly distributed in deep marine waters with depths greater than 100–150 m (Murray, 1991; Sgarrella & Moncharmont Zei, 1993).

In the phases of 'good' oxygenation, the assemblages are composed of epifaunal and infaunal taxa. The presence of *Elphidium* and *Quinqueloculina* group, associated with *Ammonia* group, *C. carinata*, *B. marginata*, the *Uvigerina* 'costate forms' group and *Valvulineria* sp., indicates the deep position of the redox zone within the sediment column. The palaeo-oxygen curve reconstructs a high oxic regime, thus, confirming the oxygen penetration at great depth. In the shallow areas of the Mediterranean Sea, the trophic levels are higher than in the deep areas (Jorissen *et al.*, 1992; Schmiedl *et al.*, 2000). This means that the consumption of oxygen is very high. In the northern and shallow Adriatic Sea, Jorissen *et al.* (1995) observed that, under eutrophic conditions, the depth of the microhabitats is not deeper than 1–2 cm below the sediment surface. In the phases of 'poor' oxygenation, one observes an increase in the infaunal position. As mirrored by the palaeo-oxygen curve, oxygen availability at the bottom–water interface and in the sediment pore-water, decreases. Consequently, the redox zone rises, thus, causing the disappearance of the epifauna.

It is interesting to observe the distributional patterns of the *Uvigerina* 'costate forms' group. With respect to Interval A, the *Uvigerina* group is frequent in the 'poorly' oxygenated intervals and disappears in the 'good' oxygenated phases. The cause that may explain this contradictory behaviour is the ability of *Uvigerina* to change its living depth. Studies conducted by Loubere *et al.* (1995) on the microhabitats of *U. peregrina* indicate that this species has productive populations at superficial and deeper infaunal levels within the sediments. Where bottom water oxygen content is low and the anoxic boundary in the sediment is shallow, the microhabitat of the *U. peregrina* population is shallow. If oxygen penetrates deeper into sediment, the population remains deeper infaunal. Accordingly, in Interval B, its major occurrence in 'poorly' oxygenated phases supports the minor depth of the redox zone in the sediment column. In Interval A, its major frequency is related to the deeper position of the redox zone.

Also of note are the distributional patterns of the keeled and unkeeled *Elphidium* sp. These taxonomic groups, although living at different depths with respect to the sediment surface, are shown to have the same distribution in the stratigraphic interval. Since the unkeeled species can tolerate low oxygen conditions (Murray, 1991), their presence (at least with low frequency) should be plausible in the phases of 'poor' oxygenation. Furthermore, the oxygen decline is not so strong, i.e. medium oxic regime, to justify their total disappearance. The same dilemma emerges for *Valvulineria* sp. This taxon is an opportunistic species able to tolerate conditions of oxygen stress characterized by high percentages of organic matter and low oxygen concentration in the sediment (Jorissen, 1987; Bergamin *et al.*, 1999). In this stratigraphic interval, the taxon shows an opposite trend to the other shallow infaunal taxa tolerating low oxygenated conditions. *Valvulineria* sp., from 55 m up to 75 m and, in the last 50 m, decreases and/or disappears, contrarily, to *C. carinata* and *B. marginata*.

From the above observations, the author concludes that in a similar shallow sedimentary basin as the one reconstructed for Interval B in which wide sea-level fluctuations are recognized, the bathymetric effect cannot be ignored. In Figure 9 the oxygen fluctuations are plotted against the palaeodepth drawn from

the stratigraphic distribution of the benthic foraminiferal assemblages (Stefanelli, 2003) and the oxygen isotope record (Brilli *et al.*, 2000, and unpublished data). In Interval B, the sedimentary cyclicity has been linked to climate control (Ciaranfi *et al.*, 2001). In the glacial periods, the shallowing phases correspond to the highly-oxygenated intervals; by contrast, in the interglacial period, the deepening phases correspond to the low oxygen conditions. As a consequence, the disappearance of *Elphidium* sp. and the increase in the *Uvigerina* group may be related to the shallowing of the redox zone as well as to the deepening of the sedimentary basin. The species of the genus *Elphidium* encountered in this study mainly live in shallow waters and disappear below 100 m; their optimum is in the depth-range of 0–50 m (Murray, 1991; Sgarrella & Moncharmont Zei, 1993). On the contrary, the costate forms of *Uvigerina* have an upper depth limit reported from about 100 m (Hasegawa *et al.*, 1990).

The lowering of the sea-level is predicted to be not deeper than 110–120 m (D'Alessandro *et al.*, 2003; Stefanelli, 2003). Consequently, the trophic conditions are unchanged when compared with the shallowing phases. This means that, in Interval B, the depth position of the microhabitat is not food-controlled, but is oxygen-controlled, in accordance with Jorissen *et al.* (1995).

CONCLUSIONS

The data from this study confirm that the position of the redox zone regulates the living depths of the Early–Middle Pleistocene benthic foraminifera. In the deep marine domain, the control on the composition and distribution of the fauna by the interplay between food availability and oxygen consumption is well supported. When oxygen availability is high and the anoxic boundary is deep, a distinct vertical microhabitat distribution is observed. As the trophic level increases, the oxygen demand increases and the redox zone rises. The epifauna disappears and, consequently, the infauna dominates the assemblages since it is more resistant to the low-oxygenated conditions. In consequence of a further oxygen loss, i.e. sapropels, the anoxic boundary is encountered immediately below the sediment surface and solely the opportunistic and more resistant taxa survive. By contrast, in the shallow marine domain in Interval B, which undergoes persistent eutrophic conditions, the depth of the microhabitats is controlled by oxygen availability. In addition to the oxygen-limited control, the wide sea-level fluctuations detected in this marine ecosystem also effect the vertical faunal distribution and composition.

Finally, the extracted curve of palaeo-oxygen drawn from Baas's equation, supports well the oxygen reconstruction made on the basis of taphofacies (Soldani, 2000) and macro benthic invertebrates (D'Alessandro *et al.*, 2003), which suggests that Interval B was better oxygenated than Interval A. The overlap of the curve on the graph of the sample scores of Factor 3 shows that, in Interval B, the phases of 'poor' oxygenation, although having the same extent when compared with Interval A, do not reflect the same dissolved oxygen regime. Yet, the dissolved oxygen regime estimated in the phases of 'poor' oxygenation, in Interval B, appears to be too high when compared with the faunal composition. In this ecological setting, i.e. high oxic regime, a major preference for the shallowest microhabitat

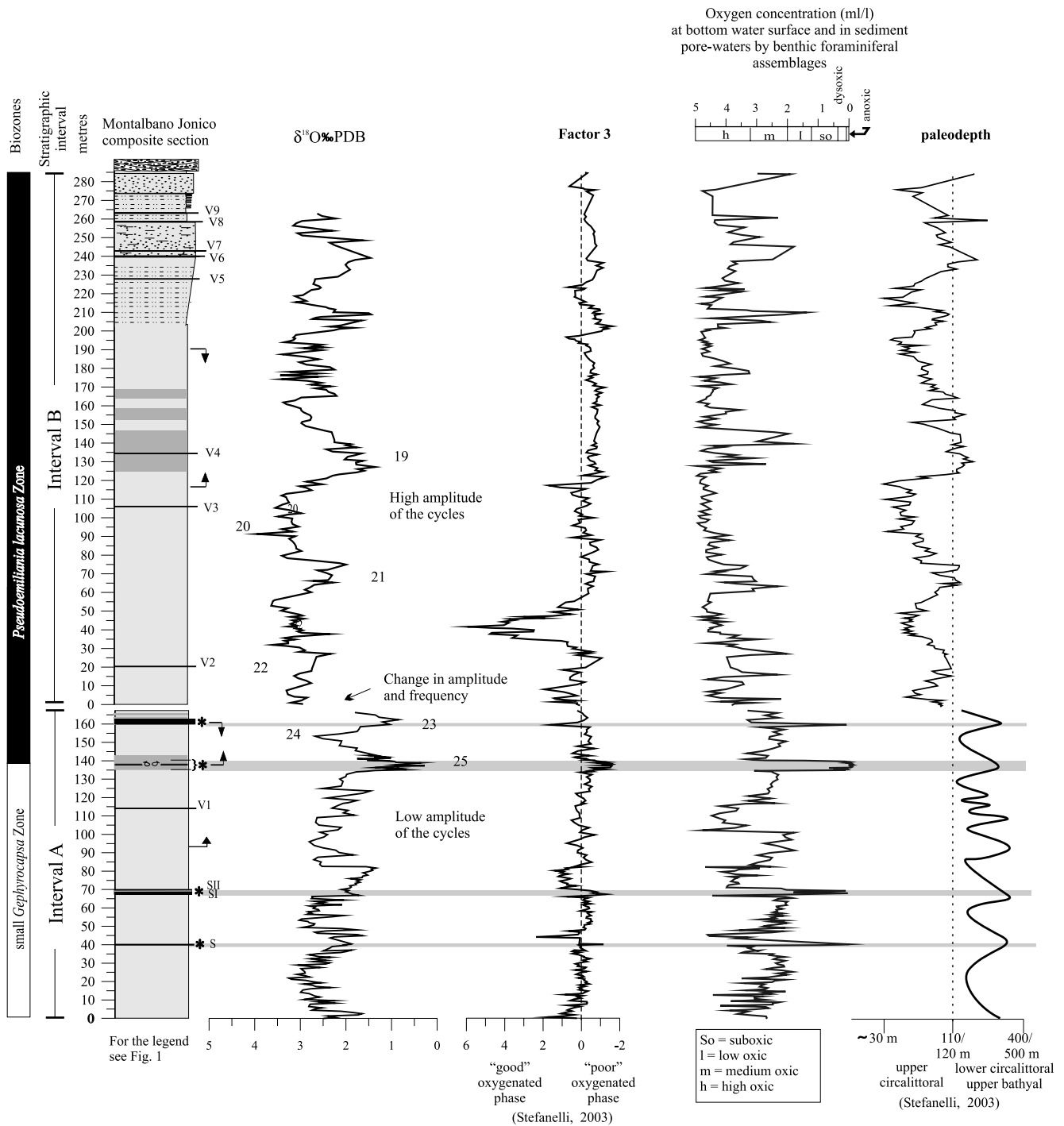


Fig. 9. Sedimentary cyclicality recognized in the Montalbano Jonico composite section. The cyclicality is linked to the different pattern of climate variation and sea-level changes between the Early Pleistocene and Middle Pleistocene (Ciaranfi *et al.*, 1997, 2001). The Early Pleistocene (Interval A) is dominated by cycles with low amplitude, linked to periodical obliquity, while the Middle Pleistocene (Interval B) is dominated by cycles with high amplitude connected to orbital eccentricity. In Interval B the glacioeustatic-controlled fluctuations are evident. For oxygen isotope analysis, the tests of *Globigerina bulloides* were used for Interval A and the tests of *Cassidulina carinata* for Interval B (Brilli *et al.*, 2000, unpublished data). The palaeodepth is reflected by Factor 1, one of the principal components extracted for the composite section performed by using PCA-analysis. Palaeodepth and Factor 3 data from Stefanelli (2003).

position should be observed. The reason that may explain this discrepancy is the BFOI estimate. A faithful application of Kaiho's criteria appears not to be possible for the upper

stratigraphic part of the composite section, probably, because of its deposition in a shallow sedimentary basin. By contrast, in the deep Interval A, generally better positive correlations can be

Epifaunal	Shallow infaunal	Deep infaunal
<i>Asterigerinata</i> spp.	<i>Ammonia beccarii</i>	<i>Amphicoryna scalaris</i>
<i>Bigenerina nodosaria</i>	<i>Bolivina alata</i>	<i>Bulimina sublimbata</i>
<i>Cibicides lobatulus</i>	<i>Bolivina dilatata</i>	<i>Globobulimina affinis</i>
<i>Cibicides refulgens</i>	<i>Brizalinaspathulata</i>	<i>Globocassidulina subglobosa</i>
<i>Cibicidoides pachydermus</i>	<i>Buccella frigida</i>	<i>Melonis barleanum</i>
<i>Cibicidoides ungerianus</i>	<i>Bulimina costata</i>	<i>Melonis soldanii</i>
<i>Elphidium advenum</i>	<i>Bulimina elegans</i>	<i>Textularia</i> spp.
<i>Elphidium complanatum</i>	<i>Bulimina elongata</i>	
<i>Elphidium crispum</i>	<i>Bulimina marginata</i>	
<i>Hanzawaia rhodiensis</i>	<i>Cassidulina carinata</i>	
<i>Hyalinea balthica</i>	<i>Criboelphidium decipiens</i>	
<i>Lenticulina</i> spp.	<i>Protoelphidium granosum</i>	
<i>Oridorsalis umbonata</i>	<i>Gyroidina</i> spp.	
<i>Planulina</i> spp.	<i>Nonion depressulum</i>	
<i>Quinqueloculina</i> spp.	<i>Pyrgo</i> spp.	
<i>Rosalina</i> spp.	<i>Pullenia</i> spp.	
	<i>Sigmoilopsis schlumbergeri</i>	
	<i>Sphaeroidina bulloides</i>	
	<i>Uvigerina</i> group costate	
	<i>Valvulineria</i> spp.	

Table A1. Taxa encountered in the study grouped according to microhabitat.

detected, although the oxygen concentrations estimated appear to be too high when compared with the fossil fauna composition.

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APPENDIX A: TAXA GROUPINGS

Table A1 lists the grouping of taxa encountered in this study on the basis of their microhabitat position. The subdivision was made following data from the literature (see text).

APPENDIX B: PLEISTOCENE OXIC, SUBOXIC AND DYSOXIC INDICATORS

Some of the Pleistocene oxic, suboxic and dysoxic indicators of Kaiho (1999) encountered in this study.

Oxic indicators

Cibicides refulgens, *Cibicidoides pachydermus*, *Cibicidoides ungerianus*, *Globocassidulina subglobosa*, *Pyrgo* spp. and *Quinqueloculina* spp.

Suboxic indicators (group B)

Bolivinita quadrilatera, *Cassidulina carinata*, *Dentalina* group, *Lenticulina* spp., *Melonis* spp., *Nonion* spp., *Oridorsalis umbonatus*, *Pullenia* spp., *Sphaeroidina bulloides*, *Trifarina angulosa*, *Uvigerina* spp. and *Valvulineria* spp.

Dysoxic indicators

Bolivina alata, *Bolivina dilatata*, *Brizalina spathulata* and *Globobulimina affinis*.

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