FORAMINIFERAL RECORD OF ENVIRONMENTAL CHANGES: PREEVAPORITIC DIATOMACEOUS SEDIMENTS FROM GAVDOS ISLAND, SOUTHERN GREECE.

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ABSTRACT

The Messinian pre-evaporitic sedimentary succession of Gavdos island (Metochia section) is a nearly uninterrupted succession of marine sediments, dominated by finely laminated diatomaceous sediments, which are cyclically alternating with marlstone and white limestone beds. The purpose of this study is to analyze in detail the benthic and planktonic foraminiferal microfauna preserved in the sediments of this section. The qualitative and quantitative analysis of the planktonic foraminifera fauna allowed the recognition of seven bioevents, which have been astronomically dated for the Mediterranean. The base of the diatomitic succession in Gavdos Island is dated at 6.696 Myr, whereas its top at 6.0 Myr. Our results suggest that two environmental parameters are the most important factors that control the community structure of the benthic foraminiferal fauna: the food availability and oxygen concentration. In addition, local upwelling phenomena evidenced by signals from the benthic foraminifera and the distribution pattern of the planktonic G. bulloides may have played a role in the faunal density and composition.

1 INTRODUCTION

Messinian evaporites in the deep Mediterranean basins and Messinian “salinity crisis” (MSC) have been the subject of several studies and speculations. Restricted environmental conditions in the Mediterranean were the main cause of the widespread deposition of evaporites. The pre-evaporitic sediments are characterized by predominantly alternations of marl/sapropel sequences (Late Tortonian to early Messinian), which pass to either diatomites (e.g. Sicily, northeastern Morocco, Algeria) or euxinic clays (e.g. northern Italy, Tyrrenian Sea, eastern Mediterranean). Palaeoenvironmental changes related to these lithological transitions are documented by faunal (e.g. Cita, 1976; Glacon et al., 1990; Benson & Rakic-El Bied, 1991; Benson et al., 1991; Sierro et al., 1993; Hodell et al., 1994) and geochemical (stable isotope) parameters (e.g. Vergnaud-Grazzini, 1983; Hodell et al., 1994; Ferretti & Terzi, 1995). The increasing accuracy of time control (Hilgen et al., 1995; Shackleton et al., 1995) improves the correlation of these phenomena throughout the Mediterranean.

The purpose of this study is to reconstruct the palaeoenvironmental trends and events leading to the MSC during the transition from the Tortonian open marine conditions to the Messinian evaporitic environments, in the Eastern Mediterranean basin. The succession of palaeoenvironments and foraminifera assemblages is analyzed from the time period before the Messinian evaporitic deposition in Metochia section, Gavdos Island.

2 MATERIAL AND METHODS

2.1 Study area

Metochia section (NE Gavdos Island, Fig. 1), is a Late Miocene hemipelagic marl succession characterized by the rhythmic alternations of poorly non-bioturbated brown-grey, organic rich lami-
nated beds (sapropels) and bioturbated, light grey-blue, homogeneous, hemipelagic marl beds. The thickness of successive sapropel and marl beds varies such that distinct small and large scale clusters can be distinguished. The upper part of this sequence is composed of 14 meters of diatomite deposits. This part consists of alternations of diatomite beds with white limestone beds, clay diatomites, diatomaceous marls and grey thin-bedded limestone (Triantaphyllou et al., 1999) (Fig. 1). Hilgen et al., (1995) have counted 38 sedimentary cycles in these deposits and dated the base of the diatomite sequence at 6.696 Ma. Perez-Folgado et al. (2003) described the lower part (6.606-6.5 Ma) of the sedimentary cycles of the diatomite sequence as typically tripartite, composed of light-brown marls (sapropel-like), a thick diatomite and an homogenous marl.

**GAVDOS ISLAND**

Fig. 1. Location map and lithostratigraphical column of the upper part of the Metochia Section.

### 2.2 Micropaleontological analysis

40 samples from the diatomite sequence of Metochia section were collected. After washing and drying, samples were sieved through 125 and 63 μm mesh. From the >125 μm size fraction 300-500 individuals of foraminifera were randomly picked. Quantitative and qualitative analysis of the benthic and planktonic foraminifera was performed in almost all the samples.

On the basis of the faunal counts, values H(s) for diversity using the Shannon-Wiener information equation (Buzas & Gibson, 1969), Species Richness (number of species), Equitability (Buzas & Gibson 1969), Dominance and the Fischer α-index (Fisher et al. 1943), were calculated. Raw data of microfossils were then transformed into percentages over the total abundance and percentage abundance curves were plotted. Species with phylogenetic affinities and similar environmental significance were also grouped to better interpret distribution patterns. Additionally, Planktonic/Benthic (P/B) ratios expressed as 100*P/(P+B), i.e. the percentages of planktonic foraminifera in the total foraminiferal assemblages, and infauna versus epifauna are used as indicators of paleobathymetry, paleoproductivity and upwelling. Paleobathymetry was also calculated for each sample by introducing P/B ratios, based on epifaunal species, in the equation of v.d. Zwaan et al. (1990).

### 3 PLANKTONIC FORAMINIFERAL BIOSTRATIGRAPHY

The quantitative distribution patterns of the most representative planktonic foraminiferal taxa are summarized in Fig.2. A quantitative biostratigraphic analysis of the planktonic foraminifera was carried out in order to pinpoint accurately the position of bio-events (Table 1).

In the lower part of the section the first abundant occurrence of *Globigerina obesa* has been recognized at around 3 m of the section, dated at 6.610 Ma (Krijgsman et al., 1999). This species
occurs almost continuously in our record. Intervals characterized by its absence or low abundances are recorded in the diatomaceous layers.

Table 1: Planktonic foraminifera bioevents in the upper part of the Metochia Section (Krijgsman et al., 1999)

<table>
<thead>
<tr>
<th>Planktonic Foraminifera events</th>
<th>Stratigraphical level (m)</th>
<th>Age (Myr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) <em>Globigerina oboesa</em></td>
<td>FAO</td>
<td>3.40</td>
</tr>
<tr>
<td>(2) <em>Globorotalia conomiozea</em></td>
<td>LO</td>
<td>5.70</td>
</tr>
<tr>
<td>(3) <em>Turborotalita multiloba</em></td>
<td>FAO</td>
<td>7.00</td>
</tr>
<tr>
<td>(4) <em>Neogloboquadrina acostaensis</em> d/s</td>
<td>8,50</td>
<td>6.337</td>
</tr>
<tr>
<td>(5) <em>N. acostaensis</em> dominance sin. forms</td>
<td>12,70</td>
<td>6.108</td>
</tr>
<tr>
<td>(6) <em>N. acostaensis</em> influx sinistral</td>
<td>14,20</td>
<td>6.099</td>
</tr>
<tr>
<td>(7) <em>Globorotalia scitula</em> influx</td>
<td>14,60</td>
<td>6.082</td>
</tr>
</tbody>
</table>

The second significant biostratigraphic event is the last occurrence of *Globorotalia miotumida* group which has been dated at 6.552 Ma (Krijgsman et al., 1995). This event is followed by two distinct influxes of the group. One is recorded around 5.7 m and the second, which is less prominent, at around 3.5 m of the section. Sierro et al. (2001), recognized also two influxes of *G. miotumida* group in Sorbas, dated at 6.552 and 6.585 Ma. In Gavdos diatomites, Perez-Folgado et al. (2003), who worked in the lower part of the section, identified only the older influx of the group on top of the diatomite cycle which lithologically corresponds to our record.

The entry of *Turborotalita multiloba* is a very useful bioevent and has been widely used for biostratigraphic correlations inside the Mediterranean. This event has been astronomically dated at 6.415 Ma (Krijgsman et al., 1999; Hilgen & Krijgsman, 1999). Short incursions of the species are recorded in our record before its regular occurrence in the section.

The distribution and coiling pattern of *Globorotalia scitula* group which comprises all the unkeeled globorotaliids (*G. scitula*, *G. nicolae*, *G. ventriosa*) of our data, are used for biostratigraphic correlation throughout the Messinian, inside and outside the Mediterranean (Krijgsman et al., 1995; Sierro et al., 1993; 2001). In our record, this group is abundant in the lower part of the section with preferentially dextral coiling and then the group shows prominent incursions and frequent shifts in coiling direction, from sinistral to dextral and vice versa, up to the top of the section. In the Mediterranean the two last influxes of *G. scitula* group have been astronomically dated (Krijgsman et al., 1999). In Gavdos diatomites, the last distinct influx of this group has been identified just above the last sinistrally coiling *Neogloboquadrina acostaensis* influx, (at 14.6 m), dated at 6.082.

*Neogloboquadrina acostaensis* is very abundant in our record reaching high abundances in the upper part, in diatomaceous marls and in the thick diatomite beds. Dextral and sinistral specimens were counted separately, in order to define a better biostratigraphic framework for the studied section. In the lower part, coiling is dominantly sinistral. A very prominent coiling change from sinistral to dextral is reported at 8.5 m which in order to define a better biostratigraphic framework for the studied section. In the lower part, coiling is dominantly sinistral. A very prominent coiling change from sinistral to dextral is reported at 8.5 m which is correlated to the astronomically date of 6,337 ma (Krijgsman et al., 1999). This event has been recognized both in the Mediterranean (Sierro et al., 1993; Sprovieri et al. 1996; and others) and Atlantic regions (Sierro et al., 1993; Benson et al., 1991 and others). Laccarino (1985) used this event to define the base of the Non- distinctive Zone in the Messinian in the Mediterranean.

Moreover, two distinct events into the distribution pattern of *Neogloboquadrina acostaensis* were recognized, one is recorded at 12.7 m where sinistrally coiled specimens are dominant, dated at 6,108 Ma, and the other at 14,20 m, dated at 6.099 Ma (Hilgen & Krijgsman, 1999) referred to the significant influx of sinistral forms.

All these events described above indicate that the studied interval ranges from 6.7 Ma as it is recorded from the onset of the diatomite sequence for Gavdos island, to 6.082 Ma according to the last influx of *Globorotalia scitula* group.
Fig. 2. Faunal abundance pattern and bioevents of the planktonic foraminifera.

4 THE BENTHIC FORAMINIFERAL RECORD

4.1 Faunal pattern

The distribution of dominant, common or significant species, which characterize the benthic foraminiferal fauna of Metochia Section, is reported in Fig.3.

The most representative species of the diverse benthic foraminiferal fauna are: Bolivina plicatella, Bolivina spathulata group (B. spathulata, B. dilatata, B. tortuosa), Bulimina aculeata group (B. aculeata, B. elongata, B. lappa), Elphidium sp, Asterigerinata planorbis and Gyroidinoidea neosoldani. Additional and significant species are Anomalinoides sp., Cibicidoides kullenbergi, C. ungerianus, Cibicides lobatulus, Cassidulina laevigata, Melonis padanum, Uvigerina sp., Valvulinera bradyana and Globocassidulina oblongus.

Bolivinidae and Buliminidae dominate throughout the succession, strongly fluctuating in the range of 0,5-79% and 1-98% respectively. Among the Bolivinidae, B. plicatella and B. spathulata group, are the most common. Bolivina plicatella is relatively abundant in the basal part of the section, displaying peak occurrences at 0,5 m and 4,2 m (76,5% and 64,6% respectively). On the contrary, B. spathulata group is abundant in the middle and upper part of the section, displaying its highest percent value at 8,5 m (49,29%). Bulimina aculeata group shows its highest frequency at 2 m (98%).

Asterigerinata planorbis and Elphidium sp. occur from the base to the top of the section with their highest frequencies in the middle of the succession, at 6,9 and 7,3 m (46% and 78% respectively).

From the faunal pattern of benthic foraminifera, the species Bolivina plicatella, Hanzawaia boueana, Cibicidoides kullenbergi, Melonis padanum, Cassidulina laevigata, Valvulinera bradyana, Globocassidulina oblongus display a decreasing trend, whereas Anomalinoides sp., Cibicidoides ungerianus, Bolivina spathulata and Uvigerina sp. show an increasing trend, up to the top of the section.
4.2 Diversity

Diversity indices expressed by Shannon diversity (H(s)), Fischer alpha, Equitability and Dominance have been measured for each sample collected from Metochia Section and are shown in Table 2. These indices are in accordance with the faunal abundance pattern implying that high diversity corresponds with low dominance and low equitability.

Table 2: Benthic foraminiferal faunal parameters

<table>
<thead>
<tr>
<th>Height [m]</th>
<th>Taxa</th>
<th>Dominance</th>
<th>Shannon index</th>
<th>Equitability</th>
<th>Fisher-α</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>18</td>
<td>76.50</td>
<td>0.97</td>
<td>0.39</td>
<td>3.56</td>
</tr>
<tr>
<td>1.4</td>
<td>11</td>
<td>68.18</td>
<td>1.09</td>
<td>0.53</td>
<td>2.08</td>
</tr>
<tr>
<td>1.5</td>
<td>8</td>
<td>88.75</td>
<td>0.56</td>
<td>0.27</td>
<td>2.06</td>
</tr>
<tr>
<td>2.6</td>
<td>4</td>
<td>98.03</td>
<td>0.11</td>
<td>0.08</td>
<td>0.84</td>
</tr>
<tr>
<td>2.7</td>
<td>13</td>
<td>34.78</td>
<td>1.75</td>
<td>0.80</td>
<td>2.44</td>
</tr>
<tr>
<td>3.2</td>
<td>14</td>
<td>28.57</td>
<td>1.74</td>
<td>0.79</td>
<td>2.46</td>
</tr>
<tr>
<td>4.2</td>
<td>13</td>
<td>67.51</td>
<td>1.16</td>
<td>0.48</td>
<td>3.12</td>
</tr>
<tr>
<td>4.5</td>
<td>13</td>
<td>67.94</td>
<td>1.02</td>
<td>0.49</td>
<td>2.07</td>
</tr>
<tr>
<td>5.6</td>
<td>11</td>
<td>24.24</td>
<td>2.05</td>
<td>0.89</td>
<td>2.81</td>
</tr>
<tr>
<td>5.9</td>
<td>33</td>
<td>16.37</td>
<td>2.28</td>
<td>0.86</td>
<td>4.58</td>
</tr>
<tr>
<td>5.4</td>
<td>18</td>
<td>25.49</td>
<td>2.19</td>
<td>0.87</td>
<td>3.67</td>
</tr>
<tr>
<td>5.6</td>
<td>22</td>
<td>24.10</td>
<td>2.15</td>
<td>0.84</td>
<td>4.15</td>
</tr>
<tr>
<td>5.7</td>
<td>14</td>
<td>40.65</td>
<td>1.78</td>
<td>0.81</td>
<td>2.45</td>
</tr>
<tr>
<td>6.1</td>
<td>9</td>
<td>63.54</td>
<td>1.05</td>
<td>0.54</td>
<td>1.70</td>
</tr>
<tr>
<td>6.2</td>
<td>12</td>
<td>22.03</td>
<td>2.01</td>
<td>0.87</td>
<td>2.79</td>
</tr>
<tr>
<td>6.9</td>
<td>9</td>
<td>32.91</td>
<td>1.34</td>
<td>0.75</td>
<td>1.40</td>
</tr>
<tr>
<td>7.3</td>
<td>5</td>
<td>78.08</td>
<td>0.81</td>
<td>0.50</td>
<td>1.11</td>
</tr>
<tr>
<td>7.5</td>
<td>10</td>
<td>92.27</td>
<td>0.38</td>
<td>0.18</td>
<td>2.07</td>
</tr>
</tbody>
</table>

Low values of Fischer-α index (at 2, 11.5 and 12.9 m of the record) suggest some deviation from the norm of the paleoenvironmental parameters (Jorissen, 1987; v. d. Zwaan & Jorissen, 1991). In addition, the availability of strong dominance of some species (at 1.5, 2, 7.5 and 12.9 m) in relation with low species diversity suggests conditions of environmental stress.

An abrupt decrease of diversity, tugged by an increase in dominance, at 4.5 m, 7.5 m, 11.2 m and 11.5 m of the record, is discerned. This is may due to the peak occurrence of the infraunal Bu-
*limina aculeata* group, which is highly tolerant to raised salinities and oxygen deficiencies (v. d. Zwaan, 1982; Jonkers, 1984; Verhallen, 1991; Rohling et al., 1993). The same stands for the interval at 12.9 m, where peak occurrence of *Bolivina spathulata* group indicates high organic content and dysoxia (v. d. Zwaan, 1982; Jonkers, 1984; Katz & Thunell, 1984; Sprovieri et al., 1986; Sen Gupta et al., 1989, Murray, 1991, Jorissen et al., 1992; Kaiho, 1994; Loubère, 1996, 1997, Kouwenhoven et al., 1999). On the contrary, in the middle or the basal part of the succession, the appearance of the epiphytic group, which constitutes up to 50% of the benthic assemblage and is represented by preferentially photofilic forms (as *Elphidium* spp. and *Asterigerinata planorbis*) implies more stable environmental conditions.

### 4.3 Infauna-Epifauna

The benthic assemblages have been divided into two major ecological categories, epifauna-shallow infauna and deep infauna, based on habitat preferences known for their recent representatives (Jorissen et al., 1995). A plot of their relative abundances (Fig. 4) shows the epifaunal component dominating the benthic community in total numbers, except of five intervals (at about 2 m, 4.5 m, 8 m, 11.5 m and 13 m), where the infaunal component rises more significantly.

![Fig. 4. Infauna versus Epifauna benthic foraminifera](http://epublishing.ekt.gr)

Dominance of the epifaunal group indicates well-ventilated bottom water environments and a rather deep position of the redox front. Van der Zwaan et al. (1999) assume that these species are not so tolerant to oxygen stress, but very well able to compete for food. This explains their prominent position at the sediment-water interface under normal conditions. According to Jorissen et al. (1995) and v. d. Zwaan et al. (1999), with increasing water depth, nutrients become limitative. As a consequence of the limited amount of organic flux reaching deep environments, less organic matter is stored in the sediment, rendering the deeper sediment layers a less profitable environment for potential infaunal species. In addition the parallels between plankton and benthos are such that the warmer relatively oligotrophic planktonic group (*Globoturborotalita aperture - Globigerinoides obliquus* group) varies together with the epifaunal group (Fig. 2).

On the contrary, it is well documented that infaunal foraminifera prefer nutrient-rich, low oxygen, muddy environments and their high abundances usually signal eutrophication in the water column (Barmawidjaja et al. 1992, Verhallen 1991). These conditions are more typical of colder or deeper waters and may occur in shallower sites with upwelling influence. Other mechanisms, which may produce a similar effect, include large-scale runoff that produces a brackish water lid and ultimately a high nutrient level.
In the first case, the upwelling suggests that cool and very productive waters characterized these parts of the section (at about 2 m, 4.5 m, 11.5 m and 13 m). The upwelling is preceded by peaks in the frequency of *Globigerina bulloides* (Fig. 2) (a species better adapted to high-productivity upwelling regimes with fairly uniform properties). Upwelling cold currents may have favored the cooling and sinking of surface waters with the subsequent upward mixing of nutrient-rich intermediate waters (Rohling & Bigg, 1998; Sierro et al., 2003). We, therefore, suggest the establishment in these parts of the section, of a small upwelling cell, probably as a result of wind strengthening. In the second case, at about 8 m height, the high abundance of infaunal species is associated with, perhaps, an enhanced river input. This is in accordance with a relatively decrease of P/B ratio. *Bolivina spathulata* group and *Bulimina aculeata* group are the most abundant species in this interval, indicating the existence of oxygen-poor, organic-rich waters at the bottom and more restricted conditions.

5 PALEOBATHYMETRY

The approximate water depth for the sediments from the Metochia Section is assessed by introducing P/B ratios based on epifaunal species, in the equation of v. d. Zwaan et al. (1990).

Based on water depth zonation of Bremer et al. (1980) and van Morkhoven et al. (1986), the depositional depth of the Section varies from around 150 to 1200 m indicating an environment in the upper to lower bathyal zone (Fig. 5a). According to v. d. Zwaan et al. (1990) the low values of depth might be due to low values of the P/B ratio (Fig. 5b) and probably represent benthic "bloom".

![Fig. 5a. Paleodepth reconstruction. 5b. P/B ratio.](http://epublishing.ekt.gr)

As the assemblages recorded from the Metochia section consist of species that are alive today, paleobathymetries have been also estimated through a direct comparison with water-depth ranges seen in their present-day counterparts. References we used include general studies (e.g. van Morkhoven et al., 1986; Murray, 1991) and a selection of papers concerning the Mediterranean Sea (e.g. Parker, 1958; Todd, 1957; Bandy & Chierici, 1966; Venec-Peyre, 1984; Jorissen, 1987; Cimerman & Langer, 1991). The depth-diagnostic benthic foraminifera taxa, selected among those having common or abundant occurrences in the Metochia Section are (Table 3): *Bolivina spathulata* group, *Bulimina aculeata* group, *Melonis padanum*, *Bolivina plicatella*, *Asterigerinata planorbis*, *Elphidium* sp., *Anomalinoidea* sp., *Gyroidinoidea neosoldanii*, *Hanzawaia boueana* and *Cibicidoides kullenbergi*. The depth range chart goes in accordance with the results extracted from the formula used for the calculation of the paleodepth, which means that the benthic foraminiferal assemblages are indicative of an upper to lower bathyal environment.
Foraminiferal assemblage distribution has been used to reconstruct the paleoenvironmental conditions that prevailed during the deposition of the diatomaceous part of the Metochia Section in Gavdos Island. These deposits, based on biostratigraphic data, have been dated at 6.69-6.082 Ma and were deposited in an upper to lower bathyal environment, characterized by a high concentration of organic matter and a generally dominance of epifaunal versus infaunal species. The intervals that infaunal species dominate may be linked to fluvial discharge or local upwelling.

Table 3: Bathymetric significance of dominant and important associated species from the Metochia Section.

<table>
<thead>
<tr>
<th>TAXA</th>
<th>SHELF</th>
<th>UPPER BATHYAL</th>
<th>MIDDLE BATHYAL</th>
<th>LOWER BATHYAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anomalinoides sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. planorbs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. plicatella</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. spathulata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. aculeata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. kullenbergi</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elphidium sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. neosoldanii</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H. boueana</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M. padanum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The basal part of the section (0-6 m) is characterized by the high percentage values of Bolivina plicatella, an indicative species of moderate paleoenvironmental stress. According to v. d. Zwaan (1982) Bolivina plicatella is highly tolerant to raised salinities and oxygen deficiencies, while v. d. Zwaan & Hartog Jager (1983) consider it as an epiphytic species. According to Seidenkrantz et al. (2000), dominance of Bolivina plicatella is a result of an increased salinity. At 1,4 m, Gyroidinoides neosoldanii is the most dominant species. This species seems to be excellent marker of organic matter and doesn't tolerate strong ecological stress due to long periods of very low oxygen levels (Mullineaux & Lohmann, 1981; de Stigter et al., 1998). High abundances of Elphidium sp. are suggestive of shallow water and probably indicative of an allochthonous fauna derived from a slump block of neritic origin (Brunner & Culver, 1992). These increased percentage values may be due to the substrate, which seems to overpass to ecological stress. In the middle part of the section (8-10 m), the paleoenvironmental conditions are characterized by intense stress due to low oxygen content. Bolivinidae and Buliminiidae dominate to the total benthic foraminifera fauna. In the upper part of the section (10-14.6 m), Bolivina spathulata group shows its highest percent values and reveal that is found is the most favourable conditions. According to van der Zwaan (1982), Verhallen (1991), Jorissen et al. (1992), Kaiho (1994), Loubere (1996, 1997), Bolivina dilatata tends to increase when the influx of terrigenous organic matter dominates the environment. Generally, zones influenced by runoff products are dominated by species with a tolerance to stressed conditions (Jorissen, 1999). But according to Phleger & Soutar (1973), Sen Gupta et al. (1989), Caralp (1989) and Gooday (1993), benthic assemblages dominated by Bolivina typify low oxygen environments with a sustained flux of organic matter in regions of high productivity, often associated with intense upwelling.

REFERENCES


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