Plio-Pleistocene shallow-marine benthic foraminifera from Katakolon section (western Greece): an attempt of quantitative paleoenvironmental analysis

Hara DRINIA¹, Assimina ANTONARAKOU¹ & Nikolaos TSAPARAS¹

Abstract
A data set, constituted by counted samples of benthic foraminifera, has been subjected to cluster and principal component analyses, in order to demonstrate the linkage between taxa distribution and paleoenvironmental gradients. The foraminiferal fauna from the Plio-Pleistocene Katakolon section in western Greece is dominated by inner to mid-shelf benthic forms, especially the rotaliids, cibicids and buliminids. A cluster analysis of the species occurrences and relative abundances identified two major assemblages, A to B, up section. Assemblage A is indicative of an oligotrophic biofacies dominated by A. beccarii whereas Assemblage B is indicative of a more eutrophic biofacies where B. marginata prevails. Our results suggest that oxygenation and trophic conditions of the near-surface sediments are the most important factors that control the community structure of the benthic foraminiferal fauna. In addition, upwelling phenomena evidenced by signals from the benthic foraminifera may have played a role in the study area.

Key-words:
Plio-Pleistocene, foraminifera, paleoenvironmental analysis, oxygenation, upwelling, western Greece.

INTRODUCTION
In the last few decades an increasing amount of paleontological research has been devoted to the problem of interpreting past sedimentary environments. In particular, benthic foraminifera can provide assessments, at varying levels of accuracy, of a number of paleoenvironmental factors of value to geological, paleoclimatic and paleoceanographic studies. Many earlier investigators concluded that there was a distinct relationship between various benthic foraminifer species and/or assemblages and bottom-water masses (STREETER, 1973, SCHNITKER, 1974, 1979, 1980, LOHMANN, 1978, CORLISS, 1979, DOUGLAS & WOODRUFF, 1981, HODELL et al., 1983, 1985, MEAD, 1985, HERMELIN, 1986, 1989, MURRAY, 1991, BORNMALM, 1995 among others). LUTZE & COULBOURN (1984) suggested that the distribution of benthic foraminifera might be controlled by the supply of organic matter to the sea floor. Therefore, fluctuations in food supply are considered to be of particular importance (JUMARS & WHEATCROFT, 1989). Furthermore, changes in oxygen concentrations at the sediment-water interface also play a major role in controlling benthic foraminifer assemblages and morphologic characteristics (KAIHO, 1994).

Availability of food and oxygen are usually closely related: the higher the organic matter supply the lower the oxygen content in the water. The amount of organic supply, on which benthic foraminifera largely depend, in turn depends on mineral nutrients (mainly phosphate and nitrate) and surface productivity (BRASIER, 1995). Additional important sources of organic matter or excess nutrient input are river discharge or man-made sewage (e.g. SEIGLIE, 1968, JORISSEN, 1987, VAN DER ZWAAN & JORISSEN, 1991).

The present study intends to delineate quantitatively how benthic foraminiferal assemblages are correlated with water masses during the Pliocene-Pleistocene interval in a part of Pyrgos Basin (western Greece). The distribution of benthic foraminifera group of the neritic Katakolon section is determined, and an analysis of the data is made in an effort to isolate and identify important relationships between the distribution of organisms studied and the parameters of the physical environment. It is the possibility of neritic paleobiological signals of productivity and upwelling that are investigated here.

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GEOLOGICAL SETTING

Katakolon section constitutes part of Pyrgos Basin, which is located in the western Peloponnesus (Fig. 1). The studied area is located in the outer Hellenic Arc, which is part of the southern branch of the Alpine Orogenetic System (HAGEMAN, 1977, 1979; KAMBERIS et al., 1992; KAMBERIS et al., 1998). In front of this area an active subduction is taking place since Upper Neogene, where the Ionian Ocean Crust is subducted beneath the outer Hellenic Arc.

In Katakolon Peninsula, the Neogene-Quaternary sediments are laying on the Triassic evaporates of the Ionian zone. This abnormal contact is due to the diapiric movements of Triassic evaporates, which penetrated the whole carbonate series. The diapiric movements have been active—From time to time—since Pliocene in various places of the Neogene basin, controlling the paleogeography and consequently the depositional areas. These caused considerable changes regarding geomorphology, water depths, salinity variations etc.

The Upper Cenozoic succession of the Pyrgos Basin shows an extremely complex pattern of predominantly terrigenous-clastic deposits, which witness of repeated changes in marine influence and in sediment-supply in a paleogeographic configuration dominated by fluvial-lacustrine and lagoonal systems.

The sedimentological, tectono-stratigraphical, geophysical and geomorphological background of the broad area of Pyrgos Basin have been established by many researchers (e.g. DERCOURT, 1959; DUFARNE, 1977; HAGEMAN, 1977, 1979; WINTER, 1979; VOULGARIS, 1991; KAMBERIS et al., 1992; LEKKAS et al., 1992; KAMBERIS et al., 1998).

The studied section belongs to the Vounargon Formation, which consists of repeated alternations of silty clays and sands, most of which are thought to reflect deposition in marginal marine environments. On the Katakolon peninsula and along the coast to the north, the Vounargon Formation is unconformably overlain by maximally 5 m of bioclastic limestones. The limestones are composed of algae, corals, bryozoa and mollusks. The occurrence of Strombus babinus in the limestone would indicate a "Eutyrrhenian age" (KERAUDREN, 1970, 1971).

The silty clays of Katakolon section may contain intercalations of thin lignite seams. Pyrite is nearly always present in relatively large quantities in and near lignite seams.

The macrofossil content of the clays is highly variable. Layers with a rich and diversified marine mollusk assemblage may alternate intervals, which are barren or contain a fauna of low diversity. There is a negative correlation between the grain-size and the number of mollusks. The upward overall increase in the silt content goes together with a decrease in the number of mollusks.

MATERIAL AND METHODS

Samples were collected from the Katakolon section (Fig. 2) at spacing between 0.5-1.0 m. The 0.125 mm coarse fraction from each sample was obtained by wet-sieving. Foraminifera were then hand-picked under a binocular microscope from randomized splits of each dried sample, and mounted on a slide. Except for barren or particularly sparsely microfossiliferous samples, one or more splits were processed until approximately 200 specimens were obtained. Assemblages were then sorted, identified and counted and the data compiled on to an Excel spreadsheet.

Taxa at the species or genus level that amounted to <0.5% averaged across the data set were removed from the data matrix so that statistical analyses of the data were based on the common and abundant taxa.

Planktonic Foraminifera

Planktonic Foraminifera have been used for the biostratigraphic determination of Katakolon section. In order to provide an accurate time spanning of the studied sediments and to determine and calibrate the bioevents recognized, we proceeded in a detailed qualitative and semiquantitative analysis of the planktonic foraminifera, which were handpicked and identified in the collected samples.

For the establishment of a detailed biostratigraphic framework of the section we first refer some taxonomic comments in order to calibrate the bioevents and correlate the section with others of the same time spanning in Italy (Singa and Vrica). These two sections are suitable for correlation because they can provide an accurate high-resolution chronology for upper Pliocene-lower Pleistocene based on the calibration of dominantly precession-controlled sedimentary cycles (sапрепел) to astronomical curves which describe past variations in the Earth’s orbit (HILGEN, 1991).

Benthic Foraminifera

As far as benthic foraminifera are concerned, calculated from the data are abundances of species and species groups, simple diversity, Shannon-Wiever (Hs) index and dominance, which are used as additional indications for normal marine versus restricted bottom water conditions.

The first measure is species richness which is simply the number of species at each sample.

The Fischer α-index (FISHER et al., 1943) which shows the relationship between the number of species and the number of individuals in an assemblage is also reported.
Fig. 1: Geological map of the studied area (after HAGEMAN, 1977, 1979, modified).

LEGEND
- Holocene Formations
- Peristeri Form.
- Katakolos Form.
- Oinoi Form.
- Erymanthos Form.
- Platiana Form.
- Keramidia Form.
- Prodromos Form
- Vounargo Form.
- Alpine Form.

IONIAN SEA

IONIAN SEA

GREECE
Finally the Shannon-Wiever index which is based on information theory (MARGALEF, 1958, MACARTHUR & MACARTHUR, 1961) and has recently received considerable attention in foraminiferal studies, because it brings out a more meaningful pattern of species diversity than is obtained by using the other measures, is also calculated. This index is given by the following equation:

\[ H(s) = -\sum_{i=1}^{s} p_i \ln p_i \]

where \( s \) is the number of species in a sample and \( p_i \) is the proportion of the \( i \)th species of that sample.

The species Dominance indicates the species that is dominant, or numerically most abundant, at a particular sample.

Additionally, 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 paleoproductivity and upwelling.

A principal component factor analysis using the varimax method is also implemented. A species proportion (percentage) matrix was prepared from raw assemblage counts.

R-mode analysis, where species are compared with each other for all the samples is employed for biofacies analysis.

In the interpretation of the dendrogram, successively lower-order clusters were grouped together until faunal differences between clusters were readily discernible and of likely ecological significance within the resolution of the interpretive technique used in this study. These clusters are termed associations, each of which can be characterized by one or more dominant or common species. Key species abundances are examined individually with respect to combinations of environmental variables, with the goal of assigning an environmental interpretation to their dominance in fossil assemblages.

RESULTS

Planktonic Foraminifera

The following biostratigraphically significant taxa or groups of taxa are recorded: Globigerinoides obliquus-extremus group, Globigerinoides saccifer, Globigerinoides ruber group, Globorotalia crassaformis group, Globorotalia inflata group, Neogloboquadrina sp., Neogloboquadrina pachyderma. Specimens identified in Neogloboquadrina group are mainly consisted by the species N. acostaensis, N. acostaensis-humerosa type and N. dutertrei while typical N. pachyderma were also recognized. Dextral and sinistral forms were counted separately. The percentage of sinistrally coiled neogloboquadridinds of the total neogloboquadridinds has been determined in order to correlate the section with Vrica and Singa section. The dextrally coiled form is the most abundant morphotype in the lower part of the section (Fig. 3). A first significant increase in left-coiling neogloboquadridinds is consistently observed above the sample K14, the level which marks the Pliocene/Pleistocene boundary (1.799 Ma, LOURENS et al., 1996). Percentages of sinistrally coiled neogloboquadridinds display a highly fluctuating pattern from the P/P boundary up to the top of the section and give the possibility to compare biostratigraphically the section
with the Italian ones. We also mark the peak occurrences of left-coiling neogloboquadrinids which in Vrica and Singa have been correlated with the glacial isotopic stages of the northern Atlantic, Site 607 (LOURENS et al., 1996).

The *G. obliquus-extremus* group, mainly occurs in the lower part of the section, but it is almost absent in the upper part. According to ZIJDERVELD et al., (1991) and SERRANO et al., (1999) the Last Common Occurrence of this group is referred above the reappearance of the *G. inflata* group (1.99 Ma) in the Mediterranean.

Specimens identified as *G. crassaformis* are identical to *G. crassacrotonensis* dextrally coiled, found also in Crete. Its range comprises the upper part of *G. bononiensis* Zone and the *G. inflata* Zone of ZACHARIASSE (1975). This group is found in the lower part of the section (samples K1- K5) and then shows a short influx around the K20-K21 samples. All specimens identified in this group are dextrally coiled, while specimens of *Globorotalia scutula* are very rare in the samples and are sinistrally coiled. The short influx of *G. crassaformis* is dated in Vrica and Singa at 1.72 Ma and this is in agreement with our studied section.

Finally, *Globorotalia inflata* is almost continuously present up to the top of the section while in the lower part of the section some *G. bononiensis* morphotypes are found together with the typical *G. inflata* morphotypes.

In concluding, the absence of *Globorotalia truncatulinoides* (at around 2.00 Ma, ZIJDERVELD et al., 1991) and also the absence of the *Hyalinea baltica* (FCO at 1.373 Ma, LOURENS et al., 1996), in combination with the identified bioevents and the distributional pattern of the sinistrally coiling neogloboquadrinids of the section, point out that the section covers the time interval from 2.00 to 1.66 Ma.

<table>
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<td>%</td>
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<td>0 50 100</td>
<td>50 100 150 200</td>
<td>1.8</td>
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</table>

K26 K24 K22 K20 K18 K16 K14 K12 K10 K8 K6 K4 K2

SAMPLES
Benthic Foraminifera

Faunal succession
The abundances of major foraminiferal species and groups are graphed in Fig. 4. A comparison of these metrics suggests a change in benthic foraminiferal composition through time.

The lower part of the section is characterized by the predominance of Ammonia beccarii, which co-occurs with Nonion depressulum, Elphidium crispum and Rosalina globularis. It particularly predominates in the samples K1, K5, K6, K8 and then disappears. Uvigerina peregrina is also represented by relatively high percentage values, whereas Cassidulina neocarinata, Cibicides dutemplei, Bulimina marginata, Milolids and Agglutinants are well represented in the whole section.
High frequency values of Uvigerina mediterranea and C. dutemplei and the disappearance of A. beccarii and N. depressulum characterize K2 sample. The same pattern is observed in samples K3 and K4 with peak abundances of C. neocarinata, Bolivina spatulata, B. marginata and U. peregrina.

The upper part of the section is characterized by the complete disappearance of A. beccarii and N. depressulum, the decreasing frequency of U. peregrina and U. mediterranea and the predominance of Bulimina marginata in association with C. dutemplei. In addition, C. neocarinata, B. spatulata and Melonis pompioliiids present an increase in abundance.

Finally, representatives of the miliolids and agglutinants show fluctuating patterns in frequency for the whole section, with peak abundances in sample K18 and K6 respectively.

The benthic foraminiferal species have been also divided into two major ecological categories, infauna and epifauna, based on habitat preferences known for their recent representatives (CORLISS, 1985; MURRAY, 1991). A plot of their relative abundances (Fig. 5) shows the epifaunal component dominating the benthic community in total numbers except in three intervals (samples K3, K7, K8), where the infaunal component rises more significantly.

P/B ratio-Paleobathymetry
Paleobathymetry was calculated for each sample by introducing P/B ratios based on epifaunal species, in the equation of VAN DER 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 45 to 500 m indicating a rather shallow environment in the middle neritic to upper bathyal zone.

Species diversity and Dominance trends
The general faunal characteristics expressed by the Fischer-α index, Shannon diversity and Dominance show predictable patterns (Fig. 6): high (low) diversity corresponds with low (high) dominance. Dominances range from 0.1 to 0.4 (Table 1) with highest dominances occurring in K1 and K5 levels where A. beccarii predominates. In this part of the section, low diversity values and high dominance trend represent a shallow shelf area which is subject to less stable environmental conditions, and therefore display less diversified benthic foraminiferal assemblages characterized by higher dominances. Dominances in the intervals with high benthic diversity are less than 0.2 and an average 0.1-0.15 corresponding to low levels of ecological stress (Table 1).

One of the most prominent characteristics in levels K3, K7, K8 of the section is that infaunal forms are abundant. The associated faunas in these parts of the section are less diverse but abundant in individuals.
Values of Fischer-α5 (Table 1) generally indicate brackish or hypersaline marginal environments but may also indicate normal marine environments with a high dominance of a single species.
From the data of H(S) (Table 1) values >2.1 indicate normal marine environments.

Statistical analysis
Cluster analysis shows that taxa with similar distribution patterns are grouped by hierarchical clustering into two main assemblages which can be further subdivided into discrete sub-assemblages (Fig. 7).
Assemblage A (cluster A) is characterized by the predominance of Ammonia beccarii which co-occurs with Nonion depressulum, E. crispum and R. globularis. It particularly predominates in the lower part of the section (Fig. 8, samples K1, K5, K6, K8) and then disappears. According to JORISSEN (1987, 1988) this assemblage is characteristic of the nearshore zone, with coarse substrate, rich in calcium carbonate and poor in organic matter. Particularly, in the present day Mediterranean region, A. beccarii occurs with N. depressulum, which is a species that can tolerate relatively low salinities in oligo-mesohaline basins (KRUIT, 1955).
In Assemblage B, clusters B1, B2, B3 and B4 are important faunal constituents. The species of Assemblage B are also present in the earlier part of the section, but only in lower percentages (Fig. 8). Many of the species in this assemblage consist of taxa that are tolerant to high environmental stress, especially a low oxygen content (VAN DER ZWAAN, 1982; SEN GUPTA et al., 1981, MURRAY, 1991, SEN GUPTA & MACHAIN-CASTILLO, 1993).
Cluster B1 is characterized by the predominance of B. marginata which can be considered an excellent marker for a large benthic productivity, which often goes hand in hand with environmental (low-oxygen) stress (JORISSEN, 1987). Its coexistence with C. dutemplei, -
Fig. 4: Relative frequency data of the most abundant taxa and groups of benthic foraminifera.
Cluster B3 is characterized by the high dominance of *C. neocarinata*, which, according to HAGEMAN (1979), reaches its highest value in sediments, that were deposited in the most marine of the shallow environments. *C. neocarinata* is a cosmopolitan species but usually occurs where the organic carbon content of the sediment is high because of higher input of terrestrial organic carbon and higher sedimentation rates (MEAD, 1985; MIAO & THUNNELL, 1993).

*Uvigerina mediterranea*, *U. peregrina*, *B. spathulata* and *C. imgerianus* are the main components of cluster B4 which is mainly found in clayey substrata. Although this cluster is mainly composed of species, which are known as rather deep-living, they are found in nearshore sediments. Earlier studies often associated *Uvigerina* with low-oxygen bottom waters (PFLUM & FLERICH, 1976; LOHMANN, 1978; SCHNITKER, 1979; STREETER & SHACKLETON, 1979). However, more recent studies indicate that *Uvigerina* in general may vary independently of the dissolved oxygen content of the bottom water and is generally associated with high sedimentary organic-carbon content (MILLER & LOHMANN, 1982, ROSS & KENNEDY, 1983, GUPTA & SRIKANTHI, 1992, WOODRUFF, 1985, CORLISS *et al.*, 1986, MEAD & KENNEDY, 1987, HERGUEIRA, 1992, BOYLE, 1990, BURKE *et al.*, 1993).

From the paleoecological attributes of the dominant species of Assemblage B, it may be said that the frequencies of the four faunal clusters are mainly determined by factors relating to the percentage of organic matter in the sediment. All these clusters appear to reflect conditions of enlarged food availability and suggest conditions of lowered oxygen concentration.

Finally, it is worth mentioning that Assemblage A seems to increase at the expense of Assemblage B (Fig. 8).

The dataset was also subjected to a standardized principal component analysis in order to determine the benthic foraminiferal faunal changes within the section (Fig. 9). The PCA, which has been carried out considering only the foraminiferal species frequencies, can test the validity of the assemblages defined through cluster analysis.

The first two varimax-rotated principal components account for 66.16% of the total variability (the first axis explains 53.03% and the second represents 13.13%).

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<td>2</td>
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The first score axis divides *A. beccarii*, *N. depressulum*, *miliolids*, *agglutinants* and *C. dutemplei* from a cluster of the other species. The second axis does not show any significant separation.

From the histograms of Fig. 10, showing the variable
Fig. 6: Faunal parameters (species diversity and dominance).

Table 1: Faunal parameters

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Fig. 7: Dendrogram resulting from cluster analysis. Clustering divided the benthic foraminiferal faunas into two main groups and five clusters.

![Dendrogram](image)

**Clusters:**
- A
- B1
- B2
- B3
- B4

Fig. 8: The record of benthic foraminifera clusters percentage.
loadings, it can easily be seen which are the variables which play a major role in the variance of the data set. The sample loadings on the first PCA axis and the general faunal characteristics allow a subdivision of the fauna into two different assemblages. One assemblage is diverse and predominates in samples showing high negative loadings, whereas the other assemblage is a low diversity assemblage, found in samples showing positive loadings.

The second axis represents trophic conditions. The negative values are represented by samples dominated by species, which are known to prefer higher organic carbon fluxes. Positive values are mainly represented by forms, which are characteristic of oligotrophic environments.

**DISCUSSION**

**Paleobathymetry**
It is well known that the P/B ratio (Fig. 4) can be regarded variously as a measure of depth of deposition (e.g. GRIMSDALE & VAN MORKHOVEN, 1955; VAN DER ZWAAN et al., 1990), a paleoproductivity index (BERGER & DIESTER-HAASS, 1988; HERGUERA, 1992) or as measure of preferential loss of planktonics by dissolution. The latter may occur at or within the sea-bed where bottom- or porewater is undersaturated by CaCO₃ (e.g. ADELSECK & BERGER, 1975) or due to diagenesis and outcrop weathering (e.g. MURRAY 1991).

Furthermore, VAN DER ZWAAN et al. (1990) demonstrated that the applicability of planktonic/benthic foraminiferal ratios in paleobathymetry is considerably improved if it is based on the ratio between planktonic and supposedly epifaunal benthic foraminifera.

However, it should be emphasized that bathymetrical reconstructions are less sensitive at the shallow (~0 m) and deep end (~1200 m) of the reconstructed range, and evidence of (oxygen) stress is a reason to regard the reconstruction with the utmost caution (see VAN DER ZWAAN et al., 1990). Therefore, we must select species having a restricted depth range and to use them for the estimation of the paleodepth.

A more detailed estimate of the depositional depth of the Katakolon sediments maybe made by using data from the literature on the recent bathymetric distribution of their most important species (Fig. 11). Therefore, many Rotaliidae and Elphidiidae constitute the infralittoral assemblage where species normally living in shallow marine environment, which may be abundant near river mouths (JORISSEN, 1987, 1988, BELLOTTI et al., 1994).

In particular, A. beccarii is a very common cosmopolitan species dwelling in littoral and neritic environments from the tropic to temperate regions.
Fig. 10:  
a. Variations in loadings of the samples along the first principal component axis.  
b. Variations in loadings of the samples along the second principal component axis.
Faunal pattern

All the associations identified have a neritic affinity and are characterized by generally low abundances of planktonic foraminifera. Moreover, the groups of species determined by R-mode analysis are indicative of a eutrophic biofacies dominated by *B. marginata* and a more oligotrophic biofacies dominated by *A. beccarii*. The very shallow conditions which prevailed in the environment in which the lowermost sands were formed, are reflected by the extreme dominance of *A. beccarii*. The increase of the relative numbers of *A. beccarii* and the relatively low numbers of Buliminidaceae may point to deteriorated connections with the open sea, which possibly indicate a marine environment with a salinity greater than 33%. (LE CAMPION, 1968, ROUVILLOIS, 1978, DEBENAY, 1978, REDOIS, 1996, DEBENAY et al., 1998). Its strong occurrence in Association A together with minor representation of other innermost shelf species such as *Elphidium crispum* indicates estuarine, tidal flat or shallow subtidal conditions and water depths of 0-10 m (cf. HAYWICK & HENDERSON, 1991).

Conversely, *Bulimina marginata* associations are composed by species primarily representing relatively "normal" conditions, with a preference for high food availability with a tolerance for low oxygen concentrations. Such sequences seem to be determined by the interplay of two parameters, the limiting effect of the oxygen decrease and coincidental effect of the increase of organic matter, which provides an abundant food supply (MILLER & LOHMANN, 1982, POAG, 1981, PHLEGER & SOUTAR, 1973, LUTZE & COULBOURN, 1984).

Moreover, it is well established that *B. marginata*, *U. mediterranea* and *U. peregrina* are the most opportunistic species found in the Mediterranean. These taxa should be dependent on an important supply of fresh organic matter, with a high nutritious value. This fact allow us to suppose that high frequency of *Bulimina marginata* in infralittoral environment is mainly due to the concentration of organic matter and the related levels of oxygenation of the bottom.

The epifaunal/infraunal ratio is explored a little more. Although it is likely that many species of foraminifera can change their food, hence their habitats (LINKE & LUTZE, 1993), their dominance in certain microhabitats permits a first order grouping into infraunal and epifaunal (ALTENBACH & SARNTHEIN, 1989). The infra fauna flourishes in quiet environments well supplied with organic carbon as beneath oxygen-poor waters where the trophic profile is high (ZAHN et al., 1986, GOODAY, 1986).

Abundant infraunal forms, which tolerate organic-matter, oxygen poor sea floor and which are infrequent at shallow depth, characterize the shallow-water deposits of the Katakolon section.
In samples K3, K7, K8, infralittoral species are abundant with frequent infaunal forms among which *U. mediterranea*, *B. marginata* and *C. neocarina* prevail. These species are known by maximum abundance in circumlittoral environment, in areas characterized by muddy substrates and low dissolved oxygen content. The results of this work suggest that the significant frequency of these species in infralittoral environments is not merely determined by the presence of fine sediments, because samples K3, K7, K8 are constituted by sandy silt, but are probably related with conditions of scarce oxygenation at the bottom and high organic matter.

Upwelling phenomena may have played a role, but it may as well be argued that this high productivity was caused by nutrient supply that was related to fresh-water input (SEN GUPTA et al., 1981, POAG & LOW, 1985). In the benthic foraminifera, these bottom conditions are expressed by high percentage values of some more tolerant species like *B. spatulata* and *C. neocarina*. More generally, the bivalvins and the buliminids, well represented in the study area, are characteristic of upwelling activity (PHLEGGER & SOUTAR, 1973, BASOV, 1974, 1976).

Upwelling and productivity are closely related but not necessarily interdependent. Upwelling brings cool, nutrient-rich waters into the mixed layer and the photic zone, resulting in high productivity. Faunas, particularly those in the plankton, are less diverse but may be numerically very high (Sample K1, BOJE & TOMCZAK, 1978). It is worth mentioning sample K1, in which together with the high predominance of *A. beccarii*, there is a planktonic/benthic ratio as high as 73%. According to BERGER & DIETER-HAASS (1988), a high productivity is commonly associated with a high P/B ratio.

The P/B ratio values together with the characteristics of the planktonic forms, mainly represented by thick walled genera, suggest that calcium carbonate dissolution partially affected the sediment.

Diversity (expressed in Fischer – α values) and Dominance usually correlate negatively (MURRAY, 1991). These parameters are generally regarded as proxies for ecological stress.

Species diversity can be viewed as a gross measure of the effect of environmental stresses on benthic foraminiferal communities.

High diversity and low dominance correspond to low levels of ecological stress, as commonly met in relatively stable and well-ventilated deep-sea environments. Usually, shallow shelf areas are subject to less stable environmental conditions, and therefore display less diversified benthic foraminiferal assemblages characterized by higher dominances (e.g. BOLTOVSKOY & WRIGHT, 1976, MURRAY, 1991). In general, interpretations of fossil faunal diversity are not simple because many biotic and abiotic factors affect the composition of fossil assemblages. However, some important factors controlling species diversity include changes of trophic (resource) level and stability of the environment (GAGE & TYLER, 1991, SANDERS, 1969, VALENTINE, 1973).

Therefore, H(S) diversity index remains rather constant with small-scale fluctuations (Table 1), indicative of short-term changes which can substantially disturb the sediment surface. This in association with the faunal pattern of the studied section, shows that the trophic level is influenced by the seasonal input of phytodetritus, which increases the abundance of the opportunistic species (e.g. *Bulimina marginata*) and generally promotes benthic activity (GOODAY, 1994).

**CONCLUSIONS**

The microfaunistic composition and the development of the species assemblages in the Katakolon section point to a relatively shallow marine environment. Foraminiferal paleobathymetry confirms the conclusion from analysis of lithofacies (sandy marls and silty clays with lignite seams and pyrite moulds) and macrofauna that Katakolon section developed within a relatively narrow spectrum of shelf depths, extending from shoreface to the mid- to outer shelf boundary. This mainly inner-shelf range is well constrained by the paucity of diagnostic species characteristic of marginal marine (e.g. *A. beccarii*) and mid- to outer shelf (e.g. *Bulimina marginata*) environments. Also, the uniformly low proportion of the planktonic foraminifera present is consistent with inferred inner-shelf depths.

Our results suggest that the trophic conditions and the oxygenation of the near surface sediments are the most important factors that control the community structure of the benthic foraminiferal fauna. Oxygen concentrations in the sediment pore water become a limiting ecological factor in these environments and foraminiferal assemblages are composed largely of low-oxygen tolerant species (SEN GUPTA & MACHAIN-CASTILLO, 1993). Since the ability of foraminifera to withstand oxygen deficiency varies among major taxa and species (e.g. BERNHARD et al., 1997), reduced oxygen concentrations will influence both the taxonomic composition and species diversity of foraminiferal assemblages by eliminating the less tolerant species, generally those which exhibit epifaunal adaptations (DE STIGTER, 1996). In addition small salinity changes normally have no influence on assemblage characteristics. It appears that in shallow water realm only substantial differences lead to hyper- or hyposaline assemblages.

Finally the record of the infaunal benthics constitute a signal of high productivity that was driven by either local upwelling or a strong river discharge or both.
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