

Original article

Late Pliocene benthic foraminifera and mollusks from the Atsipades Section, Central Crete; Palaeoecological distribution and use in palaeoenvironmental assessment

Foraminifères benthiques et mollusques du Pliocène supérieur de la Section Atsipades, Crête centrale : distribution paléoécologique et implication paléoenvironnementale

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Abstract

Changes in benthic foraminiferal and mollusk assemblages from the lower part of the Upper Pliocene of the Atsipades Section (Iraklion Basin, central Crete) were studied. The Atsipades Section represents a shallowing-upward sequence from outer shelf blue–gray clays at the bottom of the sequence, deposited below the storm wave base, to shallow inner shelf deposits affected by storm waves at the top. The foraminiferal assemblage at the bottom of the sequence is dominated by *Bolivina spathulata*, *Bolivina dilatata* and Uvigerinidae, a microfossil assemblage corresponding to the deepest deposits formed under dysoxic sea-floor conditions. Foraminiferal assemblages of the middle part of the section are highly diversified, predominantly *Haynesina depressula*, *Cassidulina carinata* and *Reusella spinulosa*. The top of the section is mainly characterised by *Asterigerinata planorbis*, *Bolivina pseudoplicata*, *Cibicides lobatulus* and *Elphidium* sp., a typically epiphytic foraminiferal assemblage which can be correlated with the presence of an algal covered sea-bottom. Within this general environmental trend, a minor shallowing cycle can be differentiated. The boundaries of this cycle can be inferred, based on a substantial microfossil assemblage change and on the coincidence of species diversity maximum and a planktonic/benthic (P/P + B) ratio peak. Nonetheless, upwelling currents and/or over-abundance of nutrients due to continental outflow could also contribute to increased diversity and P/P + B ratio. The character of the mollusk assemblages is in accordance with these trends. Moreover, the increase in diversity and in sculpture constitutes a clear indication of an increase in hydrodynamic energy related to a shallowing-upward trend.

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Résumé

L'évolution des assemblages de foraminifères benthiques et de mollusques de la base du Pliocène supérieur de la Section Atsipades (Bassin d'Iraklion, Crête centrale) est étudiée. De la base au sommet, la Section Atsipades présente des niveaux de moins en moins profonds, partant d'argiles bleu–grises de la plate-forme externe, déposées sous la profondeur limite d'action des vagues de tempêtes, jusqu'à des dépôts de plate-forme interne affectés par les vagues de tempêtes. En base de la séquence, les foraminifères dominants sont *Bolivina spathulata*, *Bolivina dilatata* et les Uvigerinidae, un assemblage micro fossile correspondant à des dépôts profonds formés en conditions disoxiques. Les assemblages de foraminifères de la partie médiane de la section sont très diversifiés, dominés par *Haynesina depressula*, *Cassidulina carinata* et *Reusella spinulosa*. Le sommet de la section est principalement caractérisé par *Asterigerinata planorbis*, *Bolivina pseudoplicata*, *Cibicides lobatulus* et *Elphidium* sp., un assemblage épiphyte typique qui peut être corrélé à l'existence d'un fond marin couvert d'algues. Au sein de

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cette séquence, un cycle mineur de diminution de la profondeur peut être isolé. Les limites de ce cycle peuvent être inférées sur la base d'un changement substantiel de l'assemblage microfossile ainsi que de la coïncidence du maximum de richesse spécifique avec un pic du rapport d'espèces planctoniques (P/P + B). Les caractéristiques des assemblages de mollusques sont en accord avec cette séquence environnementale. De plus, l'augmentation de diversité et d'ornementation constitue une indication claire de l'accroissement de l'énergie hydrodynamique reliée à la diminution de profondeur.

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Keywords: Late Pliocene; Crete; Sea-level; Palaeoproductivity

Mots clés : Pliocène supérieur ; Crête ; Niveau marin ; Paléoproductivité

1. Introduction

The Atsipades Section is located in the southern part of the Iraklion Basin (sensu Meulenkamp et al., 1994) on central Crete (Fig. 1). In contrast with other Cretan regions, the Iraklion Basin contains an almost complete Middle Miocene

to Pliocene succession. This area has been subject to many studies concerning the stratigraphic development of the Neogene basin fill (e.g. Sissingh, 1972; Zachariasse, 1975; Meulenkamp et al., 1979; Thomas, 1980; Jonkers, 1984; Frydas, 1985, 1986; Driever, 1988). Meulenkamp et al. (1994) recently addressed the late Neogene vertical motions and

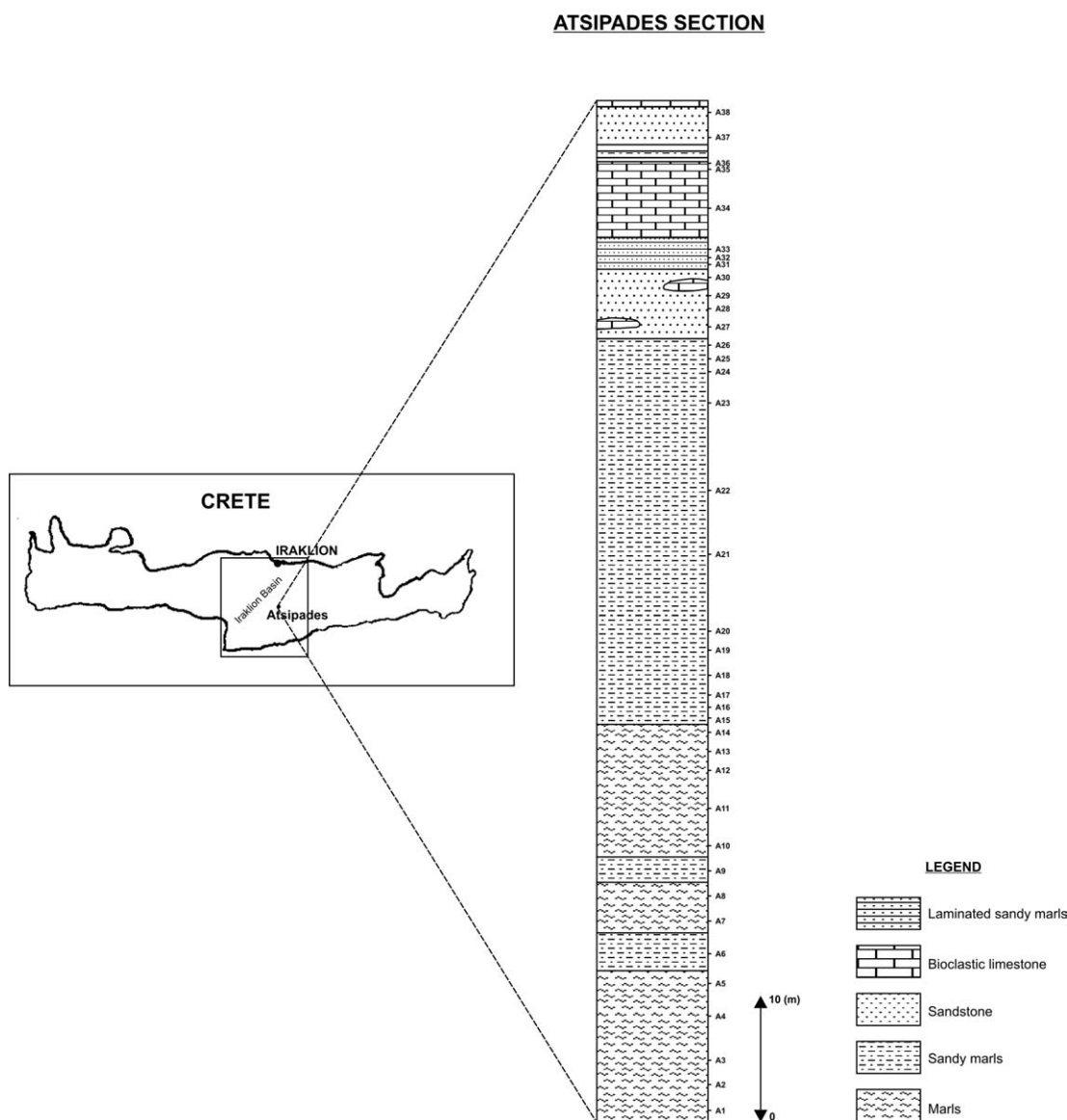


Fig. 1. Lithostratigraphical column of the Atsipades Section.

Fig. 1. Colonne lithostratigraphique de la Section Atsipades.

documented initial (late Miocene) subsidence followed by staggering amount of Plio–Pleistocene uplift coupled with tilting to the north.

In the southernmost part of the Iraklion Basin sensu Meulenkamp et al. (1994), which corresponds to our study area, sediments of the lowermost Pliocene *Sphaeroidinellopsis* Acme Zone, as a rule, overlie lower Messinian limestones. The lowermost Pliocene consists of whitish marls and marly limestones of deep-water origin, reflecting the effects of the Pliocene flooding which terminated the Mediterranean Salinity Crisis. These deep-water deposits pass upward into more sandy and conglomeratic deposits. The sequence portrays overall shallowing and even emergence in response to tilting to the north (Meulenkamp et al., 1994). This shallowing sequence has been found in the Atsipades Section.

The Atsipades Section (Fig. 1), approximately 80 m thick, represents a shallowing-upward sequence beginning with outer shelf blue–gray clays at the bottom of the sequence, deposited below the storm wave base, grading into shallow inner shelf deposits affected by storm waves at the top. Using the biochronology given by the nannofossil record and the planktonic foraminifera record (Koskeridou et al., 2002) the base of the section is dated as 3.61 Ma and the top extends up to 3.21 Ma.

The rich fossil assemblages in the Atsipades Section includes Bivalves, Gastropods, Brachiopods, Echinoids, Foraminifera and have been known for many years (e.g. Symeonidis and Konstantinidis, 1967; Zachariasse, 1975; Dermitzakis and Georgiades-Dikeoulia, 1983; Koskeridou, 1997; Koskeridou et al., 2002).

Although a great deal of documentation of its palaeobiodiversity has already been done, a palaeoenvironmental reconstruction based on organism distribution patterns has not been attempted up to date.

The intention of the present study was to quantify for the first time the fossil data for Foraminifera and Mollusks in the area and to use this information for palaeoenvironmental reconstruction. The aim of this paper is to describe the typical benthic foraminiferal assemblages, contained in fine sediments (silty clay) of late Pliocene age in central Crete (Messara Plain, Iraklion Basin), to understand their ecological significance and to infer a behavioural model related to particular environmental conditions.

Emphasis is given to the parameters of climate, sea-level and nutrient relating biotic change to environmental change. The possibility of using neritic palaeobiological proxies for productivity and upwelling are investigated here.

2. Material and methods

For this study, a total number of 38 samples from the Atsipades Section (Fig. 1) were collected. For the micropalaeontological analysis, samples were washed with mesh diameters of 63 and 125 μm . The > 125 μm fraction was examined for its benthic foraminiferal content. Foraminifera were then

hand-picked under a binocular microscope from randomised 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. Samples with fewer than 30 benthic specimens were excluded from plots and statistical treatment. Each fraction was analysed for benthic and planktonic foraminifera at the species level. From the counts we calculated foraminiferal relative abundance for faunal analysis. Species richness (number of species), diversity (Shannon, 1949), equitability (Buzas and Gibson, 1969) and dominance were determined for all samples. 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.

Additionally, P/B ratios expressed as $100 \cdot P/(P + B)$, i.e. the percentages of planktonic foraminifera in the total foraminiferal assemblages, and infauna versus epifauna are used as indicators of palaeobathymetry, palaeoproductivity and upwelling.

Finally, we applied foraminiferal sequence biostratigraphy (sensu Li et al., 1999) by selecting forms representing inner and outer neritic groups and calculating their abundance differences. The trends in their abundance differences from objective counts of taxa can be used to interpret sea-level changes.

As far as the macrofauna is concerned, quadrats 3 m² perpendicular to the bedding were used as sampling units in each bed. Since the qualitative analysis has already been done (Koskeridou et al., 2002), a quantitative approach is assessed in this study in order to obtain further information on the palaeobathymetry and palaeoproductivity. For each sample, the relative abundance of specimens was calculated whereas in the case of disarticulated shells (bivalves) the larger number of either right or left valves was counted. In addition, species richness, diversity, dominance, sculpture and trophic characteristics were determined for all samples.

3. Results

3.1. Benthic foraminifera

3.1.1. General faunal characteristics

A rich, diverse benthic foraminiferal fauna occurs in most of the Atsipades Section. The most abundant taxa are cibicids (20–50%) and other species commonly found on the middle to outer shelf. These abundance trends are closely followed by other epifaunal taxa. A contrasting pattern was found in the lower part of the section where the bolivinids (range also 20–60%) predominate. Textulariids and discorbids are less common whereas sporadic miliolid forms occur only in a few samples.

The frequency distribution of important taxa is illustrated in Fig. 2. Quantitatively important taxa are *Asterigerinata planorbis*, *Bolivina spathulata*, *Cibicides lobatulus/refulgens*,

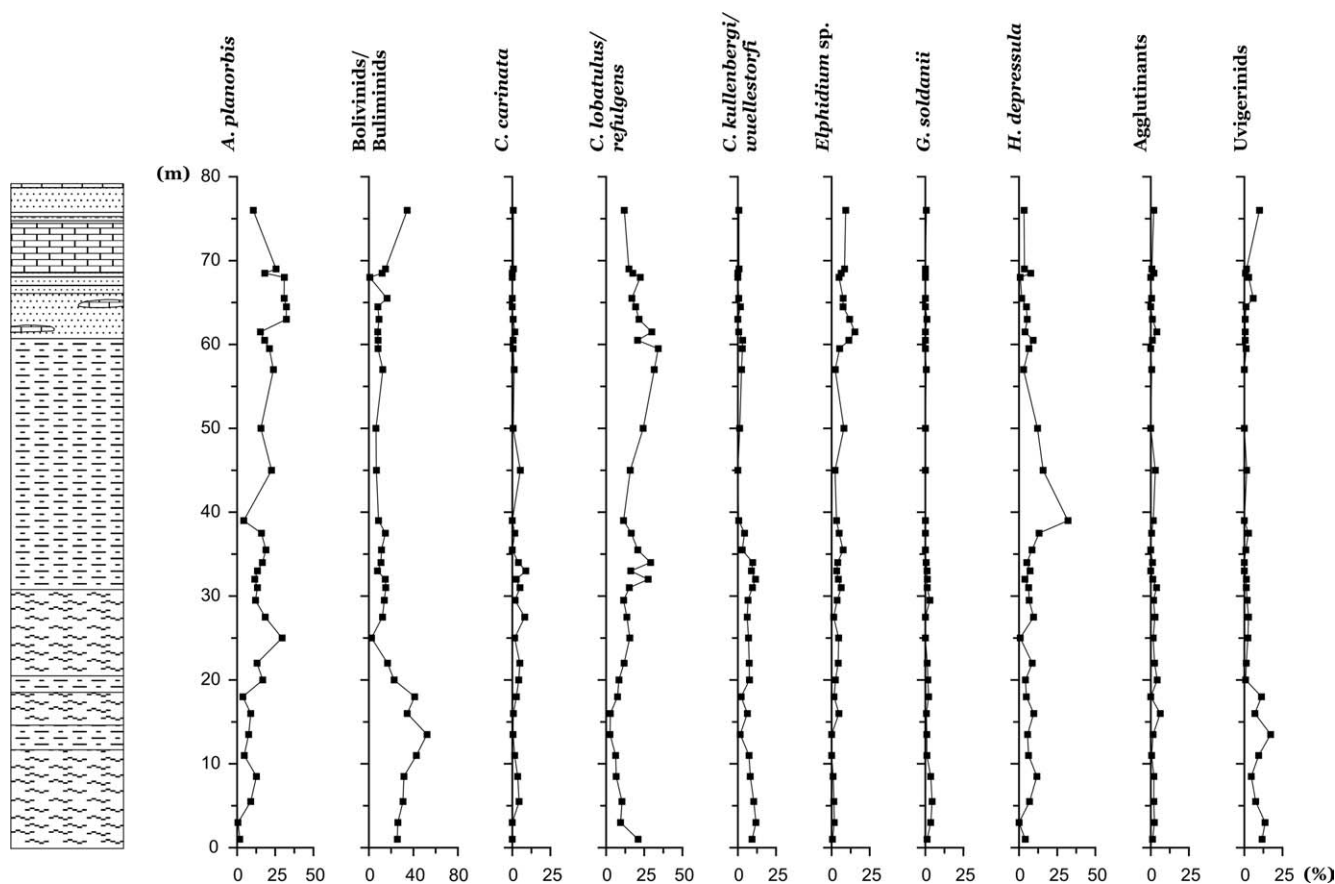


Fig. 2. Relative frequencies of the selected benthic foraminifera from the Atsipades Section.

Fig. 2. Fréquences relatives des foraminifères benthiques sélectionnés de la Section Atsipades.

Cibicidoides kullenbergi/wuellerstorfi, *Elphidium* sp., *H. depressula* and *Uvigerina peregrina*. They all display peak abundances of about 20%.

The foraminiferal assemblage at the bottom of the sequence is dominated by *B. spathulata*, *B. dilatata* and *Uvigerinidae*, a microfossil assemblage corresponding to the deepest deposits formed under dysoxic sea-floor conditions. Foraminiferal assemblages of the middle part of the section are highly diversified, predominantly *H. depressula*, *Cassidulina carinata* and *Reussella spinulosa*. The top of the section is mainly characterised by *A. planorbis*, *B. pseudoplicata*, *C. lobatulus* and *Elphidium* sp., a typically epiphytic foraminiferal assemblage which can be correlated with the presence of an algal covered sea-bottom.

The general faunal characteristics expressed by the Fischer- α index, Shannon diversity and Dominance show predictable patterns (Fig. 3): high (low) diversity corresponds with low (high) dominances. Dominances range from 11.5% to 32.3% (Table 1) with highest dominances occurring in A27 and A28 levels where *A. planorbis* predominates. Intervals with high benthic diversity contain about 40–50 different taxa with dominances being on average between 11% and 18%. In low-diversity intervals, the number of taxa decreases to 20. In this part of the section, lower diversity values and higher dominance represent a shallow shelf area which is subject to less stable environmental conditions. Dominances in

the intervals with higher benthic diversity are less than 15% and average 11.5%, reflecting lower levels of ecological stress (Table 1).

3.1.2. Palaeobathymetry

The approximate water depth for the sediments from the Atsipades Section is assessed by means of the plankton/benthos ratio ($100P/P + B$), where P is the planktonic foraminifera and B is the benthic foraminifera (Fig. 3). According to Murray (1976), this ratio gives a measure of proximity to or isolation from the open ocean and/or information about marine currents.

In the Atsipades Section, we identify an inner shelf environment (values not exceeding 20%) corresponding to 35.5, 57, 63, 64.5 and 68 m, which yield the shallower assemblage, and a slope to outer shelf environment (values between 20% and 60%).

The outer shelf is identified in the lower part of the section and corresponds to samples yielding the higher abundance in *Bolivina* spp.

Comparing the preferred depth distribution of benthic foraminifera reported in the literature (Parker, 1958; Berggren and Haq, 1976; Massiota et al., 1976; Cita and Zocchi, 1978; Lohmann, 1978; Wright, 1978; Barbieri, 1998; De Rijk et al., 1999) we interpret a water depth of approximately 50–500 m for the Atsipades Section.

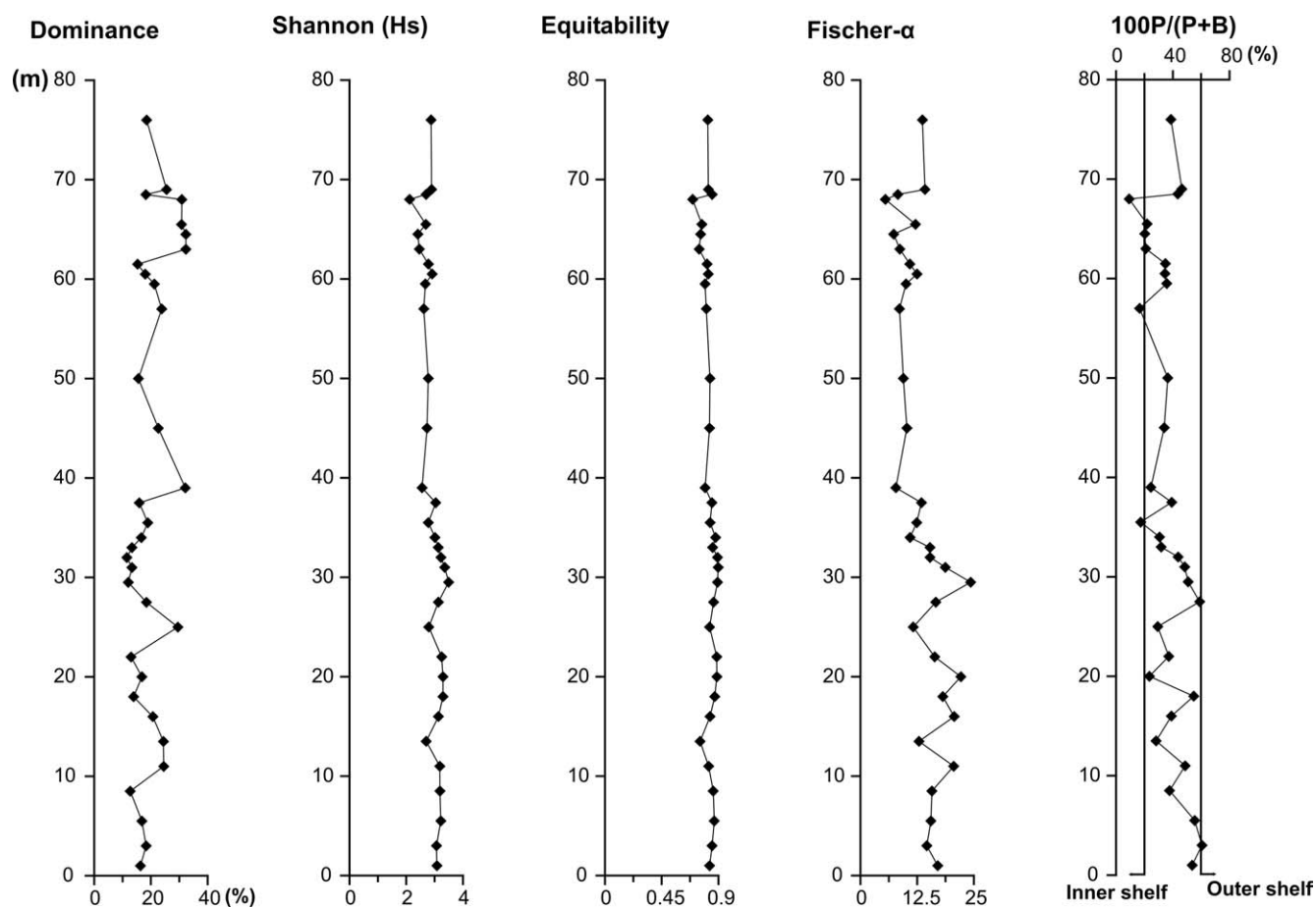


Fig. 3. Faunal parameters (diversity, equitability, dominance and P/B ratio) of the Atsipades Section.

Fig. 3. Paramètres fauniques (diversité, équitabilité, dominance et rapport P/P + B) de la Section Atsipades.

Table 1

Faunal parameters (species richness, dominance, diversity and equitability)

Paramètres fauniques (richesse spécifique, dominance, diversité et équitabilité)

	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12	A13	A14	A15	A16	A17
Richness	41	37	41	41	48	36	43	44	41	39	29	38	50	42	37	39	31
Individuals	172	169	202	197	192	197	145	187	119	161	129	147	166	158	156	180	175
Dominance	16.3	18.3	16.8	12.7	24.5	24.4	20.7	13.9	16.8	13.0	29.5	18.4	12.0	13.3	11.5	13.3	16.6
Shannon	3.08	3.07	3.22	3.19	3.18	2.70	3.14	3.29	3.30	3.25	2.79	3.13	3.49	3.36	3.22	3.13	3.01
Equitability	0.83	0.85	0.87	0.86	0.82	0.75	0.83	0.87	0.89	0.89	0.83	0.86	0.89	0.90	0.89	0.85	0.88
Fisher-α	17.04	14.62	15.53	15.75	20.54	12.91	20.65	18.14	22.13	16.37	11.64	16.61	24.29	18.70	15.33	15.32	10.94
	A18	A19	A20	A21	A22	A23	A24	A25	A26	A27	A28	A29	A31	A32	A33	A36	
Richness	28	36	25	27	28	26	29	35	31	27	24	33	21	24	34	34	
Individuals	106	182	184	133	173	168	170	194	177	186	186	172	246	143	141	151	
Dominance	18.9	15.9	32.1	22.6	15.6	23.8	21.2	18.0	15.3	32.3	32.3	30.8	30.9	18.2	25.5	18.5	
Shannon	2.78	3.04	2.56	2.73	2.78	2.62	2.67	2.91	2.78	2.46	2.41	2.69	2.12	2.70	2.89	2.88	
Equitability	0.83	0.85	0.79	0.83	0.83	0.80	0.79	0.82	0.81	0.75	0.76	0.77	0.70	0.85	0.82	0.82	
Fisher-α	12.42	13.45	7.81	10.23	9.46	8.61	10.05	12.47	10.88	8.68	7.34	12.13	5.49	8.25	14.23	13.66	

3.1.3. Palaeoproductivity

In order to evaluate the preferred microhabitat, species of total assemblages were divided in two groups, epifauna-shallow infauna and deep infauna (e.g. Jorissen et al., 1995), considering only the species with frequencies greater than 2%. The species that generally live within the top two centimetres of surficial sediment were attributed to the former group; those living deeper were assigned to the latter group

(Buzas et al., 1993; Corliss, 1985; Corliss and Chen, 1988; Barmawidjaja et al., 1992).

A plot of their relative abundances shows the epifaunal component dominating the benthic community in total numbers except in four intervals, where the infaunal component rises more significantly (Fig. 4). The infauna is characterised by species with elongate tests such as *Uvigerina* spp. and *Bolivina* spp. The species *B. spathulata* is so abundant in the

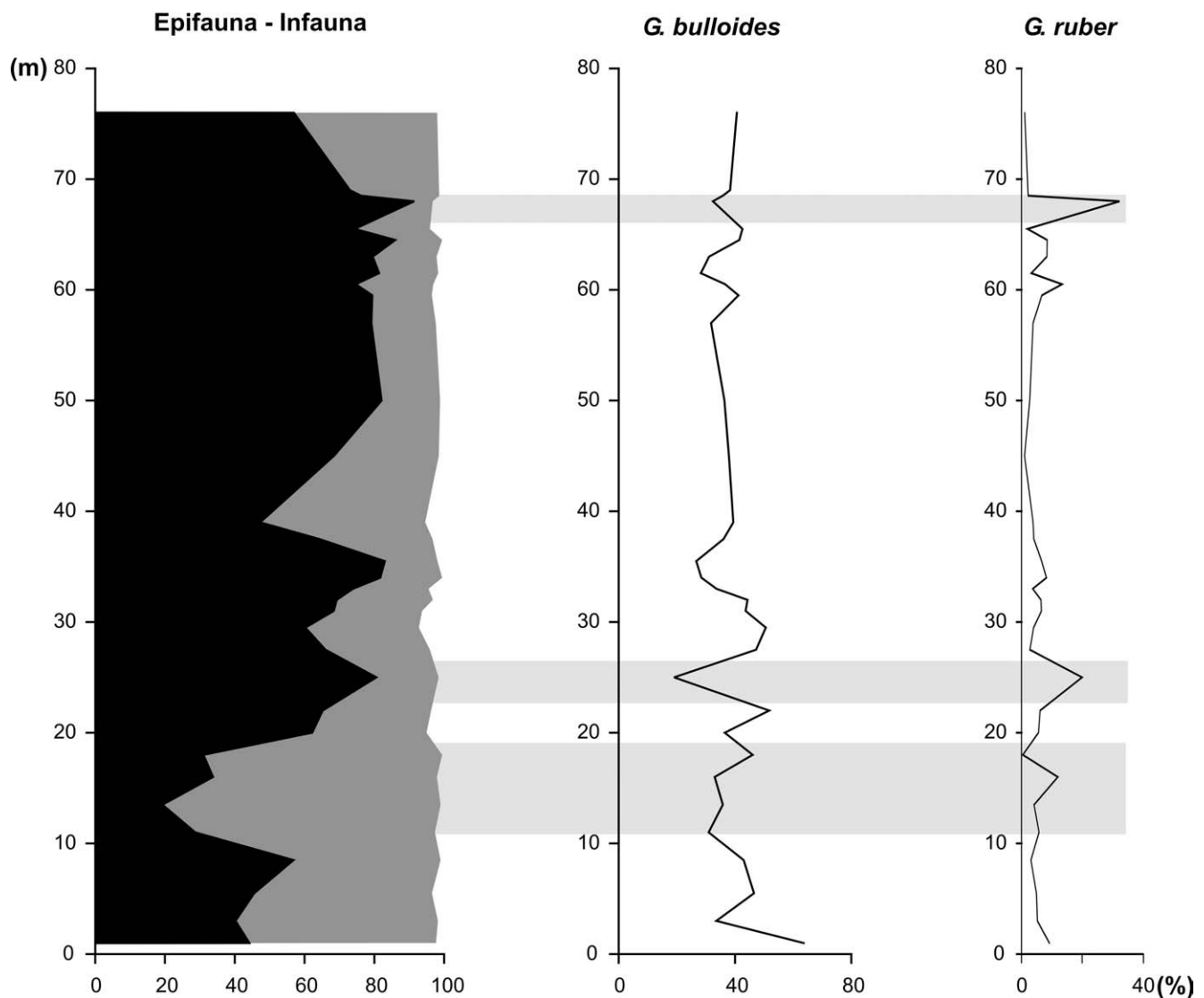


Fig. 4. Benthic foraminiferal microhabitat preferences compared with the quantified profiles of *G. bulloides* and *G. ruber*.

Fig. 4. Microhabitats préférentiels des foraminifères benthiques comparés à l'abondance relative de *G. bulloides* et *G. ruber*.

lower part of the section that it can constitute as much as 25% of the total benthic foraminiferal assemblage.

Infaunal species primarily inhabit muddy sediments under deep or cold waters, but they may also occur at shallower depths when conditions are suitable (Murray, 1991). They prefer nutrient-rich, low oxygen, muddy environments, and their high abundances usually signal eutrophication in the water column. These conditions are more typical of colder or deeper waters, and may occur at shallower sites with upwelling influence. Other mechanisms that may produce a similar effect include large-scale runoff which produces a brackish water lid and ultimately a high-nutrient level.

In order to determine which environmental factor makes the infauna flourish we used the quantified profiles of the spinose *Globigerina bulloides* group and *Globigerinoides ruber*.

G. bulloides and *G. ruber* have a widespread distribution in the world ocean and they are used as indicators of environmental changes in surface conditions and, in particular, for

palaeoceanographic reconstructions of upwelling intensity (Prell and Curry, 1981; Kroon et al., 1990; Venec-Peyre and Caulet, 2000; Peeters et al., 2002).

G. bulloides dominates the planktic foraminifera assemblage in terms of relative abundances (Fig. 4). This species is conventionally known from the sub(ant)arctic and transitional faunal province (see Hemleben et al., 1989) but has been found in significant proportions in tropical and subtropical upwelling regions of the Indian Ocean (Prell and Curry, 1981; Rao et al., 1989; Kroon, 1991; Curry et al., 1992; Naidu and Malmgren, 1996; Guptha et al., 1997), the eastern Pacific (Sautter and Thunnell, 1991; Thunnell and Reynolds-Sautter, 1992) and the eastern Atlantic (Ganssen, 1983). It appears *G. bulloides* produces peak shell fluxes in high-nutrient and potentially high productivity regimes.

The profile of *G. bulloides* is rather constant with small-scale fluctuations, with variations on the order of ten percent relative abundance. Among several peaks in the *G. bulloides*

component, one is more significant in terms of concurrence with other upwelling indices (infaunal benthos), at 11–18 m (68–80% infaunal benthos).

Just as high numbers of the planktonic *G. bulloides* alone are an ambiguous signal of cooling, of upwelling, or of both, so too is the record of the infaunal benthics. A combined signal, however, indicates high productivity due to upwelling. Together with the predominance of Bolivinidae and *G. bulloides*, there is a planktonic/benthic ratio as high as 60% (Fig. 3). According to Berger and Diester-Haass (1988), high productivity is commonly associated with a high planktonic/benthic ratio.

Likewise, the benthic signal suggests that the planktonic signal has an upwelling component and is not simply due to cooling.

In addition, the parallels between plankton and benthos are such that the warmer relatively oligotrophic planktonic group (*G. ruber* group, Conan and Brummer, 2000) varies together with the epifaunal group. Maximum peaks in *G. ruber* record coincide with minima in the *G. bulloides* record. At around 68 m, epifaunal dominance includes larger species, which are photosymbiotic and good indicators of warming. Therefore, at 68 m, *G. ruber* increases in the plankton, epifaunal benthics increase over the infaunal species and the studied succession evidently shallows (sharp declines in P/B ratio and in infaunal percentages). All of these are consistent with shallowing and concomitant changes in circulation.

3.1.4. Predicting sequences

Many benthic forms appear to prefer certain environments—inner shelf, outer shelf or slope—in which they proliferate but decline sharply in other settings (Murray, 1991). By referring to their modern habitat preferences and assuming these preferences have changed little since the Pliocene, we selected those representing inner and outer neritic groups and calculated their abundance differences (i.e. inner minus outer neritic) (Fig. 5). The frequency and relative amplitude of the curves should be environmentally meaningful unless these taxa were wrongly selected or their habitats have changed. These curves accordingly give us an indication of local sea-level changes. Indeed, outer neritic species increase with increasing water depth while inner neritic species become common in shallow-water environments approaching sequence boundaries. Therefore, high negative values = more neritic forms = shallower palaeodepths, and vice versa. The lows in these inferred eustatic trends could represent sequence boundaries.

In addition, high planktonic abundances (P/B ratios) indicate increased oceanic influence implying high sea-level, such as at maximum flooding surfaces, and conversely for low values near sequence boundaries. The combined evidence of biofacies and lithological discontinuities permits the subdivision of the succession into three packages. The peaks of inner neritic forms and the low P/B ratios enable us the recognition of possible sequence boundaries. Sequence boundaries should be at shallowing events and epifaunal peaks, whereas infaunal

peaks should indicate burial of organic carbon, i.e. deeper quieter water, as well as upwelling.

Boundary 1 (at 35.5 m) corresponds to an increase in coarser and more consolidated sediments. It is characterised by a low P/B ratio, frequent elphidiids, and some miliolids.

Boundary 2 (68 m) is more obviously erosional and is characterised by a collapse in P/B ratio, a decrease in deep-water benthics, many Fe-stained specimens with >11% miliolids, and a major shift in all biofacies metrics especially benthic species composition.

However, the inferred boundaries may only represent proxies to actual sequence boundaries, which should be drawn on erosional or other physical surfaces, because we did not sample the surfaces at which the actual sequence boundaries may occur. Therefore, the sequence boundaries inferred from the biofacies should be tuned on physical and sedimentological grounds.

3.2. Mollusks

From the study of species richness, diversity, dominance, sculpture and trophic characteristics of the determined mollusks in all samples from the Atsipades Section, the following considerations have been made:

The mollusk assemblage at the bottom of the sequence is poor, with a few representatives of *Neopycnodonta navicularis* (Brocchi) and fewer *Gouldia minima* (Montagu), probably due to dysoxic conditions.

In the blue–gray marls between 11 and 18 m, 12 species have been identified and 54–56.8% of the population constitutes infaunal burrowers (Fig. 6). Suspension feeders (52.6–53.4%) predominate over deposit feeders (47–48%). The byssally-attached forms are totally absent. The ecological categories presented in the clays confirm that these facies effectively correspond to an environment rich in organic matter, which is a shelter for numerous turritellids (*Haustator* (*Miohaustator*) *turris* (Basterot), *Archimediella* (*Torculoidella*) *subangulata* (Brocchi), Scaphopods (*Dentalium* (*Dentalium*) *sexangulum* Scroeter, *Dentalium novercostatum* Lamarck) and herbivorous gastropods (*Astrea rugosa* Linné, *Rissoia variabilis* Megerle von Muhlfeldt). It is an environment in which the infaunal burrowers can be mostly developed. The abundance of *Amussium cristatum* (Bronn), the unique species of the free-lying Bivalve epifauna corroborate this situation. The offshore settings are the preferred habitat of present-day *Amussium* (Kauffman, 1969; Gould, 1971; Stanley, 1972; Hayami, 1991) and the accompanying fauna in our assemblage reinforce this interpretation.

The assemblages of the following beds (20–30 m) are composed of a great variety of fossils reflecting different life strategies. The epifauna is 64.2–65.4% and the suspension feeders are 79–82%. There is an abundance of Pectinidae (*Chlamys varia* (Linné), *Chlamys scabrella* (Lamarck), *Chlamys pesfelis* (Linné), *Flabellipecten flabelliformis* Brocchi etc.), *Pecten jacobaeus* (Linné), *Anadara pectinata* (Brocchi), *Acanthocardia echinata* (Linné). Among the infaunal

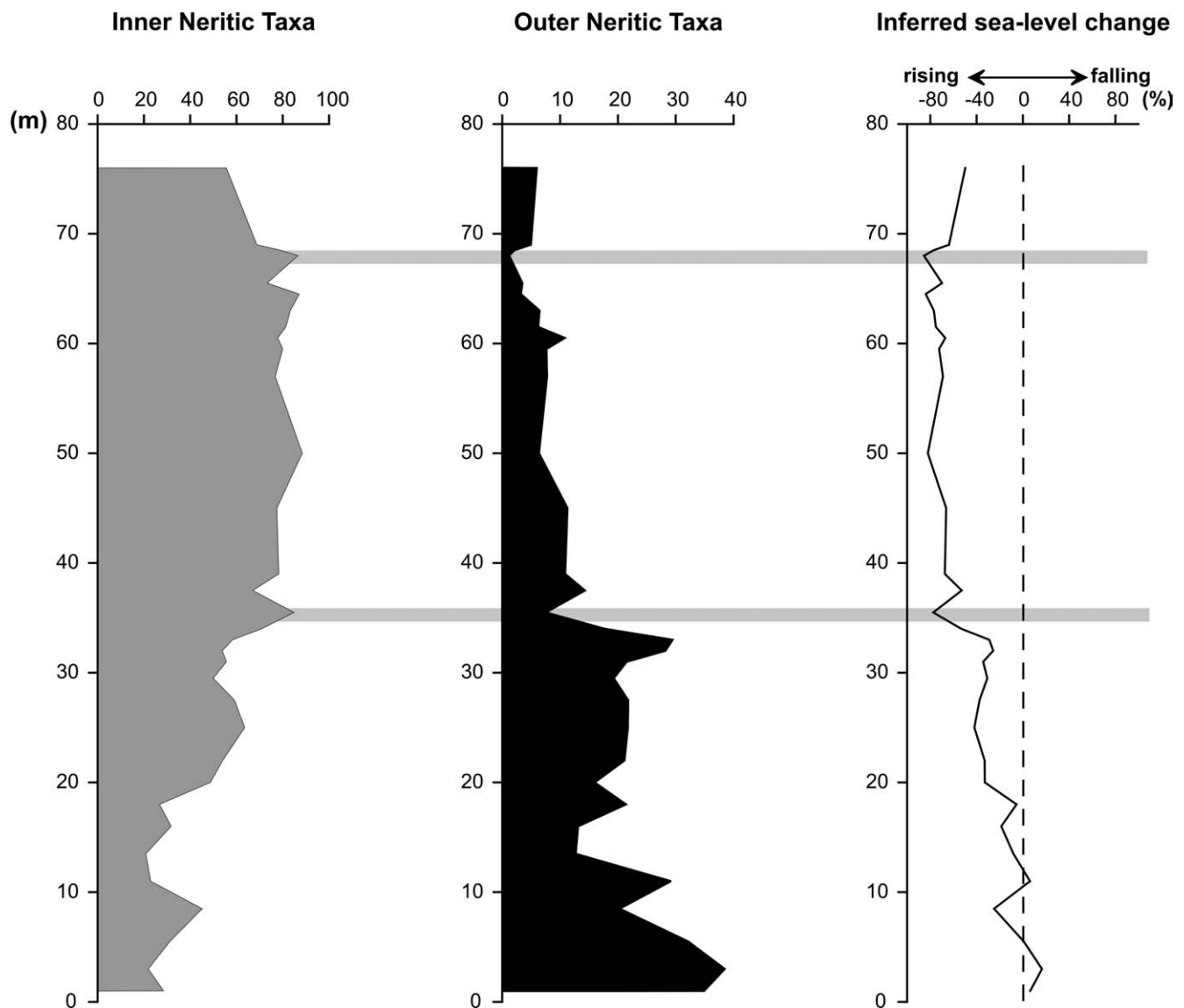


Fig. 5. Abundances of the major groups of inner and outer neritic taxa through the Atsipades Section. Changes in their abundance generate a curve depending on the composition of the “inner neritic” category. The curve is consistent with the possibility that it is reflecting changes in sea-level.

Fig. 5. Abondance relative des taxons des domaines néritiques interne et externe de la Section Atsipades. Les changements d'abondances génèrent une courbe reflétant les fluctuations du niveau marin.

deposit feeders, *Megaxinus transversus* (Bronn) displays great abundance. The abundance of Pectinidae (which are photosensitive) and *Megaxinus*, indicate very good ecological conditions of normal salinity, rich in oxygen.

The mollusk assemblage in the following beds of the section is dominated by Pectinids, Pinnidae, Naticidae, Turritellids, a small number of *Terebra acuminata* (Borson) and Conidae, Terebratulidae etc. The epifaunal component dominates the benthic community in these deposits.

At around 68 m, the marly sand level mainly contains the suspension feeder *Ostrea (Ostrea) lamellosa* Brocchi. These deposits contain also a small percentage of *Theridium vulgatum* (Bruguier) and *Mitrella subulata* Brocchi. The species *Ostrea (Ostrea) lamellosa* Brocchi characterises an environment of the medio-infralittoral zone, rich in oxygen and usually prefers low salinity waters (Gitton et al., 1986). It is a

suspension feeder, which prefers high-energy currents. The coexistence with the herbivorous *T. vulgatum* (Bruguier) and the carnivorous *M. subulata* Brocchi indicates this is an environment of the mediolittoral zone, rich in oxygen, with high turbulence.

4. Discussion–conclusions

The Upper Pliocene Atsipades Section at the southern part of Iraklion Basin in central Crete contains a well-preserved foraminiferal fauna dominated by benthic cibicidids, uvigerinids and bolivinids. A lack of foraminifera commonly found on the outer shelf and slope suggests that the sequence was mainly deposited in inner to mid-outer shelf environments.

All the parameters investigated in this study appear to be closely correlated and depict two different ecological situa-

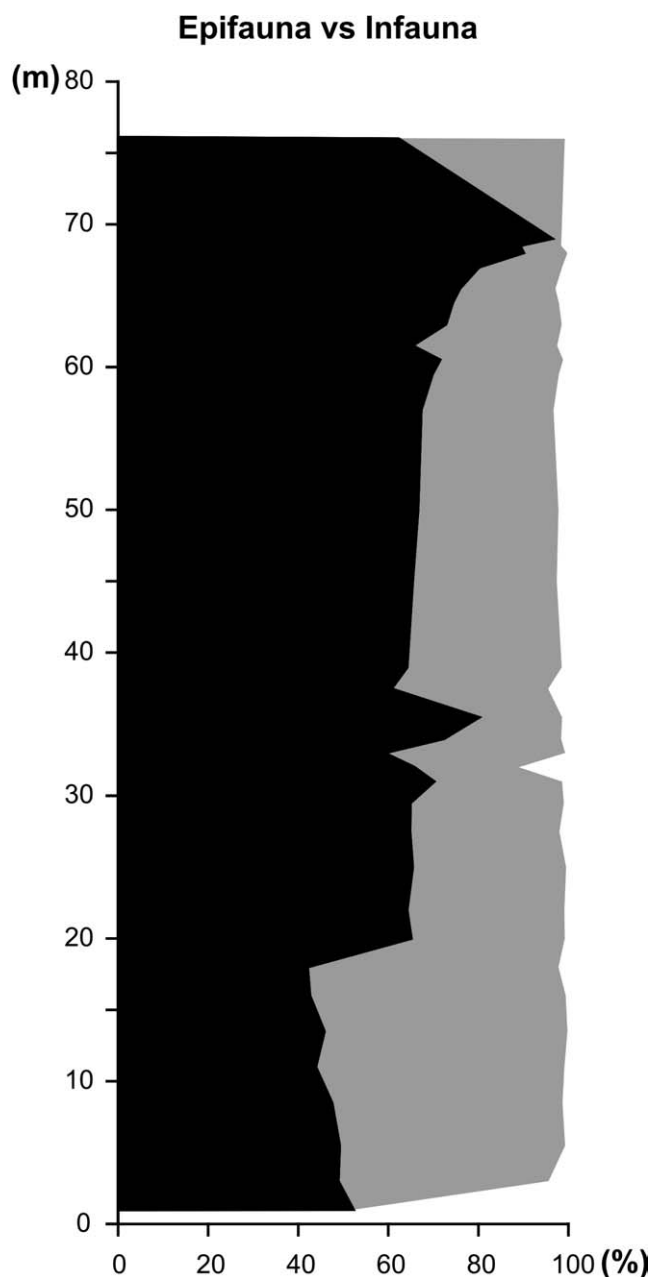


Fig. 6. Epifaunal versus infaunal mollusks in the Atsipades Section.
Fig. 6. Abondance relative des épi- et endo-malacofaunes de la Section Atsipades.

tions. According to palaeoecological data inferred through the present study the palaeogeographic position of the Atsipades Section is well supported. Indeed, at the Atsipades Section a relatively shallow environment was detected reflecting the basinal position. In addition, the section reflects a shallowing-upward trend as indicated by the foraminiferal record.

The essentially parallel trends in the dominating benthic groups—epifaunal cibicidids and infaunal uvigerinids and bolivinids—allow us to identify one upwelling event on one hand, and two warmer oligotrophic periods on the other.

The fluctuating differences in relative abundances between inner and outer neritic taxa can be quantified as a curve

enabling the recognition of possible sequences with boundaries placed at the peaks in inner neritic forms. Indeed, the collapse in the P/B ratio, a decrease in deep-water benthics, and an increase in elphidiids may indicate the position of sequence boundaries.

Moreover, the character of the mollusk assemblages is in accordance with the trends indicated by the Foraminiferal assemblages. It is obvious that the infaunal component dominating the benthic fauna in the lower part of the section points to an environment rich in organic matter, whereas the epifaunal component dominating upwards points to very good ecological conditions of normal salinity and high oxygenation.

As far as the sculpture of mollusks is concerned, the species *A. cristatum* (Bronn) is rather thin-valved while *Chlamys* and *P. jacobaeus* (L.) are moderately thick-valved with *P. jacobaeus* (L.) more sculptured than the others. This points to an increase in energy (Peres, 1961; Kauffman, 1969) upward in the section. The increase in diversity and in sculpture indicates clearly an increase in hydrodynamic energy related to a shallowing-upward trend.

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