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Polychaete Communities of Greece: An Ecological Overview

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With 7 figures and 1 table

Key words: Polychaeta, Aegean Sea, communities, diversity, multivariate analysis.

Abstract. Benthic samples were collected from 188 stations distributed over the Aegean and Ionian Seas (Greece, Eastern Mediterranean). Sampled substrata represented a variety of biotopes in soft bottoms with depths ranging from 3 to 380 m. The samples yielded a total of 398 species of polychaetes. Detrended Correspondence Analysis was applied to the whole set of data as well as to three bathymetric groups into which the data was divided. The results showed that in each bathymetric group, different factors determine the spatial distribution of species. Over the whole data set the type of substrata proved to be the major factor, whereas depth is the second most important. Other controlling factors were the substratum type and exposure to hydrodynamism in the shallow group, depth and substratum in the intermediate, and sediment granulometry and depth in the deep one. Diversity, species number and density tended to decrease with depth, while diversity and species number are favoured by coarse material in the sediment.

Problem

Polychaetes are a qualitative and quantitative key component of the benthic fauna in soft substrata (Fauchald, 1977; Gambi & Giangrande, 1986; Bellan, 1987). Soft-bottom polychaetes have been extensively studied in the Western Mediterranean, especially along the Italian coasts, and the importance of the group as a descriptor of environmental conditions has been well established (Gambi *et al.*, 1984; Giangrande & Gambi, 1985; Gambi & Giangrande, 1986). Studies in undisturbed soft-bottom marine ecosystems around Greece have shown that the average percentage of polychaete species is 53%, varying from 28–73 %, while the respective mean density is 55 %, ranging from 23–85 % (Zenetos, 1989; Papathanassiou, 1992; Anagnostou & Papathanassiou, 1994;

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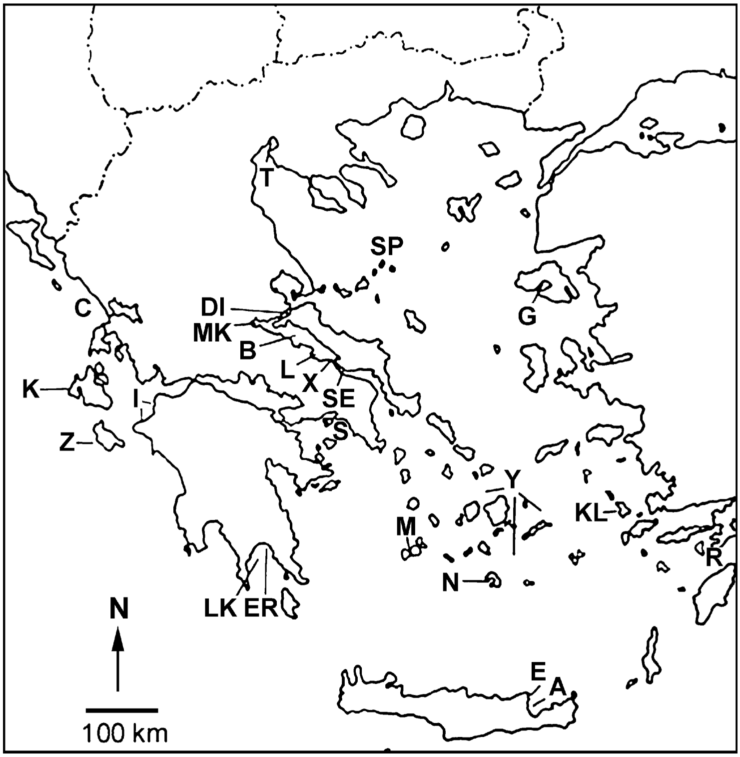

Fig. 1. Map of Greece with areas sampled. Abbreviations: Chalkis-N. Evvoikos Gulf (X). Chalkis-S. Evvoikos Gulf (SE). Kyclades Plateau (Y). Geras Gulf (G). Kalamitsi (C). Kefalonia Island (K). Kalymnos Island (KL). Kriti-Elouda (E). Kriti-Agios Nikolaos (A). Lakonikos Gulf-Evrotas Mouth (ER). Lakonikos Gulf-Gytheio (LK). Larymna (L). Maliakos Gulf (MK). Milos Island (M). N. Evvoikos Gulf (B). N. Sporades (SP). Oreos Channel (DI). Rodos Island (R). Santorini Island (N). Saronikos Gulf (S). Thermaikos Gulf (T). W. Peloponissos Coasts (I). Zakynthos Island (Z).

Friligos, 1994; Simboura, 1998; Pancucci-Papadopoulou *et al.*, 1999; Zenetos *et al.*, 1997; Simboura *et al.*, 1995a, b).

As with the whole benthic community (Fredj *et al.*, 1992) the number of polychaete studies in the Western Mediterranean outnumbers that of the Eastern. The present paper compiles data from a large number of stations distributed over the Aegean and Ionian Seas (Greece) in an attempt to examine the major ecological and/or anthropogenic factors governing the distribution and relationships of this essential benthic component.

Material and Methods

A set of 188 stations (Fig. 1) representing a variety of biotopes was sampled. The sites were distributed over the Aegean and Ionian Seas (Greece, Eastern Mediterranean) on soft substratum and at depths ranging from 3 to 380 m. Sampling was carried out during 1982–1993 using mainly the RV ‘Aegeo’ of the National Centre for Marine Research (NCMR) and various fishing vessels. At each station sediment was sampled by means of various benthic samplers such as a 0.2 m^2 and 0.1 m^2 van Veen grab, a 0.05 m^2 Ponar grab, a 0.1 m^2 Smith-McIntyre grab and a 0.05 m^2 Reineck grab. In some regions of the Ionian Sea, namely Kalymnos, Zakynthos, Kefalonia islands and western Peloponnisos coasts, sampling was qualitatively carried out using a Foster's anchor dredge. Sampling effort ranged from 2 to 20 samples per station. This variation in the sampling effort and sampling method was unavoidable due to the great number of samples, the extended geographic area and the long period of time. This drawback was overcome with the use of transformation techniques in the statistical analyses.

Part of the sediment was retained for grain-size analysis and sediments were classified according to Folk (1954). The percentage of coarse material in the sediment (grain diameter > 63 μm) was used for the statistical correlations. Special symbols were used for the graphical representation of different sediment and substrata types.

After sieving the sediment over a 1mm mesh the residue was preserved in 4 % formalin, stained with Rose Bengal and stored for subsequent laboratory analysis. Samples were sorted in the laboratory and polychaetes were identified and enumerated at the species level.

In order to manage with the great volume of data, which is a restricting factor when applying statistical packages, and to facilitate interpretation of results, the data were classified into four bathymetric groups corresponding to the biocoenotic zonation according to Pérès & Picard (1964). Thus the first group of stations corresponds with the upper infralittoral zone (3–9 m), the second with the lower infralittoral (10–30 m), the third with the circalittoral (36–150 m) and the fourth with the upper bathyal zone (185–380 m). Statistical analysis of the data included:

(a) The multivariate statistical method of Detrended Correspondence Analysis (DECORANA) (Hill, 1979). This is a modified Correspondence Analysis which has the advantage of avoiding the arch or horseshoe effect, which is a tendency of the second axis to be strongly related to the first axis of an ordination plot. This method is recommended for voluminous data treatment and facilitates interpretation of ecological relationships. Abundance data were transformed to presence/absence data in order to overcome the heterogeneity of the sampling method and sampling effort. The analysis was first performed on the whole data set (188 stations and 398 species) to detect possible bathymetric and/or geographical trends. DECORANA was then applied to each group of stations separately except for the deepest, which comprised only 9 stations and was excluded.

(b) The non-parametric Spearman's rank correlation coefficient (Zar, 1984) for the evaluation and statistical confirmation of the DECORANA plots interpretation. Correlations are evaluated according to the significance level values ($P < 0.001$, $P < 0.01$ or $P < 0.05$).

(c) Calculation of some ecological indices, the Shannon-Wiener (Shannon & Weaver, 1963) diversity index and the Pielou evenness index J (Pielou, 1969). Abundance data were expressed as number of individuals $\cdot$ m^{-2}, lumping all replicate samples at each station.

Results

1. The polychaete fauna

A total of 57,307 specimens were enumerated and 398 species were identified, with 18 of these being identified only to the genus level. These species belong to 49 families. The list of species is available on request. Certain species need further research to fully determine their taxonomic status. For example, at least two new species are included in the genus *Chaetozone* Malmgren, 1867. The systematics of this genus in the Mediterranean has not been fully assessed yet, so presently all species belonging to this complex are treated as a single taxonomic unit. Other species remain unidentified due to unresolved taxonomic problems that will probably lead to new descriptions, namely: *Aquilaspio* sp., *Clymenella* sp., *Leitoscoloplos* sp., *Meiodorvillea* sp. and others.

2. Detrended Correspondence Analysis

The results of DECORANA are presented as plots of stations against the first two major axes. The reverse analysis of the species was also performed but the resulting plots are not presented here. In order to interpret the DECORANA plots of the stations, however, information concerning both the environmental parameters of the stations and the ecological characteristics of the species (taking extreme scores on the axes of the reverse DECORANA analysis) was used.

a. Whole data set (3–380 m)

The ordination of the 188 stations is shown in Fig. 2. To simplify interpretation of this complex diagram, stations are marked according to their bathymetric grouping and not the substratum type. Along axis II a polarization of stations caused by some high-scoring stations on the Kyclades plateau (Fig. 2) is observed. These stations belong to the deepest bathymetric group (185–380 m) or are among the deepest stations of the third bathymetric group (36–150 m). In the most dense part of the diagram the ordination of stations along axis II follows a general bathymetric grouping: shallower stations of the first group (3–9 m) score lower on axis II, second group stations (10–30 m) have medium scores, while third group stations (36–150 m) score higher on axis II.

As to axis I, ordination of stations follows a general gradient, though this is not obvious in Fig. 2. In the left part of the axis, stations with muddy bottom ordinate, further right group stations with sandy mud, then muddy sand and sand. In the right part of axis I, stations with *Posidonia*, sand or gravel ordinate. A grouping of identical bathymetric symbols in more or less descrete areas is apparent in Fig. 2: first group stations aggregate in the right part of axis I and the lower part of axis II. Third group stations gather more or less in the left part of axis I and the upper of axis II, while second group stations are distributed all along axis I and in between these two groups. This pattern indicates that the arbitrary bathymetric grouping set for methodological reasons corresponds well with the classical benthic bathymetric zonation.

Spearman correlation analysis was applied among the eigenvalues of the axes and the available abiotic parameters. Axis I correlates with depth and coarse sediment percentage ($r = -0.5716$, $P < 0.01$ and $r = 0.4065$, $P < 0.001$, respectively) and axis II only with depth ($r = 0.4946$, $P < 0.001$). These results combined with the DECORANA analysis suggest that axis I represents the type of substratum and axis II the depth factor.

b. The first bathymetric group of stations (3–9 m)

Forty stations are included and 218 species were found. Figure 3 presents the plotting of the stations against the first two major axes. To facilitate ecological interpretation of the DECORANA plot, the stations were symbolized according to the substratum type. Clearly, stations with high scores in axis I are those with substratum composed of biogenic calcareous fragments, gravel or stones, muddy sand or *Posidonia oceanica* meadows. Stations with low scores on axis I are muddy stations, whereas medium scores

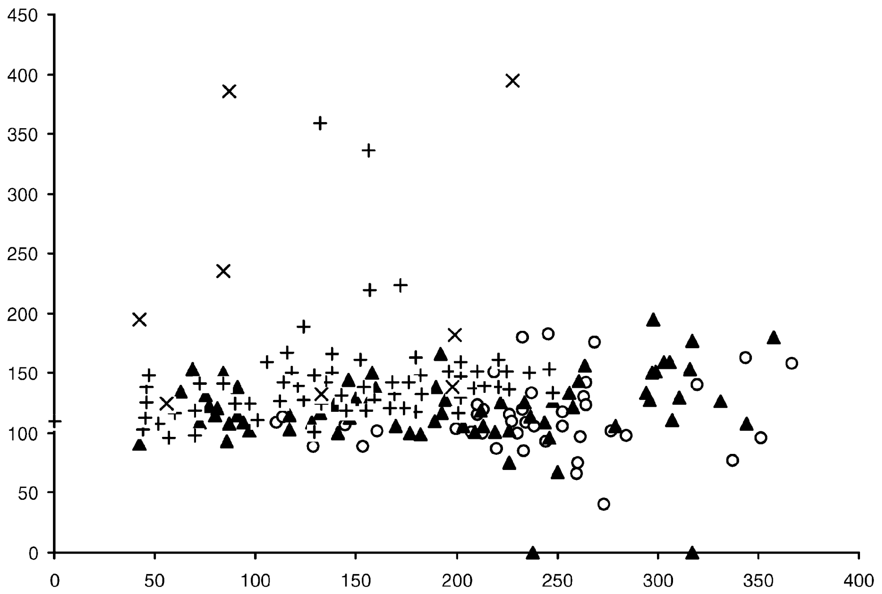

Fig. 2. DECORANA plot of all (188) stations against the first two major axes. Symbols represent bathymetric groups: ❍ 3–9 m, ▲ 10–30 m, + 36–150 m, × 185–380 m.

correspond to stations with sandy and mixed sediments such as muddy and gravelly sand.

Regarding axis II, stations scoring high are those exposed to high-energy conditions, *e.g.* some of Zakynthos Island stations. Stations scoring low on axis II include those found in closed protected bays, as for example stations of Geras Gulf (Lesvos Isl.), South Evvoikos Gulf, *etc.*

In the same bathymetric group the reverse plot of the species against the axes, not presented here, provided complementary information on the nature of the main two factors governing the distribution of polychaete species in the study area. Thus, most species with high scores on axis I characterise sciaphilous hard-bottom communities of the infra- and circalittoral zones such as *Dorvillea rubrovittata* (Sarda, 1986) and *Eurysyllis tuberculata* (Abbiati *et al.,* 1987). Species with low scores on axis I are mud-preferring species, namely *Aedicira mediterranea* (Castelli, 1987) and *Rhodine loveni* (Reyss, 1966); species preferring sandy sediments such as *Armandia cirrosa* (Picard, 1965) and *Euchone rubrocincta* (Giangrande, 1989); or species of mixed sediments such as *Spiochaetopterus costarum* (Llanso, 1992). High scores on axis II were attained by *Armandia cirrosa,* characteristic of coarse sand under bottom currents, and the sand-preferring *Prionospio caspersi* (Picard, 1965; Lardicci, 1989). Among species having low scores on axis II are the mud-preferring *Glycera unicornis, Maldane glebifex, Maldane sarsi* (Picard, 1965; Intes & LeLoeuff, 1986)*, Pherusa plumosa* (Castelli, 1989) and *Ophelina aulogaster* (Picard, 1965) .

Spearman correlation analysis showed that axis I is not statistically correlated with depth and coarse sediment percentage ($P > 0.05$), whereas axis II is positively corre-

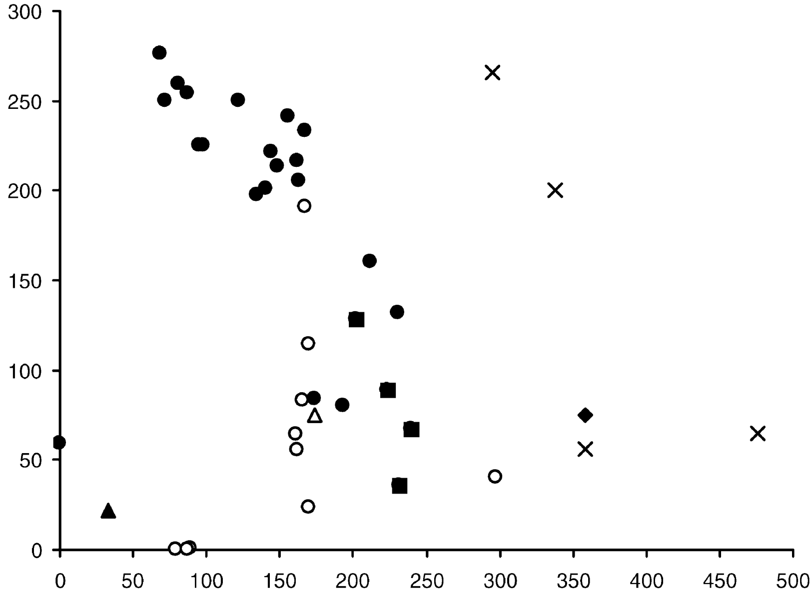

Fig. 3. DECORANA plot of the stations belonging to the bathymetric group 3–9 m against the first two major axes. Symbols represent type of substratum: ▲ mud, ❍ muddy sand, Δ sandy mud, ● sand, ■ gravelly sand, × stones-gravel-biogenic fragments, ◆ *Posidonia* beds.

lated with coarse sediment percentage and negatively with depth ($r = 0.6535$, $P < 0.001$ and $r = -0.6046$, $P < 0.001$, respectively).

Combining the results of the multivariate (DECORANA) and non-parametric (Spearman's rank correlation) statistical analysis, axis I apparently relates to substratum type and axis II to the prevailing hydrodynamic conditions, a factor also influencing the type of substratum.

c. The second bathymetric group of stations (10–30 m)

Here, a total of 75 stations yielded 354 polychaete species. Figure 4 shows the DECORANA plot of 75 stations against the first two major axes. Stations scoring high on axis I are stations with coarse sand, *Posidonia* beds, sandy gravel, muddy sand or gravelly sand. Stations with low scores on this axis are relatively deep with muddy or sandy muddy sediment.

Along axis II stations seem to ordinate according to substratum type. Thus, low scores on this axis were attained by stations with *Posidonia* beds and sediments with biogenic fragments, medium scores by stations with muddy and mixed sediments, and higher scores by sandy and sandy gravel stations.

Among species scoring high on axis I are those characteristically found among photophilous algae: *Odontosyllis ctenosoma* (de Gaillande, 1968), *O. gibba* (Alos & Pereira,

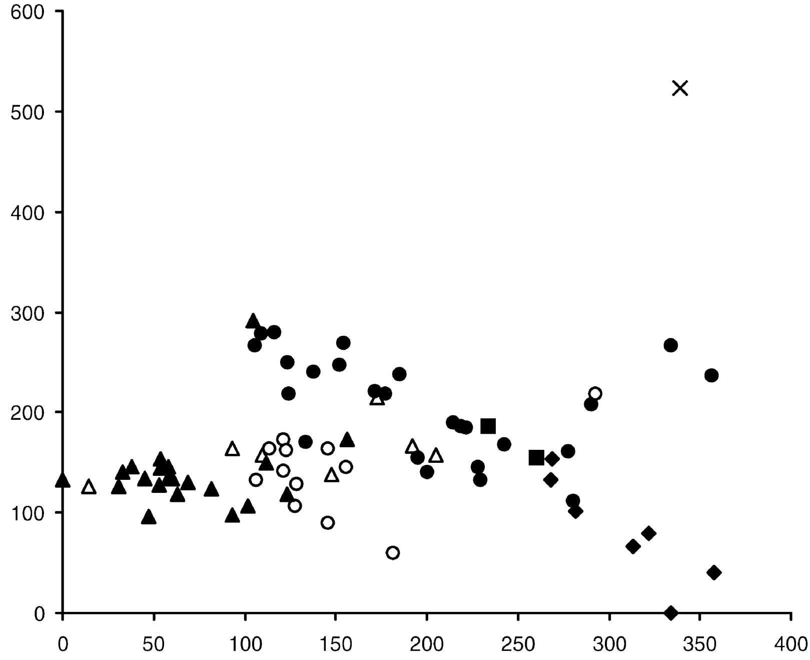

Fig. 4. DECORANA plot of the stations belonging to the bathymetric group 10–30 m against the first two major axes. Symbols represent type of substratum: ▲ mud, ❍ muddy sand, Δ sandy mud, ● sand, ■ gravelly sand, × stones-gravel-biogenic fragments, ◆ *Posidonia* beds.

1989), *Grubeosyllis limbata* (Sarda, 1990), *Syllides fulva* (Alos *et al.*, 1982), *Pseudosyllis brevipennis* (San Martin *et al.*, 1981). Also high scores are given to species typical of sandy communities that reflect euphotic and strong hydrodynamic conditions such as *Ophelia roscoffensis, Thalenessa dendrolepis* (Picard, 1965), *Paradoneis armata* (Castelli, 1987), *Pisione remota (*Duineveld *et al.,* 1991) and species characterizing *Posidonia* meadows such as *Exogone rostrata, Parapionosyllis brevicirra* (Alos & Pereira, 1989), *Amphicorina armandi* (Alos, 1983), *Xenosyllis scabra* (Pérès, 1954). Among species scoring low on axis I are generally included those associated with sandy sediments or muddy sands such as *Diplocirrus glaucus* (Giangrande & Gambi, 1985; Gambi & Giangrande, 1986; Castelli, 1989), *Heteromastus filiformis, Marphysa sanguinea* (de Gaillande, 1968), *Lanice conchilega* (Bergman & Hup, 1992), *Spiochaetopterus costarum* (Llanso, 1992), *Spiophanes kroyeri* (Giangrande & Gambi, 1985) or species associated with muds or sandy muds such as *Levinsenia gracilis* (Desbruyeres *et al.*, 1973), *Maldane glebifex, Sternaspis scutata* (Picard, 1965), *Sthenolepis yhleni* (Bellan, 1961). Most of these species are eurybathic and some indicate organic pollution or instability of the environment (FAO/UNEP, 1986; Diaz-Castaneda & Safran, 1988; Diaz-Castaneda *et al.*, 1989; Lastra *et al.*, 1990; Crema *et al.,* 1991; Moore & Rodger, 1991; Chang *et al.*, 1992; Dewarumez *et al.*, 1992). Regarding axis II, high-scoring species are sand-preferring ones such as *Diopatra neapolitana, Glycera tridactyla, Mysta siphonodonta, Sigalion mathildae* (Picard, 1965), *Prionospio caspersi, Scolelepis squa-*

mata, Spiophanes bombyx (Lardicci, 1989), *Peresiella clymenoides* (Harmelin, 1968). Low scoring on axis II are sciaphilous species, or species characteristic of the coralligenous community, namely *Amphitrite variabilis* (Bellan, 1961; Sarda, 1986), *Dorvillea rubrovittata* (Sarda, 1986), *Haplosyllis spongicola, Serpula concharum* (Abbiati *et al.,* 1987), *Polyphysia crassa* (Laubier, 1959), *Protula ampullifera* (Bianchi, 1981), *Syllis ferrani* (Alos & San Martin, 1987). Indeed, these species characterise stations with precoralligenous or corraligenous substratum or stations with *Posidonia* beds.

According to the results of Spearman correlation analysis, axis I correlates, in descending order of significance, first with depth ($r = -0.4725$, $P < 0.001$) and second with coarse percentage ($r = 0.3207$, $P < 0.001$), while axis II correlates first with coarse percentage ($r = 0.3075$, $P < 0.01$) and second with depth ($r = -0.2727$, $P < 0.05$). This suggests an inverse relationship between depth and coarseness of sediment which is, indeed, proved by a significant negative correlation between them ($r = -0.3385$, $P < 0.01$). Combining the results of the above analyses axis I probably represents mainly depth and axis II the type of substratum (including type of sediment).

d. The third bathymetric group of stations (36–150 m)

The 64 stations belonging to this group yielded a total of 333 species. The ordination of stations along the first two axes is shown in Fig 5. Low scores on axis I are held by stations with the higher percentage of sand, medium scores by stations with sandy mud, while stations with muddy sediments score high on this axis. Ordination of stations along axis II is not determined by either bathymetry or granulometric composition of sediment. Stations scoring high have sediment characterized as sandy mud without biogenic fragments or with biogenic fragments presenting low structural complexity. Lower values are exhibited by stations with sand or muddy sand or stations with heterogeneous biogenic fragments. Axis II apparently represents the structural complexity of the substratum. Species scoring low on axis I include: *Hyalinoecia fauveli, Euclymene palermitana, Sthenelais boa*, characterising detritic bottoms with high percentage of mud (Picard, 1965; Intes & LeLoeuff, 1986); *Pionosyllis dionisi, P. weismanni, Notopygos megalops* associated with the coralligenous community (Fauvel, 1927; Ben-Eliahu, 1977; Parapar *et al.*, 1993); and the gravel-preferring species *Psammolyce arenosa* (Picard, 1965). Species scoring high on axis I are mainly mud-preferring: *Marphysa bellii, Lumbrineris fragilis, Nephtys hystricis, Maldane glebifex, Sternaspis scutata* (Picard, 1965), *Ninoe armoricana* (Giangrande & Gambi, 1985), *Pseudopolydora pulchra* (Eleftheriou, 1970), *Ancistrosyllis groenlandica* (Augier, 1982), *Rhodine loveni* (Reyss, 1966), *Marphysa kinbergi* (Intes & LeLoeuff, 1986). As to axis II, species with high scores could not be classified in a single category regarding their substratum preference. Among them are species characterizing circalittoral or bathyal communities, including *Brada villosa* (Picard, 1965), *Chaetopterus variopedatus* (Sarda, 1986), *Hyalinoecia fauveli, Maldane sarsi* (Intes & LeLoeuff, 1986), *Pionosyllis dionisi* (Parapar *et al.*, 1993), *Serpula lobiancoi* (Abbiati *et al.*, 1987) or species with a wide bathymetric distribution. Species characterising coralligenous communities and others associated with mud or having a mixicole character also belong here. Species scoring low on axis II show various preferences as to substratum type and depth.

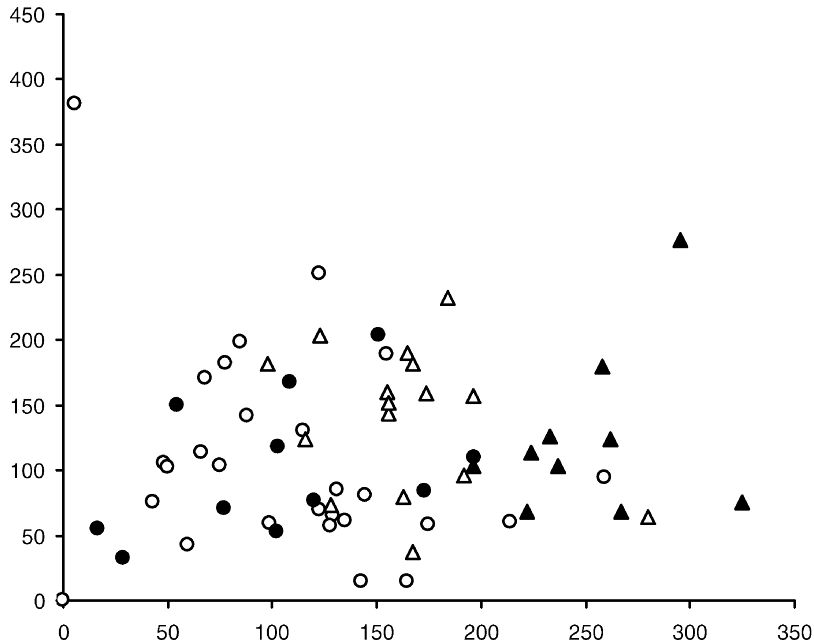

Fig. 5. DECORANA plot of the stations belonging to the bathymetric group 36–150 m against the first two major axes. Symbols represent type of substratum: ▲ mud, ❍ muddy sand, Δ sandy mud, ● sand.

The Spearman correlation shows that axis I is negatively correlated with sand percentage ($r = -0.5291$, $P < 0.001$) and axis II positively with depth ($r = 0.3751$, $P < 0.01$). Based on the results of the DECORANA plot and the Spearman correlations, axis I probably represents the granulometric composition of the sediment, whereas axis II is related to depth and the structure and heterogeneity of the substratum (in our case this latter is mainly associated with the quantity and type of biogenic fragments on the bottom). Note that there is no correlation between depth and coarseness of sediment in this group of stations ($r = -0.0584$, $P > 0.05$).

3. Ecological indices

The ecological indices of general diversity H' (Shannon & Weaver, 1963), evenness J (Pielou, 1969), species number (S) and individual's density per m^2 (N) were calculated for each station. The correlation of the indices with depth and coarse sediment percentage was determined using the Spearman's rank correlation coefficient. Table 1 presents the minimum and maximum value of each index and its correlation with the measured abiotic factors.

The minimum diversity (H' = 1.266) and evenness (J = 0.366) values were measured in Elefsis Bay (Saronikos Gulf), an area with heavy organic pollution. The respective values calculated on the basis of all macrobenthic species present were H' = 1.626 and

Table 1. Minimum and maximum values of the ecological indices measured. Spearman's rank correlation coefficient values among the indices, depth and coarse sediment percentage.

indices	min.	max.	depth	% coarse
H'	1.266	5.999	–0.0876	0.3725 ***
J	0.366	1.000	0.4289 ***	0.0863
S	3	123	–0.2445 **	0.3317 ***
N	5	7080	–0.3692 ***	0.1519

** = P < 0.01; *** = P < 0.001

J = 0.390 (Simboura *et al.*, 1995a). Low diversity values (H' < 3) were found in stations with high hydrodynamic regime and very coarse sediment (as in N. Sporades Islands, where also the lowest species richness was measured), in stations with very fine sediments (Maliakos, Lakonikos Gulfs), in stations with anthropogenic disturbance caused by urban effluents (inner Saronikos Gulf) or metalliferous wastes (Larymna Gulf; Simboura, 1998) and in stations with great depth and volcanic substratum (Kyclades Plateau, Santorini Island; Zenetos *et al.*, 1993).

High diversity values (H' > 5.4) (and maximal number of species) were found in stations with high structural complexity and substratum heterogeneity (mixed sediments with biogenic fragments or algal cover) belonging to various depths (18–91 m). The highest diversity value was measured in an Ionian station (western Peloponnisos coasts) at 40 m depth and sandy sediment covered with biogenic fragments of *Cladocora* and bivalve shells.

The highest evenness value (J = 1.0) was measured in stations of the Kyclades plateau and Santorini Island at depth below 178 m, while the minimum density value (5 indiv. $\cdot$ m^{-2}) occurred in the deepest station of all (Santorini Island, depth = 380 m). The maximal density value (7080 indiv. $\cdot$ m^{-2}), measured in an Ionian station, is attributed to the high density of serpulids and sabellids found in bundles of tubes. The total macrobenthic faunal density at that station was 7930 indiv. $\cdot$ m^{-2} (Zenetos *et al.*, 1997).

The results of linear correlation among the ecological indices and the abiotic parameters measured show that diversity (H'), and species number (S) increase with increasing percentage of coarse material in the sediment. Evenness increases with depth, while species number and specimen density decrease. Diversity did not correlate significantly with depth.

A graphical representation of the variation of the ecological indices H', S and N with depth and coarse material percentage was obtained by the distance weighted least squares method (Figs. 6 and 7). Species number (S) and diversity (H') apparently increase with coarse material percentage (Fig. 6), which is in agreement with the Spearman correlation results (Table 1). The graphical representation indicates no change of density in relation with sediment percentage in coarse material. As for depth (Fig. 7) the three ecological indices (H', S and N) present a similar pattern of variation. The general trend is a decrease with depth, but all three lines present a remarkable change of slope at two points corresponding approximately to 25 and 70 m. Though the Spearman correlation did not show any statistically significant correlation of diversity with depth, Fig. 7 clearly shows a non-linear pattern of correlation among these two parameters.

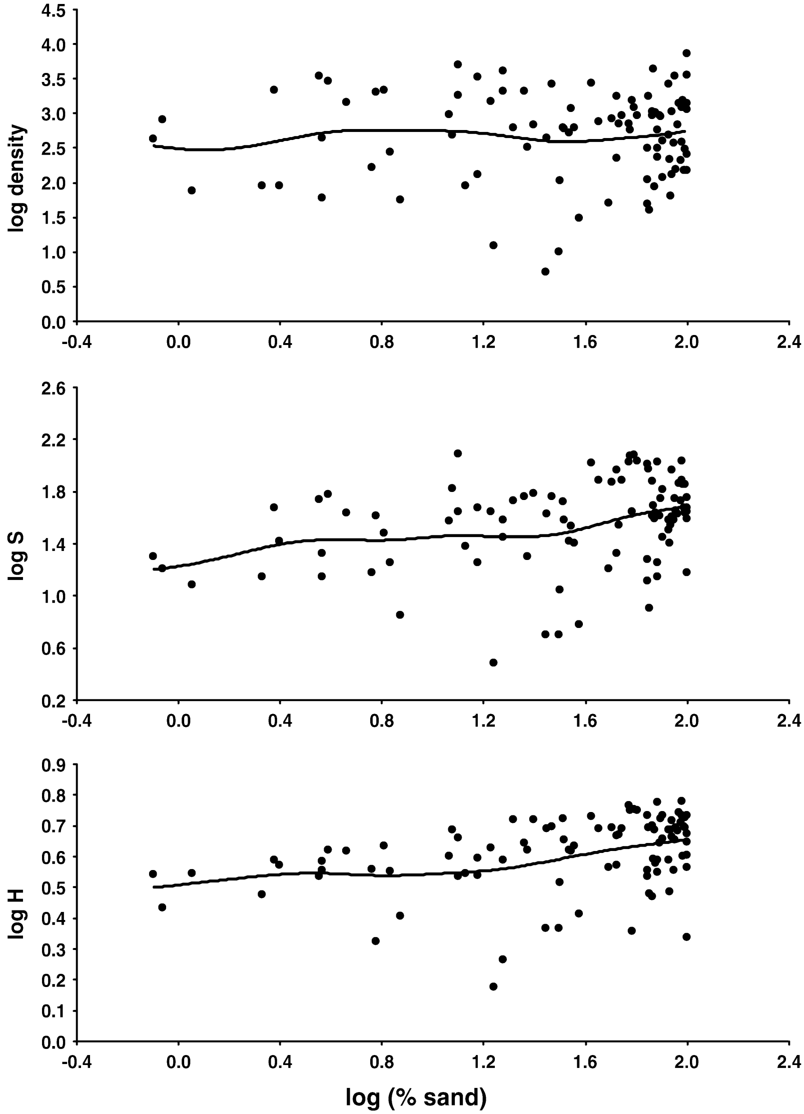

Fig. 6. Graphical representation of the variation of specimen density (indiv. · m^{-2}), species number (S) and diversity (H') with sediment percentage in coarse material.

Discussion

The importance of depth and substratum type in shaping polychaete communities varied in the three bathymetric groups. The most significant effect of depth was observed in the second bathymetric group between 10 and 30 m, although its influence cannot be distinguished from that of substratum. Indeed, in the infralittoral zone, factors controlling the distribution of benthic fauna such as light intensity, hydrodynamic energy induced by wave action and granulometric composition of sediment (Pérès &

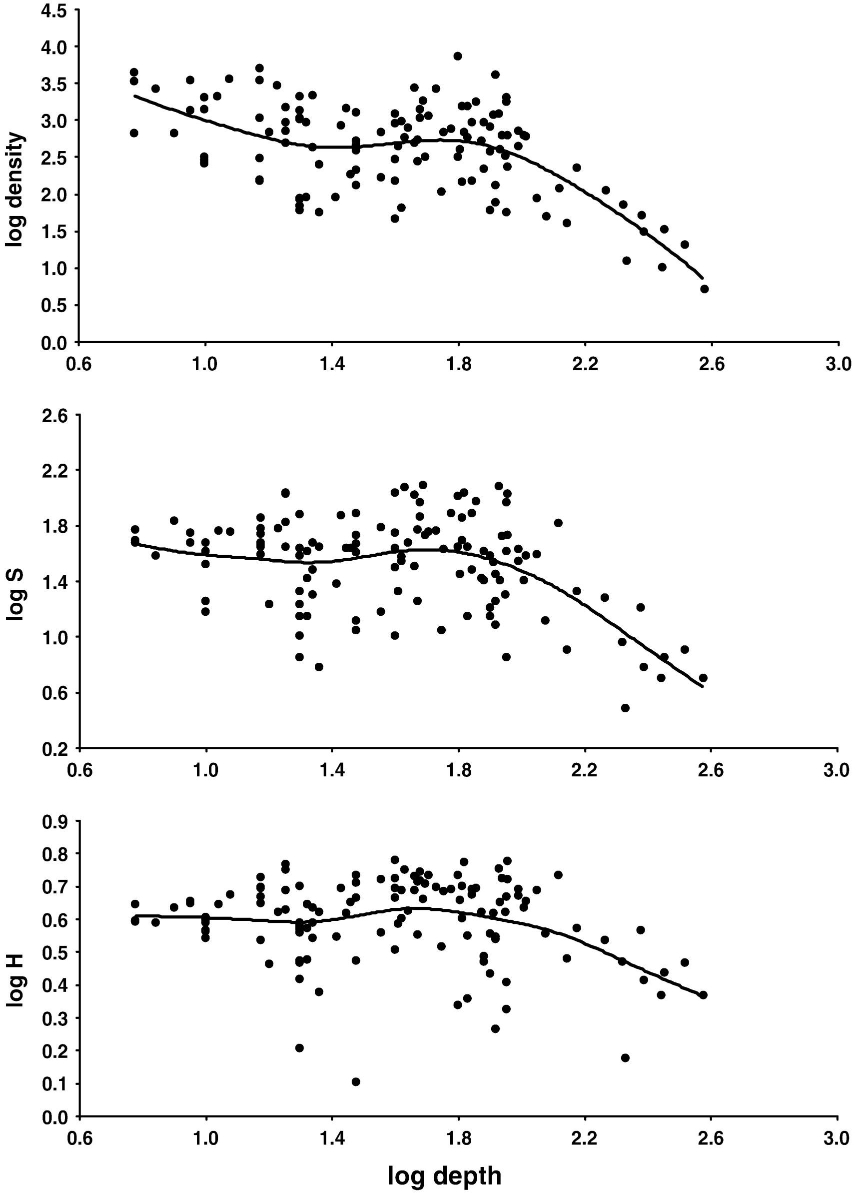

Fig. 7. Graphical representation of the variation of specimen density (indiv. · m^{-2}), species number (S) and diversity (H') with depth.

Picard, 1964; Pérès, 1982; Bellan-Santini, 1994) usually present strong variations correlating with depth. Significant correlation between depth and coarse percentage was also observed in the present study in this group of stations. Thus the influence of these factors acts as a sub-component of a complex super-factor, which is depth in that zone.

In the third bathymetric group, corresponding to the circalittoral zone 36–150 m, factors controlling polychaete distribution are the granulometric composition, including heterogeneity of the sediment, and depth. The lack of correlation between sediment coarseness and depth may be, because the bathymetric distribution of sediments (according to their granulometry) is no longer controlled by hydrodynamism but rather by other factors such as slope morphology, advection currents *etc.* At these depths there is a great homogeneity of environmental conditions because light intensity and wave action, components related to depth, are diminished. Depth, however, remains important and probably affects other factors such as food availability. In a study of macrobenthic community structure along the continental shelf of Crete, sedimentary characteristics such as grain size play an important role in the shallow stations, while in the deep offshore stations macrofauna was largely shaped by food quality and food availability (Karakassis & Eleftheriou, 1997).

In the bathymetric group corresponding to the upper infralittoral (3–9 m) the governing factors were the type of substratum and exposure to wave action (hydrodynamism). In this shallow zone, where depth variation is very limited, hydrodynamic energy is controlled mainly by wind and bottom morphology and less by depth. The degree of exposure to wave action in turn plays an important role in influencing the type of substratum.

Regarding the relation of the diversity indices with the parameters measured, the present study showed that diversity is favoured by structural complexity and heterogeneity of the substratum. On the other hand it is disfavoured by natural factors such as intense hydrodynamic conditions or volcanism of the substrata and by anthropogenic factors such as disturbance caused by organic pollution or metalliferous waste dumping.

Depth seems to have an overall negative influence on diversity, species number and number of individuals. A reduction of benthic diversity with depth has been demonstrated in several other cases such as in the continental shelf of Crete (Karakassis & Eleftheriou, 1997), in the South Aegean continental slope (Tselepides & Eleftheriou, 1992) and in the medio- and infralittoral zones of the Balearic Islands (Sarda, 1991). Our results indicate that this influence is less pronounced within a depth range of *ca.* 25–70 m. It is noteworthy that in the continental shelf of Crete (40–190 m), the diversity index peaked at 70 m depth, followed by a rapid decline, while chloroplastic pigments also dropped below 70 m (Karakassis, 1991). Perhaps 70 m represents a turning point below which depth significantly influences the biotic and abiotic parameters.

In the large geographical area covered by this study, changes in polychaete community structure and diversity should be influenced by complex factors which are not linearly related to depth. The poor food availability in deep water could be one such key factor in the oligotrophic Eastern Mediterranean.

Summary

Benthic samples were collected from a large geographical area covering the Aegean and Ionian Seas (Greece, Eastern Mediterranean) and the polychaete species were identified. A total of 188 stations sampled on soft substrata and at depths ranging from 3 to 380 m yielded 398 species of polychaetes. The Detrended Correspondence Analysis was applied to the data to determine the major environmental factors controlling the

spatial distribution of polychaetes. The data were grouped into three bathymetric ranges corresponding to the upper infralittoral (3–9 m), the lower infralittoral (10–30 m) and the circalittoral (36–150 m) of the Mediterranean. The resulting ordination plots of the stations were interpreted using station characteristics, the species' ecological characteristics and the Spearman's rank correlation statistics. In the shallower group of stations the governing factors were substratum type and hydrodynamic conditions. In the intermediate group (10–30 m), depth was the most significant factor, followed by the type of substratum. In the third group (36–150 m) the main controlling factors were the granulometric composition of the sediment and depth. The ecological indices of diversity, species number and abundance were calculated and were correlated with depth and sediment characteristics. Diversity is apparently favoured by structural complexity and heterogeneity of the substratum, whereas there seems to be a non-linear pattern of correlation between depth and diversity.

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