The continental shelf of Crete: structure of macrobenthic communities

Ioannis Karakassis*, Anastasios Eleftheriou

Institute of Marine Biology of Crete, PO Box 2214, GR-71003 Heraklion, Crete, Greece

ABSTRACT· The analysis of 99 quantitative macrobenthic samples taken from the Cretan shelf at depths ranging from 40 to 190 m yielded 547 species from a total of 18858 individuals. Both average abundance and biomass decreased with depth in this zone by 85 and 75% respectively. The fauna was not consistently related to the biocoenoses proposed for the Mediterranean, at least with regard to the distribution of characteristic species in the sampled stations. Diversity also decreased with depth, resulting in a rather impoverished fauna towards the outer shelf. The main factors explaining the overall macrofaunal distribution were depth and chlorophyll a, while further analysis for the 4 different groups of stations identified by cluster analysis revealed that factors controlling the structure of the assemblages also change with depth: in the shallow stations sedimentary characteristics such as grain size play an important role while in deep offshore stations macrofauna is largely shaped by food availability and the quality of sedimenting phytoplankton biomass.

KEY WORDS: Macrofaunal community · Abundance · Biomass · Diversity · Particulate organic carbon · Chlorophyll · ATP · Redox potential · Eastern Mediterranean · Continental shelf

INTRODUCTION

Continental shelf ecosystems contribute to global carbon fixation to an extent disproportional to the area they occupy. Estimations of productivity for the worlds' aquatic ecosystems, based on Walsh & Dieterle (1988), give a productivity 5 times higher in shelf ecosystems than that of the Ocean. Unlike the deep sea, where the effect of benthos on total system metabolism is negligible (Ott 1992), or the shallow intertidal zone, where the pelagic component is insignificant and benthos dominates total system metabolism, the continental shelf ecosystem seems to be regulated by both pelagic and benthic components. The outer shelf, where the sea bottom is below the mixing depth over the greater part of the year, is dominated by deposit feeders which utilize sedimented organic material colonized by micro-organisms and stimulate microbial activity (Fenchel & Jørgensen 1977). The return of nutrients resulting from this remineralization process into the upper water column during the deep mixing period

influences pelagic production and provides indirect feedback (Wassmann 1984). In this context quantitative information on the benthic ecosystems is an important element for understanding the function of the ecosystem as a whole.

The Mediterranean, and particularly the eastern basin, is one of the most oligotrophic areas of the worlds' oceans and has often been an obstacle to researchers attempting to formulate general marine biological rules (Petersen 1985). The macrofauna of the continental shelf in the Eastern Mediterranean has received extremely little research effort in comparison to that of the western basin (Bellan-Santini 1985). Very few data sets have been published using quantitative sampling devices and none of them was coupled with geochemical data. In most benthic studies, even recently (Zenetos 1996), separation of macrofauna from the sediment has been performed by means of a 1 mm sieve, despite the fact that macrofauna of the eastern Mediterranean, and particularly in the shelf and slope, has been found to be smaller in size compared to those found generally in the same Atlantic biotopes (Bellan-Santini 1985).

*E-mail: jkarak@imbc.gr

Island communities are usually atypical due to the relatively small size of the shelf. The Cretan shelf however is rather large in comparison to most Mediterranean islands, its coastline exceeding 800 km. The continental shelf of Crete, situated in the centre of the eastern Mediterranean Basin, could be considered as a representative site for the study of the influence of the oligotrophism on the benthic ecosystem since this area is not affected by large rivers or major anthropogenic perturbations.

MATERIALS AND METHODS

A set of 99 stations was chosen on the continental shelf of Crete at bottom depths of 40, 70, 100, 130, 160 and 190 m. Sampling was carried out during May and June 1988 using the RV 'Philia'. The continental shelf along the north coast extends up to 8 miles from the shoreline which forms a number of relatively open bays. Along the south coast the shelf is very steep with the exception of only 2 areas, i.e. to the south of Ierapetra (I) and in the Gulf of Messara (MR). The sampling stations (Fig. 1) were in general chosen using a number of transects taken at right angles to the coast. Coverage of the different sub-areas of the continental shelf, in terms of sampling effort, was approximately proportional to the size of each area. At each station sediment was sampled by means of a 0.1 m^2 top-opening Smith-McIntyre grab (Smith & McIntyre 1954). Samples with less than 6 cm of sediment were rejected as recommended by Eleftheriou & Basford (1989). The redox potential (Eh) at different depth layers and temperature (at –5 cm) were measured. After sieving over a 0.5 mm mesh the residue was preserved in 10% formalin and stored for subsequent laboratory analysis. A second sample taken at each station was subsampled for particle size analysis, plant pigments total organic carbon (TOC) and adenosine triphosphate (ATP) content. These data, which will be reported elsewhere (Karakassis & Eleftheriou unpubl.), were used for the determination of relationships between macrofaunal and environmental variables.

Samples were sorted in the laboratory after being stained with Rose Bengal for 24 h. Macrofaunal organisms were identified and enumerated at the species level, and the wet biomass was weighed in total for 6 major taxonomic groups (Polychaeta, Mollusca, Crustacea, Echinodermata, Sipuncula and miscellanea); the dry biomass was calculated using the conversion factors given by Eleftheriou & Basford (1989). Animals of excessive weight (>50% of the total station biomass) were weighed separately, and their biomass excluded from the data analysis.

Cluster analysis of community data was performed using the Bray-Curtis similarity index (Bray & Curtis 1957) and the group average linkage technique (Clarke & Warwick 1994); in order to normalize the data and avoid skew a square root transformation was applied on the abundance data prior to cluster analysis (Field et al. 1982). Results are expressed in the form of a dendrogram in which samples have been arranged into groups of increasingly greater similarity based on species abundance. In order to detect statistically significant differences between the groups obtained by the cluster analysis the ANOSIM (ANalysis Of SIMilarity) method was used (Clarke & Green 1988, Clarke & Warwick 1993).

Multidimensional Scaling (MDS) ordination analysis (Field et al. 1982) was performed with the same configuration as in cluster analysis with respect to similarity index and transformation. In order to identify relationships between community and other environmental data, the technique described in Kruskal & Wish (1978) was used. For each environmental variable measured, a linear multiple regression was performed using this variable as the dependent variable and the coordinates of the MDS configuration as the independent variables. This process provided a weighted combination of the coordinates which explained the variable as well as possible, the goodness-of-fit being given by the multiple correlation coefficient. Regression weights were transformed to the corresponding angles and consequently are plotted in a 2-dimensional plot comprising sampling units and environmental variables. Despite the fact that this method is based on linear regression (and in general linearity is not the usual case in most ecological situations), this method seems to us appropriate for the examination of animal-sediment relationships in a case where several environmental parameters are strongly intercorrelated (Karakassis & Eleftheriou unpubl.). An alternative method, based on non-para-
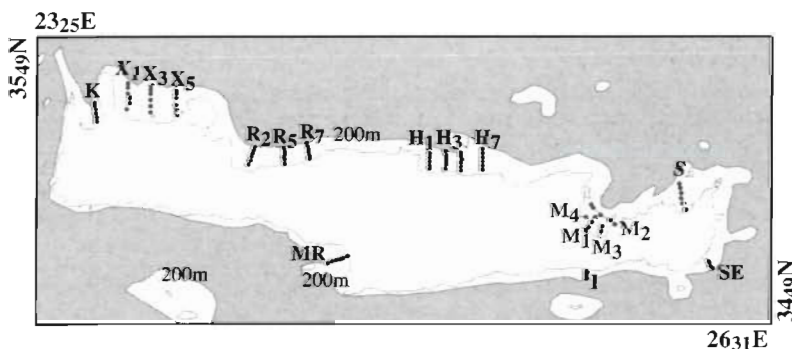

Fig. 1. Sampling stations on the continental shelf of Crete

metric statistics, described by Clarke & Ainsworth (1993) would require the elimination of most of the environmental parameters from this data set since they are correlated with depth. Species richness for each group of stations was calculated using the S_∞ method (Karakassis 1995) while the $(\log_2)$ Shannon information index H' (Shannon & Weaver 1949) and the associated evenness component J (Pielou 1966) were calculated for each sample. Cluster analysis, ANOSIM and MDS were performed by means of the PRIMER software package (developed in Plymouth Marine Laboratory).

RESULTS

Fauna

A total of 18858 individuals were identified as belonging to 547 species. Among these 238 were polychaete species, 165 crustaceans, 89 molluscs, 23 echinoderms, 14 sipunculans and 18 miscellanea (not always identified down to species level). In all the individual samples taken the polychaetes comprised most of the species found. On average, the number of polychaete species found in the shallow (40 m depth) stations was 48.1% of the total species number identified in this depth zone. This number increased up to 53.4% at the deeper (190 m) stations. Crustaceans decreased with depth from 31 to 20% while molluscs remained a relatively stable component of the community contributing 13.2 to 14.4% of the species found at any depth with the exception of 190 m, where their percentage decreased to 11.5%.

Table 1. Combinations of simultaneous occurrence of characteristic species from different bicoenoses (after Pérès 1967) in the samples taken on the Cretan shelf. DC: coastal detritic; VTC: terrigenous mud; DE: muddy detritic bottom; VP: bathyal mud

Combination	Samples	Total
None	3	3
DC	4	
VTC	5	
DE	5	
VP	4	18
DC-VTC	7	
DC-VP	1	
DC-DE	–	
VTC-DE	10	
VTC-VP	10	
DE-VP	7	35
DC-VTC-DE	5	
DC-VTC-VP	6	
VTC-DE-VP	24	
DE-DC-VP	–	35
DC-VTC-DE-VP	8	8

In order to test if the biocoenoses proposed by Pérès (1967) were readily recognizable in our samples a presence-absence analysis of occurrence of 'characteristic species' was performed with all the 99 samples. Four different types of biocoenoses were found, i.e. coastal detritic (DC), terrigenous mud (VTC), muddy detritic bottoms (DE) and bathyal mud (VP). The results of this analysis (Table 1) imply that there is a considerable amount of overlapping between different biocoenoses since in 78% of the samples simultaneous presence of more than 1 category of characteristic species was found.

Classification and analysis of similarity

On the basis of numerical classification of samples (Fig. 2), 4 major station groups (I to IV) could be distinguished reflecting depth and sediment-related differences in macrofaunal species composition plus 1 pseudogroup (V) comprising a heterogeneous assemblage of samples.

Group I consisted of 14 deep stations (160 to 190 m) with silt and clay content exceeding 80% of the sediment weight. Group II (20 stations) also consisted of deep stations (130 to 190 m) with coarser sediments than in Group I. Group III included 30 stations with intermediate depth (70 to 130 m) and silty sediment. All the samples taken at 100 m depth were included within this group. Group IV comprised all the 40 m depth stations as well as the 70 m ones with coarser sediment (silt < 80%). Group V comprised stations characterized by very coarse sediments ranging from Amphioxus sand to Maerl, from various depths and locations on the Cretan shelf as well as from deep stations with impoverished fauna from Messara on the south coast. Although the same criteria were used for the collection of samples, this heterogenous group could not be considered as a distinct unit and therefore it was excluded from subsequent analyses concerning the determination of animal-sediment relationships.

The analysis of similarity between groups showed significant differences between all the possible pairs of groups (p < 0.001). Therefore it could be argued that these groups reflect more or less distinct environmental conditions and accordingly subsequent analysis should take this classification into account rather than depth alone.

Abundance

Average total macrobenthic abundance decreased with depth from 4248 ind. m^{-2} at the 40 m stations to

663 ind. m^{-2} at 190 m. In all cases polychaetes comprised more than 55% of the abundance (up to 79% at the shallow stations) while sipunculans reached maxi-

mal abundance (250 to 270 ind. m^{-2}) in the 70 to 100 m zone and maximal relative abundance (20%) at the 160 m stations. The abundance of crustaceans, mol-

Table 2. Dominant macrofaunal species based on abundance rank (P: Polychaeta, S: Sipuncula, M: Mollusca, C: Crustacea, E: Echinodermata, Ne: Nemertinea). Densities are averaged over all samples in each station group identified by cluster analysis

| Species	Ind. m^{-2}	Cum. %	Species	Ind. m^{-2}	Cum. %
Group I			**Group II**		
Sarsonuphis sp. (P)	52.0	9.4	Golfingia murina (S)	125.4	10.1
Tauberia gracilis (P)	24.9	13.9	Tauberia gracilis (P)	58.9	14.9
Golfingia procera (S)	21.5	17.8	Sarsonuphis sp. (P)	58.9	19.6
Golfingia murina (S)	40.2	25.0	Golfingia procera (S)	63.6	24.8
Aricidea catherinae (P)	12.5	27.3	Hyalinoecia bilineata (P)	36.7	27.7
Nephasoma sp. (S)	16.6	30.3	Kelia sp. (M)	31.5	30.3
Prionospio steenstrupi (P)	12.5	32.5	Hyalinoecia brementi (P)	34.1	33.0
Notomastus latericeus (P)	12.5	34.8	Ampharete acutifrons (P)	25.3	35.0
Hyalinoecia brementi (P)	13.2	37.1	Axinulus croulinensis (M)	21.2	36.8
Mysidacea (C)	13.2	39.5	Chloeia venusta (P)	21.7	38.5
Nemertinea (Ne)	9.7	41.3	Nemertinea (Ne)	24.3	40.5
Glycera capitata (P)	11.1	43.3	Myriochele heeri (P)	19.1	42.0
Tharyx heterochaeta (P)	10.4	45.2	Pseydopolydora antenata (P)	19.6	43.6
Asychis biceps (P)	8.3	46.7	Bathyarca grenophia (M)	23.3	45.5
Euclymene palermitana (P)	9.0	48.3	Nephasoma sp. (S)	23.3	47.3
Spiophanes bombyx (P)	7.6	49.7	Cirrophorus lyra (P)	15.0	48.6
Ampharete acutifrons (P)	9.0	51.3	Tachytrypane jefreysii (P)	15.0	49.8
Amphioura filiformis (E)	8.3	52.8	Lumbrineris gracilis (P)	15.0	51.0
Terebellides stroemi (P)	6.9	54.0	Aricidea catherinae (P)	11.4	51.9
Eurydice truncata (C?)	6.9	55.3	Phthisica marina (P)	13.4	53.0
Lumbrineris emandibulata (P)	7.6	56.7	Chone duneri (P)	14.5	54.1
Rhodine loveni (P)	7.6	58.1	Rhodine loveni (P)	13.4	55.2
Euclymene oerstedii (P)	6.9	59.3	Prionospio steenstrupi (P)	12.4	56.2
Cirrophorus lyra (P)	6.9	60.6	Euchone rosea (P)	15.5	57.5
Poecilochaetus serpens (P)	6.3	61.7	Chrysopetallum debilis (P)	11.9	58.4
All other (111) species	218.7	100.0	All other (207) species	526.9	100.0
Group III			**Group IV**		
Onchnesoma steenstrupi (S)	96.3	6.6	Tharyx heterochaeta (P)	290.9	7.6
Golfingia procera (S)	83.5	12.3	Lumbrineris gracilis (P)	216.1	13.2
Tharyx heterochaeta (P)	81.3	17.8	Tauberia gracilis (P)	197.8	18.4
Tauberia gracilis (P)	85.0	23.6	Magelona minuta (P)	113.8	21.4
Prionospio steenstrupi (P)	25.4	25.4	Pseudoleiocapitella fauveli (P)	131.8	24.8
Hyalinoecia brementi (P)	38.0	27.9	Micronephthys maryae (P)	123.4	28.0
Myriochele heeri (P)	24.3	29.6	Aricidea catherinae (P)	164.0	32.3
Sarsonuphis sp. (P)	28.3	31.5	Onchnesoma steenstrupi (S)	102.3	35.0
Caudofoveata (M)	22.0	33.0	Hyalinoecia brementi (P)	82.0	37.1
Axinulus crulinensis (M)	24.6	34.7	Cossura soyeri (P)	83.5	39.3
Tharyx marioni (P)	21.0	36.1	Notomastus latericeus (P)	50.2	40.6
Chone duneri (P)	20.4	37.5	Chone duneri (P)	88.9	42.9
Mysidacea (C)	19.3	38.9	Lumbrineris nonatoi (P)	58.6	44.5
Lumbrineris gracilis (P)	19.3	40.2	Rhodine loveni (P)	47.1	45.7
Golfingia murina (S)	13.6	41.1	Ampelisca typica (C)	62.1	47.3
Aspidosiphon kovalevski (S)	18.0	42.3	Thyasira flexuosa (M)	41.8	48.4
Nemertinea (Ne)	19.1	43.6	Tharyx marioni (P)	30.3	49.2
Asychis biceps (P)	16.7	44.8	Melinna palmata (P)	39.5	50.2
Sipuncula sp.3 (S)	14.7	45.8	Notomastus sp. (P)	44.5	51.4
Ampharete acutifrons (P)	17.3	47.0	Terebellides stroemi (P)	26.4	52.1
Turitella communis (M)	13.3	47.9	Ampharete acutifrons (P)	33.3	52.9
Euclymene palermitana (P)	11.7	48.7	Cirrophorus furcatus (P)	38.7	53.9
Cirratulus filiformis (P)	15.4	49.7	Pista cristata (P)	31.4	54.8
Notomastus latericeus (P)	16.0	50.8	Ditrupa arietina (P)	50.6	56.1
Glycera rouxii (P)	12.6	51.7	Ehlersia cornuta (P)	23.4	56.7
All other (278) species	708.5	100.0	All other (366) species	1659.8	100.0
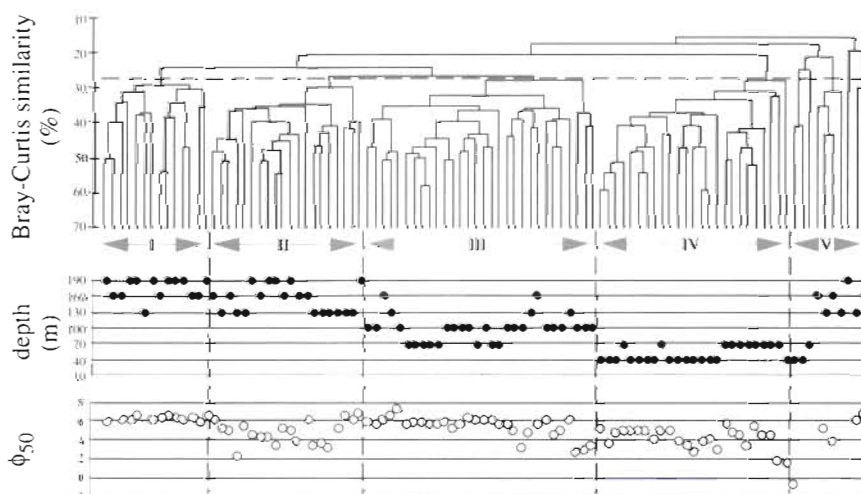
Fig. 2. Dendrogram of station classification showing the corresponding depth and ϕ_{50} |= $-\log_2$(MD), where ϕ_{50} is median grain size and MD is median diameter| of each station

luscs and echinoderms decreased with depth by factors of 10, 5 and 3 respectively.

For each of the groups (I to IV) of samples obtained by cluster analysis the 25 most abundant species were determined by means of ranking each of the 20 most abundant species within each sample; each species was given a rank score ranging from 20 down to 1 and the scores were subsequently added together within each group. Results showed (Table 2) that in all the groups there was a weak dominance with the first species hardly exceeding 10% of the total abundance within the assemblage. The cirratulid *Tharyx heterochaeta* dominated the shallow stations (Group IV), decreasing in density with depth, while the small paraonid *Tauberia gracilis* seems to have a wide distribution throughout the Cretan shelf, being among the first 4 dominant species in all station groups. The sipunculid *Onchnesoma steenstrupi*, which inhabits empty gastropod shells, reached high densities (ca 100 ind. m^{-2}) in Groups III and IV but its population declined rapidly at the deeper stations. Two sipunculan species, namely *Golfingia procera* and *G. murina*, were among the top 4 species in Groups I and II, the latter comprising 10.1% of the total abundance in Group II. At the deeper stations the onuphid polychaete *Sarsonuphis* sp. was found to be among the top 3 species with densities ranging between 50 and 60 ind. m^{-2}

For each of the groups of stations defined by cluster analysis, the total number of species found exclusively in that group and the name of the species found at more than one station in each group are presented in Table 3. The number of exclusive species found decreases from 87 in Group IV to 8 in Group I and so does their percentage of the total number of species in the group (22 to 6%). It should be noted that most of the exclusive species were found at 1 station only and

even those that were present in 2 or more stations had rather low densities in comparison to those of the dominant species (Table 2). The examination of both tables implies that at least between 'adjacent' groups (i.e. Groups I–II, Groups II–III and Groups III–IV) the faunistic differences are quantitative rather than qualitative. Therefore it could be argued that the entire data set is more or less a continuum with 2 extremes

Table 3. Species found exclusively in one group of stations identified by cluster analysis. TES: total number of exclusive species, P: Polychaeta, E: Echinodermata, C: Crustacea, M: Mollusca. Densities are averaged over all samples in each group. Presence indicates the number of samples in which the species was found

Group (TES)	Species	Ind. m^{-2}	Presence
I (8)	*Scolelepis ciliata* (P)	2.9	2
II (17)	*Labidoplax bouski* (E)	5.0	6
	Ampelisca vervecei (C)	2.0	4
	Fauveliopsis sp. (P)	2.0	3
	Epimeria cornigera (C)	1.0	2
III (26)	*Ophelina aulogaster* (P)	3.3	5
	Tanaopsis sp. (C)	1.3	3
	Cuspidaria cuspidata (M)	1.0	3
	Trachythyone elongata (E)	0.7	2
	Leptosynapta sp. (E)	0.7	2
	Phylo latreilli (P)	0.7	2
IV (87)	*Aricidea claudiae* (P)	22.0	9
	Tellina pulchella (M)	12.4	9
	Protodorvillea kefersteini (P)	11.2	5
	Glycera unicornis (P)	9.2	5
	Monoculodes subnudus (C)	4.4	4
	Tharyx multibranchiis (P)	4.4	4
	Leptaxinus sp. (M)	4.0	4
	Sosane sulcata (P)	2.8	4
	Paranaitis kosteriensis (P)	2.0	4
	Nuculana pella (M)	6.4	3

(Groups I and IV) while Groups II and III could be considered as intermediate zones.

Biomass

Average macrobenthic biomass (dry weight) decreased with depth, from 1.46 g m^{-2} in Group IV to 0.35 g m^{-2} in Group I (Fig. 3). Polychaetes contributed most of the biomass at all depths, their percentage decreasing with depth from 70% of the total biomass at the 40 m stations down to 40% at stations situated between 130 and 190 m. Crustaceans and molluscs exhibited larger biomass at the nearshore stations and decreased with depth while sipunculans reached their maximal absolute biomass in the 160 m depth zone (22% of the biomass) and they comprised 25% of the biomass at the deeper stations.

Feeding types

Surface deposit feeders were the dominant feeding type accounting for 55 to 60% at all depth zones (Table 4) while carnivores followed with ca 20% at the shallow stations and 30% at the deeper ones. Subsurface deposit feeders and filter-feeders accounted for 8 to 12% at all depth zones, and herbivores never exceeded 3% at any depth zone.

The main carnivores-scavengers with respect to abundance were polychaetes belonging to the families Lumbrineridae (*Lumbrineris gracilis*, *L. nonatoi* and *L. emandibulata*) and Onuphidae (*Sarsonuphis* sp., *Hyalinoecia brementi* and *H. bilineata*); the main filter-feeders were the polychaetes *Ditrupa arietina* and *Fabricia sabella* as well as several bivalve species; the group of deposit feeders comprised all the sipunculans
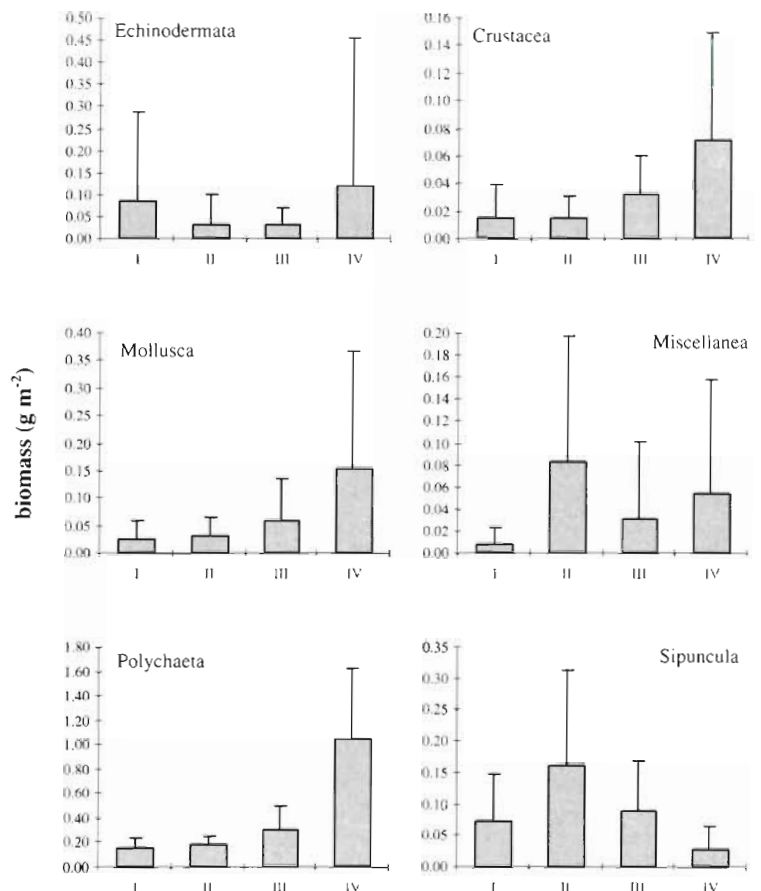

Fig. 3. Biomass (dry weight) distribution of the main macrofaunal groups within groups of stations (I to IV), defined by cluster analysis

and numerous polychaete species, the most abundant being *Tharyx heterochaeta*, *Tauberia gracilis*, *Aricidea catheninae*, *Pseudoleiocapitella fauveli* and *Magelona minuta*. Most of the polychaete species which showed higher abundance belong to genera (e.g. *Tharyx*) or families (Paraonidae, Onuphidae) that have been

Table 4. Average abundance (%) of feeding types in each group of stations defined by cluster analysis

Feeding type	Station group			
	I	II	III	IV
Herbivores	0.3	0.3	0.3	1.1
Detritus feeders	4.5	4.3	6.5	6.6
Filter feeders	4.3	11.9	9.6	8.2
Carnivores	26.2	24.6	18.3	19.7
Scavengers	2.2	1.8	2.0	1.0
Surface deposit feeders	50.3	48.2	52.9	51.4
Below surface deposit feeders	12.3	8.9	10.4	12.0

Table 5. Diversity indices (H', J) and estimated S_∞ values for each group of stations

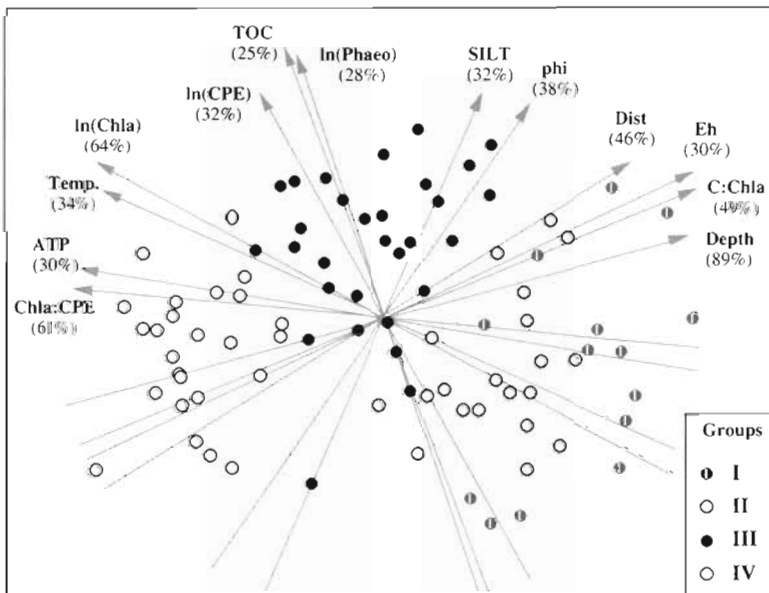| Group	Species no./0.1 m^2		H'		J		S_∞
	Mean ± SD		Mean ± SD		Mean ± SD		
	Min	Max	Min	Max	Min	Max	
I	29.21 ± 4.85		4.49 ± 0.27		0.93 ± 0.04		152.6
	21	37	4.16	4.92	0.83	0.97	
II	48.45 ± 10.56		4.96 ± 0.37		0.89 ± 0.05		240.0
	32	80	4.18	5.49	0.78	0.94	
III	52.77 ± 12.93		5.07 ± 0.36		0.89 ± 0.03		305.9
	30	80	4.41	5.75	0.80	0.95	
IV	75.00 ± 15.00		5.22 ± 0.38		0.84 ± 0.04		407.9
	55	111	4.44	6.12	0.75	0.92	

Fig. 4. Two-dimensional space obtained through the MDS (multidimensional scaling) ordination (stress 0.19) for 89 sampling stations. Cluster groups identified in Fig. 2 are denoted with different symbols. Lines drawn on the configuration show directions of best fit for the most significant (p < 0.001) environmental variables. Arrows denote direction of increase for each variable. Percentages (in parentheses) indicate the fraction of variance explained by each variable. Dist.: distance from the coast. Other abbreviations as in Table 6

Ordination and multiple regression

The results of the MDS ordination along with the significant environmental variables are presented in Fig. 4 while the results of the regression analysis for the entire data set are given in Table 6. Prior to ordination the stations comprised in the pseudogroup V were removed from the data set to obviate problems associated with the presence of 'outliers', e.g introducing bias to the ordination by compressing the distribution of the remaining sites (Hosie & Cochran 1994). The arrows plotted in Fig. 4 point towards increasing values, while their direction was calculated from the regression weights of each parameter; they could be seen as indicating the 'direction' of each gradient in the data set and therefore perpendicular directions could be considered as explaining different parts of the variance in the data. The results imply that the faunal distribution is determined by a 'network of gradients' the most important being those associated with depth, which alone explains 89% of the variance in macrofaunal data. Distance from the coast is also related to depth in most cases and so is redox (Eh), which tends to show higher values in offshore areas (Libes 1992).

reported as successful inhabitants of the deep sea according to Fauchald (1977) and Fauchald & Jumars (1979).

Diversity

Species diversity in general decreased from the shallow stations (Group IV) to deep silty stations (Group I) as shown by most of the results presented in Table 5. The number of species found in each sample declined on average from 75 to 29, this difference being largely dependent on the number of individuals present, which also decreased by approximately 85%. Although evenness (J) increased towards the deep stations, i.e. the dominant species were less abundant, the species richness influenced component of the Shannon index prevailed and therefore H' was higher in the shallow stations as well. The estimation (by means of the S_∞ method) of the total number of species in each group, i.e. the number of species that could be obtained by infinite sampling effort, is also presented in Table 5.

Table 6. Multiple regression analysis between environmental parameters and MDS (multidimensional scaling) scores for 2-axis ordination of comparison of sampling sites in the entire data set. Adjusted coefficient of determination (adj. R^2) gives the fraction of the variance accounted for by the explanatory variable. ANOVA values (F, df and p) are also given. Chl a: chlorophyll a; CPE Chloroplastic Pigments Equivalent; TOC total organic carbon; ϕ_{50}: median grain size; SILT: percentage of silt and clay in the sediment; Eh: redox potential; ATP: adenosine triphosphate; phaeo: phaeopigments

Variable	Direction cosines (regression weights)		Adj. R^2	F	df	p <
	x	y				
Depth	0.965	−0.264	0.886	343.62	2,89	0.000
ln(chl a)	−0.879	0.477	0.642	79.00	2,85	0.000
Chl a:CPE	−0.996	−0.094	0.609	68.80	2,85	0.000
TOC:chl a	0.919	−0.395	0.487	42.31	2,85	0.000
Distance	0.851	−0.525	0.464	39.06	2,86	0.000
ϕ_{50}	0.560	0.828	0.377	27.08	2,84	0.000
Temperature	−0.905	−0.425	0.337	19.32	2,70	0.000
SILT	0.399	0.917	0.320	21.19	2,84	0.000
ln(CPE)	−0.481	0.877	0.319	15.22	2,85	0.000
Eh	0.906	−0.422	0.301	14.35	2,60	0.000
ATP	−0.988	−0.155	0.295	9.16	2,37	0.001
ln(phaeo)	−0.330	0.944	0.279	17.87	2,85	0.000
TOC	−0.342	0.940	0.245	15.09	2,85	0.000

Sediment quantitative descriptors such as ϕ_{50} [= $-\log_2(MD)$, where ϕ_{50} is median grain size and MD is median diameter] and percentage of silt and clay at the sediment (SILT) are partly associated with depth, since in general fine sediments are found in the deeper offshore stations, but they also describe the complex regime of sediment-hydrodynamism-biota interactions which is quite unpredictable in the Mediterranean (Blanc 1968). The concentration of chlorophyll a (chl a) in the sediment is also an important factor in determining community structure (64% of the variance) and so are some indirect ratios such as C:chl a and chl a:CPE (Chloroplastic Pigments Equivalent, i.e. the sum of phaeopigments and chlorophyll a concentrations), ratios describing the condition of the sedimenting organic material and the 'freshness' of the phytoplankton cells available for the benthic organisms.

In order to examine in detail the interplay between environmental variables we repeated the above-described procedure for each of the Groups I to IV identified by cluster analysis since the absence of depth as an overwhelming determinant was expected to rearrange the MDS configuration so that fine differences would be revealed. The new MDS scores were used as independent variables for multiple regression with the environmental data. The results (Table 7) imply that different factors determine species composition at each group of stations.

In Group I it seemed that productivity-related parameters such as TOC and the quality of the sedimented phytoplankton material (ratio chl$a$:CPE) explain a large proportion of the variation in macrobenthic community structure, which is a good indication of food limitation in the deeper zone. In Groups II and III where there is an important depth element in the stations composition, depth was found to be the most important factor explaining 64 and 87% of the variance respectively. The ratio chl$a$:CPE was again among the determining factors at both groups. However in general Group III was determined by sedimentary parameters, ϕ_{50} (= $-\log_2 MD$) explaining 60% of the variance. The sediment type was even more important in the case of Group IV, where ϕ_{50} accounted for 62% of the variance and was the principal parameter determining community structure. Four out of 5 variables that gave significant correlation (at the $p < 0.05$) level in this group were sedimentary descriptors (including sorting coefficient, σ_1, and skewness, sk_1), the remaining one being depth.

The results reported here indicate that macrobenthic communities are structured by different factors at the 2 ends of this depth gradient on the Cretan shelf. The upper and nearshore part is shaped by the hydrodynamic processes and their effect on the sedimentary characteristics, while at the deeper and offshore part, food availability in qualitative and quantitative terms determines the limits of population growth for most of the benthic organisms.

Table 7. Multiple regression analysis between environmental parameters and MDS (multidimensional scaling) scores for each group of stations obtained through the cluster analysis. Adjusted coefficient of determination (adj. R^2) gives the fraction of the variance accounted for by the explanatory variable. ANOVA values (F, df and p) are also given. σ_1: sorting coefficient; sk_1: skewness; Other abbreviations as in Table 6

Group Variable	Direction cosines (regression weights) x	y	Adj. R^2	F	df	p <
I Chl a:CPE	−0.124	0.992	0.543	8.72	2,11	0.005
TOC	−0.991	−0.135	0.528	8.27	2,11	0.006
SILT	−0.842	0.540	0.452	5.53	2,9	0.027
II Depth	0.774	−0.634	0.637	17.67	2,17	0.000
Distance	0.846	0.533	0.568	13.48	2,17	0.000
Chl a:CPE	−0.250	−0.968	0.298	5.04	2,17	0.019
Chl a	−0.754	−0.657	0.220	3.69	2,17	0.047
III Depth	−0.992	−0.123	0.869	96.96	2,27	0.000
ϕ_{50}	−0.199	0.980	0.597	22.45	2,27	0.000
Temperature	0.673	−0.740	0.567	18.65	2,25	0.000
SILT	−0.020	1.000	0.529	17.20	2,27	0.000
TOC:chl a	−0.812	0.584	0.458	12.85	2,26	0.000
Chl a:CPE	0.960	−0.281	0.453	12.60	2,26	0.000
TOC	0.060	0.998	0.433	11.68	2,26	0.000
Distance	−0.372	−0.928	0.380	9.89	2,27	0.001
TOC:CPE	−0.441	0.898	0.364	9.02	2,26	0.001
TOC:Phaeo	−0.377	0.926	0.339	8.19	2,26	0.002
Chl a	0.930	−0.367	0.222	5.00	2,26	0.015
IV ϕ_{50}	−0.771	−0.637	0.621	20.63	2,22	0.000
SILT	−0.786	−0.619	0.581	17.67	2,22	0.000
Depth	0.959	−0.283	0.561	31.66	1,23	0.000
σ_1	−0.659	0.752	0.511	13.53	2,22	0.000
Sk_1	0.336	−0.942	0.208	4.15	2,22	0.030

DISCUSSION

The classification of benthic biocoenoses (Pérès 1967) had a profound impact on the development of benthic ecology in the Mediterranean. A considerable amount of information concerning the Mediterranean benthic ecosystems has been organized and presented with reference to this classification scheme. Even recent papers (Simbura et al. 1995, Zenetos 1996) have used this system for the description of benthic ecosystems in the

Aegean and Ionian shelf and despite the difficulties in the application of the scheme outside the Mediterranean (Petersen 1985) it has been considered as appropriate for the Mediterranean (Bellan Santini 1985, Petersen 1985). Pérès (1982) used the term 'organismic assemblages' to further clarify the relationship between this scheme and the old but never ending organismic-individualistic debate which has been going on since the beginning of the century (McIntosh 1995). One of the critical points in this debate is whether species are organized in distinct groups corresponding to different ecological conditions (Krebs 1985). Therefore it could be argued that the concept of characteristic species as descriptors of the environment plays a central role in the above-mentioned classification scheme.

Our results proved that in several cases characteristic species of more than 1 biocoenoses were found in the same sample. In fact all possible combinations were present in the data set except for DC-DE and DC-DE-VTC, which however were found in the last row of Table 1, where characteristic species from 4 biocoenoses occurred in the same sample. The 'casual species' concept (Pérès 1982) could be used in order to explain the co-occurrence of characteristic species of various biocoenoses in the same sample. However, the percentage of simultaneous presence of more than 1 category of characteristic species is too high (78%) to be explained in such a way. This is true especially when one considers that sampling was conducted by means of a 0.1 m² grab and therefore the patchiness effect would be much lower than when using dredges as was the case for most of the information reviewed in Pérès (1967). Of course it could be argued that the sampling methodology used in the present study was different with respect to both sampling gear and sieve mesh size and in fact most of the characteristic species found are at the low end of the size spectrum. Regarding quantitative aspects of the data set, it is worth mentioning that none of these species was dominant with respect to abundance or biomass and none was found to be responsible for the differences found among groups in previous analysis (Karakassis 1991) using the 2 indicator species analysis TWINSPAN (Gauch 1982). Although the ANOSIM results revealed significant differences between the groups identified by cluster analysis, a close examination of the data set seems to indicate that the main differences are quantitative (levels of density) rather than qualitative (presence/absence) and it therefore could be argued that the continuum concept (Mills 1969) is more applicable in this case as well. Gagnon & Haedrich (1991) investigated shelf macrobenthic communities in Labrador/Newfoundland using both taxonomic and functional approaches. They also found that samples are distributed along a primary continuum, without any evidence of well-defined clusters at a depth range of 85 to 622 m. Of course, the use of characteristic communities or assemblages is a convenient means for common reference among scientists and, up to a point, the biocoenoses described by Pérès (1967) reflect real differences among biotopes in the Mediterranean especially in the shallow inshore ecosystems. It could also be argued that an island shelf could be considered too narrow for species assemblages to be typical since gradients are steeper and the zonation components less extensive.

In terms of quantitative composition the macrofaunal assemblages on the continental shelf of Crete have similarities with comparably located faunas in the Mediterranean and elsewhere in the world. Quantitative data reported from Banyuls-sur-mer in the western Mediterranean (Bhaud & Duchene 1978) showed a certain degree of similarity with our data, i.e. 27 (out of 41) dominant species in Banyuls were also included in our species list but not with the same rank order. Desbruyeres et al. (1972) described an *Amphiura filiformis* community from the Spanish Catalan coast which bears a considerable resemblance to Group IV in the present study, i.e. both are dominated by *Tharyx heterochaeta* and *Tauberia gracilis* while *Lumbrineris latreilli* replaces *L. gracilis* on the Cretan shelf; further down the list dominance rank changes since small-sized species, such as *Magelona minuta*, *Cossura soyeri* and *Micronephthys maryae*, appear in our list.

Macrofaunal density was in general lower than that reported from other studies (Nichols & Rowe 1977, Eleftheriou & Basford 1989) but the main differences lay with the biomass which was impressively lower than that reported by other authors (Guille 1971, Bellan-Santini 1985), reaching only one-tenth of the average biomass reported by Eleftheriou & Basford (1989) from the North Sea shelf for the same depth zone. This reduced biomass is clearly related to the oligotrophy which is a characteristic of the Mediterranean Sea (Margalef 1985), and which is even more pronounced in its Eastern Basin. In fact it has been found that on the continental shelf of Crete the oligotrophic conditions of the Mediterranean offshore system prevail even at very short distances from the shore (Karakassis & Zivanovic 1995). Therefore the amount of *in situ* production of the organic material available for sedimentation on the seabed could be expected to be relatively low.

A conspicuous feature of the community structure on the Cretan shelf is the relatively high abundance of sipunculids, which are among the larger infaunal organisms; although they are considered as non-selective deposit feeders, elevated levels of organic material in their gut compared to those in the ambient sediment have been reported (Gage & Tyler 1991). The success-

Table 8. Comparative data sets from shelf and slope benthic ecosystems (S: number of species, N: number of individuals identified)

Source	Location	Depth (m)	S	N	Area (m²)	$(S-1)/\ln(N)$
Present study	Crete, shelf	40–190	547	18585	9.9	55.5
Eleftheriou & Basford (1989)	North Sea, shelf	70–200	409	21630	7.6	40.9
Coleman et al. (1997)	Australian upper shelf	11–51	803	60258	10.4	72.9
Gray (1994)	Norwegian shelf	72–305	620	39582	50.0	58.5
Hyland et al. (1991)	California outer shelf and slope	90–565	886	444989	34.4	68.0
Grassle & Maciolek (1992)	New Jersey & Delaware slope	1500–2000	798	90677	21.0	69.8

ful colonization by sipunculids of the offshore sediments on the Cretan shelf, where food availability is relatively low, may be attributed to the competitive advantages derived from their ability to cache the available food deeper in the sediment and their adaptation to environments characterized by the pulse of organic material, i.e. non-continuous sedimentation (Jumars et al. 1990). The fact that most of the dominant polychaete species belong to taxa capable of inhabiting deep sea environments along with large sipunculan densities could be attributed to the fact that the outer Cretan shelf presents to a certain extent a homology with deep environments elsewhere in the world with respect to limited sedimentation of organic material. This limitation could affect the biomass macrofauna:meiofauna ratio since meiofaunal organisms are better competitors for food than larger animals when food is scarce (Soyer 1985). Therefore it could be expected that the structure of the benthic metabolism in the Mediterranean could be significantly different to that on other continental shelves in the world. On the other hand, macrofaunal organisms have to endure not only food limitation but also high temperature, the latter inducing a higher metabolic rate and therefore higher demands for energy resources. Perhaps this is the major reason for the difficulties bathyal Atlantic fauna have in becoming established in the deeper zones of the Mediterranean as was suggested by Ben Tuvia (1983).

In comparison to other large-scale investigations of the benthic environment (Table 8) the macrofauna of the Cretan shelf could not be considered as impoverished with respect to species richness, nor are the diversity indices reported here lower than in other areas of the Mediterranean or the Atlantic. However there is a remarkable decline in species richness towards the outer shelf, the macrofauna becoming extremely scarce at the continental slope (Tselepides 1992).

Depth, not surprisingly, has been identified as the main factor controlling community structure in all the studies in the world where a considerable depth gradient was involved (such as Basford et al. 1989, Rabalais 1990). The present paper is no exception to this rule since in this 40 to 190 m depth interval everything changes with respect to physics, chemistry and biol-

ogy. This gradient is even more important in an oligotrophic system where the flux of organic material towards the sea bed is more limited.

The role of sediment type as a factor determining macrobenthic community structure has been emphasized by many authors (Sanders 1958, Gray 1974). Correlations between infaunal species and sediment types have been well documented since the turn of the century (Dayton 1984), different functional groups have been defined in association with different substrate types (Sanders 1958, Rhoads & Young 1971, Fauchald & Jumars 1979) and the role of some species in providing nutrient regeneration and structure to an otherwise relatively homogeneous substratum is well established (Dayton 1984). Macrofaunal assemblages at the shallow stations (Group IV) seem to be shaped by the sediment properties which are indeed more heterogeneous than those at the deeper offshore areas (Karakassis & Eleftheriou unpubl.). The increase in relative abundance of carnivores and scavengers towards the outer Cretan shelf seems to be compatible with their ability to exploit a variety of food resources.

At the deeper and offshore stations there are strong indications of food limitation. This is demonstrated by the strong relationship between chlorophyll a and community structure in the entire data set, as well as by the decrease in biomass and abundance of macrofauna and, in particular, of feeding types which depend on phytoplankton material such as filter feeders. In several cases, however, and in particular at the offshore deep stations, it was the ratio chla:CPE and not chlorophyll a concentration itself that showed significant correlation with the ordination results. This could imply that the quality of the sedimented plant material is at least as important as the quantity of chlorophyll a, and even if there is enough of the latter it could be of such a quality that macrofauna could not have a significant benefit.

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