

Sublittoral megabenthos along cliffs of different profile (Aegean Sea, Eastern Mediterranean)

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ABSTRACT. The sublittoral megabenthos was studied in selected areas of the Aegean Sea. Data were collected with a visual, non-destructive, method and the technique of randomly placed frames was adopted. Eighty-nine megabenthic species were recorded. The spatial and temporal variation in population density, as well as the pattern of dispersion, was estimated for the most dominant species. Spatial analysis of the population densities suggested the separation of the studied sites in three major groups, reflecting differences in cliff profile. Temporal analysis revealed the discrimination of summer samples. The pattern of dispersion for most of the examined species was random without seasonal differentiations. *Agelas oroides* and *Leptopsammia pruvoti* showed a clumped pattern, while *Halocynthia papillosa* and *Microcosmus sabatieri* were evenly distributed.

KEY WORDS : megabenthos, sublittoral, Aegean Sea, hard substrate, population density, spatial dispersion

INTRODUCTION

In the lower sublittoral zone, where light conditions are reduced, an algal-dominated community develops on hard substratum throughout the Mediterranean (AUGIER, 1982; ANTONIADOU & CHINTIROGLOU, 2005). This community, characterized by the development of sciaphilous species, constitutes a special environment, according to the typology of the European Water Framework Directive, on which few data exist for the Eastern Mediterranean (STERGIOU et al., 1997; MORRI et al., 1999; PANSINI et al., 2000; ANTONIADOU et al., 2004a; ANTONIADOU et al., 2004c). This environment is quite sensitive to anthropogenic pressure, such as coastal technical constructions (breakwaters, seawalls, docks, harbours etc.), terrigenous water outfall, toxic wastes, fishing or collection of rare species (red coral, sponges), invasion of introduced species, sport or recreational activities etc., as most megabenthic species are slow growing and long-living (WARWICK, 1993; BELLAN-SANTINI et al., 1994; GARRABOU et al., 1998, 2002; PEREZ et al., 2000; GARRABOU & ZABALA, 2001; BOUDOURESQUE & VERLAQUE, 2002; PAPADOPOULOU & KANIAS, 2003; CHINTIROGLOU et al., 2005). Many of these species are of great economic importance, either as a food source, or as potential sources of therapeutic drugs. Examples are the tunicate *Microcosmus sabatieri*, which is intensively harvested and commercially exploited at many locations in the Aegean (ANTONIADOU et al., 2004b) and the sponges of some genera such as *Agelas*, *Ircinia*, *Axinella*, *Dysidea*, which are currently studied for their bioactivity (e.g. SCHMITZ, 1994). Therefore, there is a growing need for studies focusing on the ecology and stock availability of megabenthic species, in order to establish efficient management plans for the exploitation and conservation of their populations and habitats (SALA et al., 1996; GARRABOU et al., 1998; PEREZ et al., 2000; GARRABOU & HARMELIN, 2002).

Furthermore, substrate inclination is thought to be a major factor controlling the spatial dispersion of sublittoral megabenthic species in rocky shore communities, reducing both illumination (UV radiation) and the deposition of sediment (GLASBY, 1999; PANSINI et al., 2000; BELL & SMITH, 2004). Nevertheless, its effects have been scarcely investigated directly (PRECIADO & MALDONADO, 2005). Considering this, the aim of the present investigation is to study the composition of the megabenthic fauna associated with a sciaphilic algae community along a wide range of cliff profiles in the Aegean Sea, as well as to detect the spatial and temporal variability of the most dominant species.

MATERIALS AND METHODS

Study area

The study was carried out in the northern part of the Aegean Sea (Fig. 1) at seven coastal locations sharing some common physical characteristics. These included hard substrate down to a depth of 30-40 m and inclinations greater than 50° (for details see ANTONIADOU et al., 2004c). Sampling stations were set at a variety of cliff profiles and depth ranges, which were classified in three groups: (1) vertical cliffs (85-90°), (2) moderately inclined cliffs (60-80°) and (3) gently sloping (55-60°) bio-constructed, i.e. colonies of the scleractinian *Cladocora caespitosa* (Linnaeus, 1767), cliffs (Fig. 2). The cliffs were subjected to low current intensities (5-12 cm s⁻¹), at least at the sampling depth (15-40 m). Water clarity overpassed 18 m, with the exception of station 5, where it was reduced to about 12 m, as this site constitutes a very closed and sheltered area, in which muddy sediment covers the sea bottom (ANTONIADOU et al., 2004c).

All cliffs were sampled during summer 1998 (stations 1-6) or summer 1999 (station 7) for the needs of spatial analysis. Station 3 was selected for the temporal analysis

because it is sheltered from the N, NE and NW winds that usually blow in this area during winter. Temporal sampling was carried out on a 3-month basis, from summer 1998 to spring 1999 (i.e. July 1998, October 1998, January 1999 and April 1999).

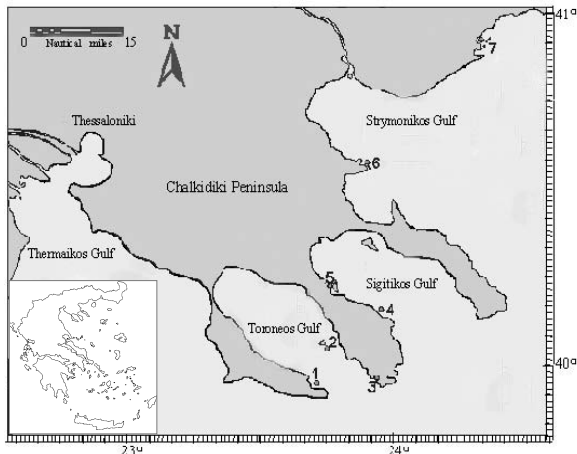


Fig. 1. – Map of the North Aegean Sea indicating sampling stations.

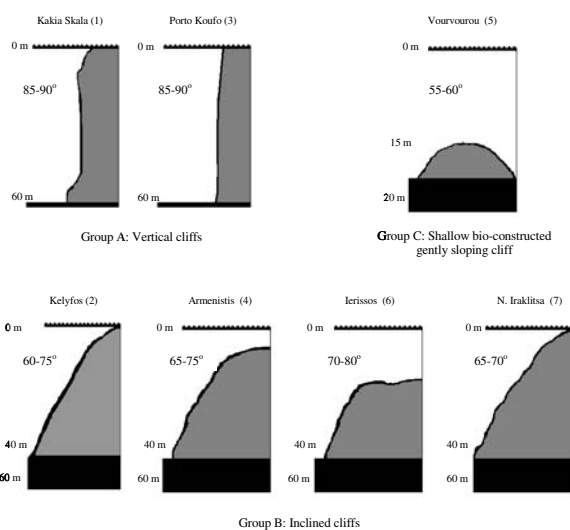


Fig. 2. – Schematic representation of the cliff profiles at the seven sampling stations.

Fauna

Preliminary sampling in all cliffs involved the collection of random qualitative samples with SCUBA diving (3 x 1 hour dives per station at a depth level of 15 to 40 m). All the collected material was identified down to the species level in the laboratory and revealed the presence of a large number of megabenthic species. The most conspicuous and abundant of these species were selected for quantitative investigation: the sponges *Agelas oroides* (Schmidt, 1864), *Axinella cannabina* (Esper, 1794), *Axinella verrucosa* (Esper, 1794), *Chondrosia reniformis* Nardo, 1833, *Diplastrella bistellata* (Schmidt, 1862),

Dysidea fragilis (Montagu, 1818), *Ircinia variabilis* (Schmidt, 1862), *Petrosia ficiformis* (Poiret, 1789), the scleractinian *Leptopsammia pruvoti* Lacaze-Duthiers, 1897, the bryozoan *Pentapora fascialis* (Pallas, 1766) and the tunicates *Halocynthia papillosa* (Linnaeus, 1767) and *Microcosmus sabatieri* Roule, 1885. All these species are epibenthic, sessile and large enough to permit a visual, hence non-destructive quantification (WARWICK, 1993; GARRABOU et al., 2002).

Data collection

Sampling was carried out by SCUBA diving at the same depth range as the preliminary sampling and a non-destructive method was used to obtain data (HISCOCK, 1987; WARWICK, 1993; RHUMOH, 1995; GARRABOU et al., 2002). To achieve this a combination of *in situ* counting and underwater photography was used. The method of randomly placed frames was employed for the estimation of population density and spatial dispersion of the 12 megabenthic species (ELLIOT, 1971; BAKUS, 1990). The number of individuals contained in 10 frame samples (1 x 1 m each) was recorded (BAKUS, 1990) for the estimation of numerical abundances. In order to estimate the pattern of spatial dispersion, preliminary sampling was performed to detect the optimal quadrat size and number, for each organism. The number of replicates depended on the precision required. For most benthic samples, a standard error ranging between 10 and 20 % is acceptable (BAKUS, 1990). In our case, 3 frames of different dimensions (30 x 30 cm, 50 x 50 cm, 1 x 1 m) were tested. Each frame was placed randomly 10 times and the mean (χ) and variance (σ) were calculated. On the basis of these data, the 30 x 30 cm frame was chosen for the estimation of spatial dispersion ($\sigma < \chi$) for all selected organisms. The number of replicates required was calculated according to the formula proposed by BAKUS (1990).

Data analysis

In order to check the null hypothesis, stating that population density of each species does not differ significantly spatially (among stations), an ANOVA test (one-way) was carried out. A logarithmic transformation ($\log(x+1)$) was used to normalize the variance of numerical abundances data (ZAR, 1984). The Fisher PLSD test was used to detect any pair of stations with significantly different abundance.

The data obtained per sampling station were analyzed using hierarchical cluster analysis and multidimensional scaling techniques, based on the Bray-Curtis semimetric distance and log transformed numerical abundances, with PRIMER package (CLARKE & WARWICK, 1994). The significance of the multivariate results was assessed using ANOSIM testing. SIMPER analysis was applied in order to identify the percent contribution of each species to the overall similarity within a site and the dissimilarity among sites (CLARKE & WARWICK 1994). Finally, Morisita's index was calculated to estimate the spatial dispersion of the 12 megabenthic species. This index equals one for a random distribution, is greater than one for a clumped dispersion, and is less than one for a regular dispersion (ELLIOT, 1971). The advantage of Morisita's index is that it does not vary with sample size (BAKUS,

1990). A chi-square test was used to determine the significance of deviation from random (ELLIOT, 1971; BAKUS, 1990). All the above techniques were employed both in spatial and temporal analyses.

RESULTS

I. Spatial Analysis

Sampling at all sites revealed the presence of 89 megabenthic species : 27 Porifera, 15 Cnidaria, 1 Echiura, 7 Polychaeta, 5 Bryozoa, 15 Mollusca, 5 Crustacea, 11 Echinodermata and 3 Tunicata (Table 1). The cliffs can be classified in three groups with respect to species richness : (1) high richness cliffs (number of species > 80 % of the total number of megabenthic species recorded) as in stations 1 and 3, (2) intermediate richness cliffs (number of species between 50 % and 80 % of the total number of megabenthic species recorded) as in stations 2 and 4, and (3) low richness cliffs (number of species < 50 % of the total number of megabenthic species recorded) as in stations 5, 6 and 7.

Population density of each megabenthic species per sampling site is given in Fig. 3. One-way ANOVA test showed that the numerical abundance was not equally distributed in space, for the majority of the species (stations in which a species was absent were not taken into account) (Table 2). The only exceptions were *L. pruvoti* and *M. sabatieri*, which showed an equal dispersion of abundance, although they occurred only at two and five stations respectively. The results of the Fisher PLSD test,

localizing the existing differences are depicted in Fig. 4. For example, *A. oroides* showed significantly decreased abundance at stations 2 and 7, in comparison to the rest of the stations, whereas *A. verrucosa* showed significantly increased abundance at stations 1 and 3 (absent from station 6), in comparison to the rest of the stations (see Fig. 4).

Hierarchical cluster and non-metric MDS indicated, at a similarity level of 65%, three groups of stations (Fig. 5). The performance of a one-way ANOSIM test gave global R : 0.81 at a significance level of $p < 0.1\%$, indicating a satisfying discrimination of the three groups. Further examination, in order to localize differences among groups by means of a pairwise test, did not reveal any significant variation in R-values between each pair of groups, but it did show the higher similarity of groups A and C. SIMPER analysis showed that in-group similarity in station group B reached 90.4%, while 5 species (*L. pruvoti*, *A. oroides*, *D. bistellata*, *C. reniformis*, *P. fascialis*) contributed 65% to the average similarity. In-group similarity in station group C reached 80.6%, with 4 species (*A. oroides*, *D. bistellata*, *H. papillosa*, *A. cannabina*) contributing 62%.

Dispersion of the megabenthic species per sampling site (except for the cases where the abundance of a species was too low to permit calculation of Morisita's index) is presented in Table 3. The majority of the species were randomly or evenly dispersed, depending on the variance of abundance.

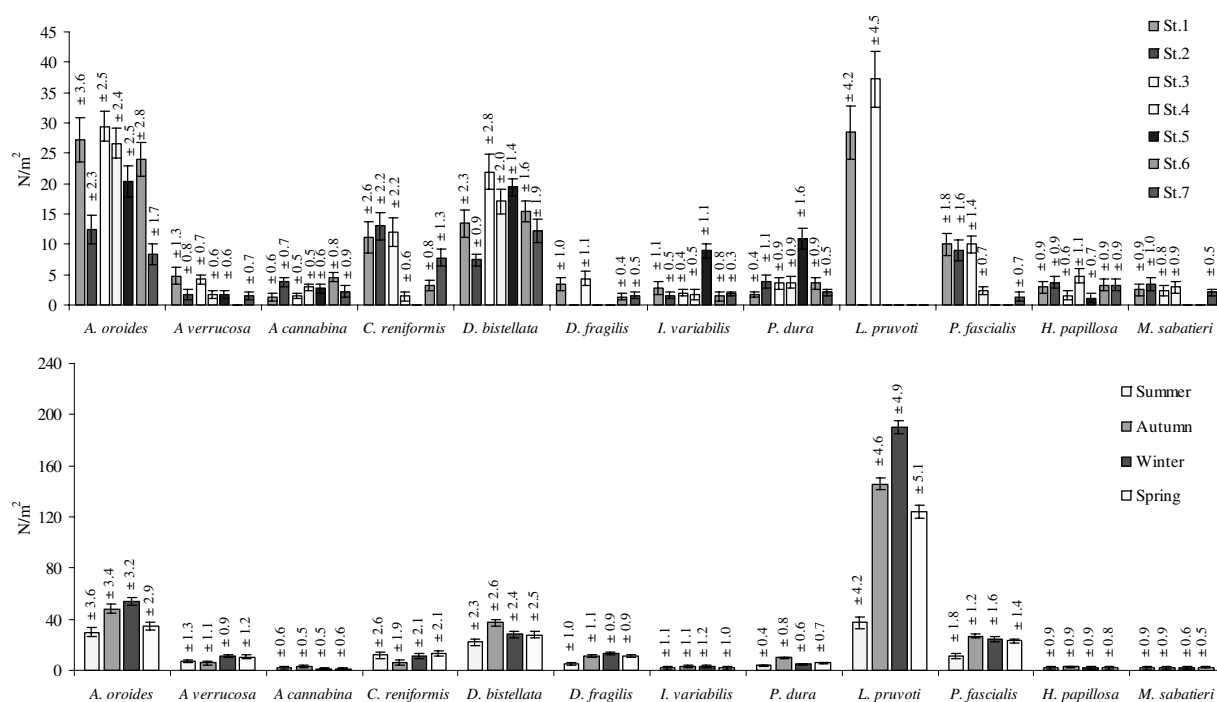


Fig. 3. – Population density (N/m²) of megabenthic species per sampling station (up) and season (down). Values are mean of ten 1m² plots and error bars represent standard deviation.

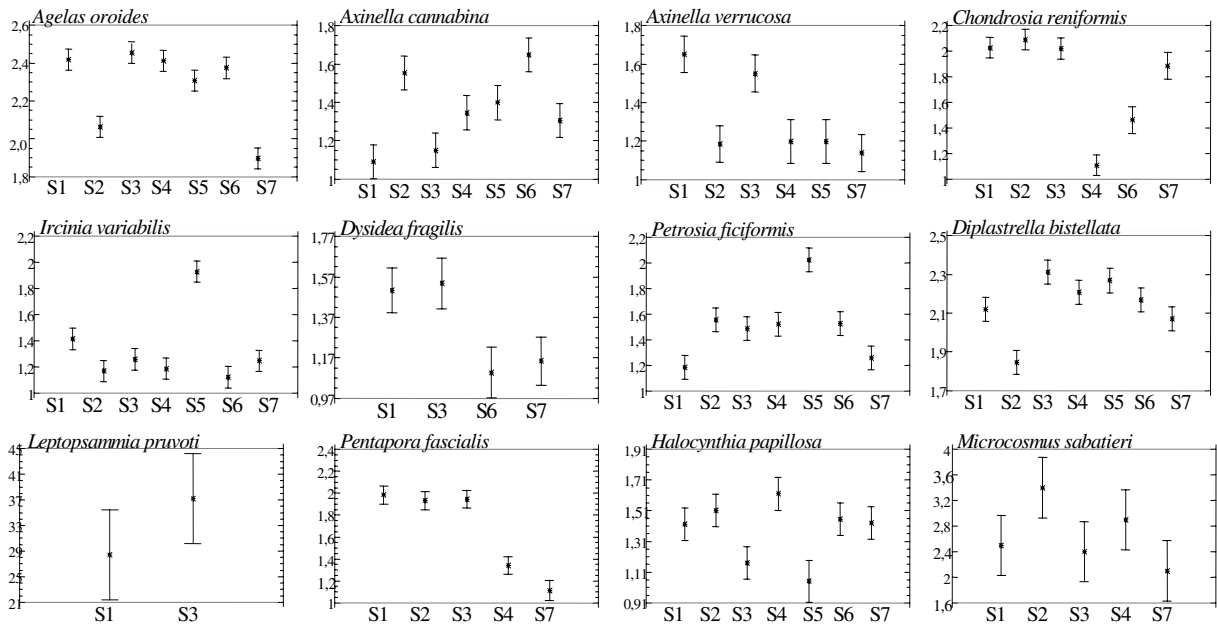


Fig. 4. – Spatial dispersion of log-transformed numerical abundances of megabenthic species showing significant differences among stations. Error bars represent standard deviation.

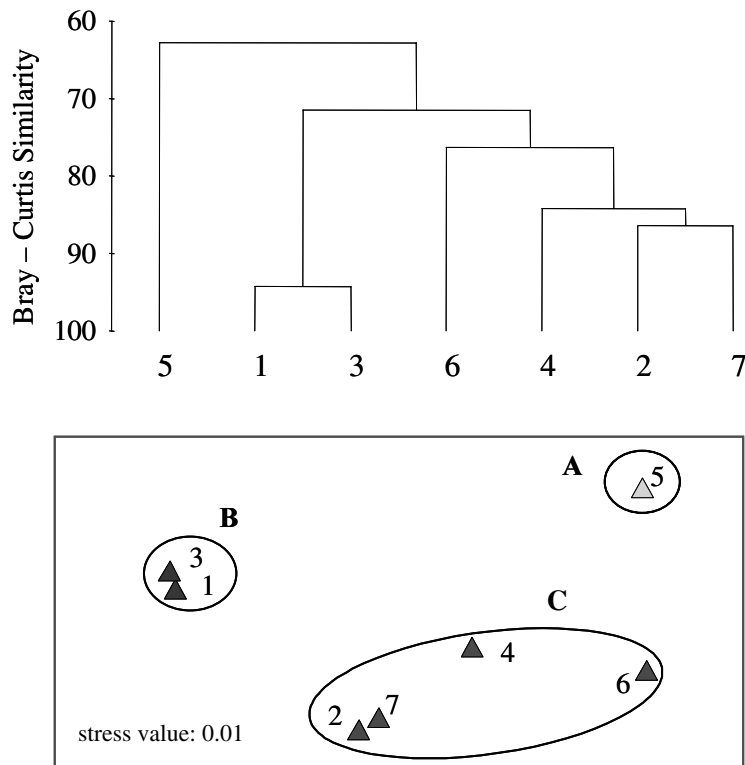


Fig. 5. – Spatial hierarchical cluster analysis and non-metric multidimensional scaling, calculated from log transformed numerical abundance data.

TABLE 1

List of megabenthic species recorded in the study area.

Species	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Porifera							
<i>Agelas oroides</i> (Schmidt, 1864)	*	*	*	*	*	*	*
<i>Aplysina aerophoba</i> Schmidt, 1862	*		*		*		*
<i>Axinella cannabina</i> (Esper, 1794)	*	*	*	*	*	*	*
<i>Axinella damicornis</i> (Esper, 1794)	*		*				*
<i>Axinella verrucosa</i> (Esper, 1794)	*	*	*	*	*		*
<i>Chondrilla nucula</i> Schmidt, 1862	*	*	*	*	*	*	*
<i>Chondrosia reniformis</i> Nardo, 1833	*	*	*	*	*	*	*
<i>Cliona</i> sp.	*	*	*	*	*	*	*
<i>Coscinoderma sporadense</i> Voults, Van Soe & Kouk., 1991			*				
<i>Crambe crambe</i> (Schmidt, 1862)	*	*	*	*			
<i>Diplastrella bistellata</i> (Schmidt, 1864)	*	*	*	*	*	*	*
<i>Dysidea avara</i> (Schmidt, 1862)	*		*				*
<i>Dysidea fragilis</i> (Montagu, 1818)	*		*			*	*
<i>Erylus euastrum</i> (Schmidt, 1870)			*			*	
<i>Halisarca dujardini</i> Johnston, 1842			*				
<i>Hemimycale collumella</i> (Bowerbank, 1874)	*	*	*	*			
<i>Hippospongia communis</i> (Lamarck, 1813)	*			*			
<i>Ircinia pausifilamentosa</i> Vacelet, 1961			*				
<i>Ircinia variabilis</i> (Schmidt, 1862)	*	*	*	*	*	*	*
<i>Oscarella lobularis</i> (Schmidt, 1826)			*				
<i>Penares helleri</i> (Schmidt, 1864)			*				
<i>Petrosia ficiformis</i> (Poirlet, 1789)	*	*	*	*	*	*	*
<i>Sarcotragus muscarum</i> Schmidt, 1862	*		*			*	
<i>Sarcotragus spinosulus</i> Schmidt, 1862	*		*	*			
<i>Spongia officinalis</i> Linnaeus, 1759	*	*	*	*			
<i>Spongia nitens</i> (Schmidt, 1862)			*				
<i>Stryphnus mucronatus</i> (Schmidt, 1868)	*		*	*			
Cnidaria							
<i>Aiptasia mutabilis</i> (Gravenhorst, 1831)	*		*	*			
<i>Alcyonium palmatum</i> Pallas, 1766	*						
<i>Balanophyllia europaea</i> (Risso, 1826)	*	*	*	*			*
<i>Calliactis parasitica</i> (Couch, 1838)							
<i>Caryophyllia smithii</i> Stokes and Broderip, 1828	*		*	*			
<i>Cerianthus membranaceus</i> (Spallanzani, 1784)	*	*	*	*			
<i>Cladocora caespitosa</i> (Linnaeus, 1767)	*	*	*	*	*		
<i>Condylactis aurantiaca</i> (DelleChiaje, 1825)	*		*	*	*		
<i>Cotylorhiza tuberculata</i> (Macri, 1778)	*	*	*	*			
<i>Eunicella cavolinii</i> (Koch, 1887)	*		*				
<i>Eunicella singularis</i> (Esper, 1791)	*	*	*	*			
<i>Eunicella verrucosa</i> (Pallas, 1766)	*		*				
<i>Leptopsammia pruvoti</i> Lacaze-Duthiers, 1897	*	*	*	*			
<i>Parazoanthus axinellae</i> (Schmidt, 1862)	*	*	*	*	*		*
<i>Paramuricea clavata</i> (Risso, 1826)	*		*				
Echiura							
<i>Bonellia viridis</i> Rolando, 1821	*	*	*	*			
Polychaeta							
<i>Arenicola marina</i> (Linnaeus, 1758)	*		*				
<i>Hermodice carunculata</i> (Pallas, 1776)	*		*	*			
<i>Myxicola infundibulum</i> (Renier, 1804)			*				
<i>Protula</i> sp.	*	*	*	*	*	*	*
<i>Sabella pavonina</i> Savigny, 1820	*	*	*	*	*	*	*
<i>Serpula</i> sp.	*	*	*	*	*	*	*
<i>Spirographis spallanzanii</i> (Viviani, 1805)	*	*	*	*	*	*	*
Bryozoa							
<i>Bugula</i> sp.	*	*	*	*	*	*	*
<i>Myriapora truncata</i> (Pallas, 1766)	*		*		*	*	*
<i>Pentapora fascialis</i> (Pallas, 1766)	*	*	*	*			*
<i>Sertella septentrionalis</i> Harmer, 1933	*	*	*	*			
<i>Smittina</i> sp.	*		*	*			
Mollusca							
<i>Aplysia</i> sp.	*						
<i>Charonia sequeziae</i> Aradas et Benoit, 1876		*					
<i>Coryphella lineata</i> (Loven, 1846)	*	*	*	*			
<i>Discodoris atromaculata</i> Bergh, 1880	*	*	*	*	*	*	*
<i>Flabellina affinis</i> (Gmelin, 1791)	*	*	*	*	*	*	*
<i>Halliotis tuberculata</i> Linnaeus, 1758	*	*	*	*	*	*	*
<i>Hypselodoris</i> sp.	*		*				
<i>Janolus cristatus</i> (DelleChiaje, 1841)	*			*			
<i>Lima</i> sp.	*		*				
<i>Luria lurida</i> (Linnaeus, 1758)	*	*	*	*	*	*	*
<i>Octopus vulgaris</i> Cuvier, 1797	*	*	*	*	*	*	*
<i>Ostrea edulis</i> Linnaeus, 1758	*	*	*	*	*	*	*
<i>Pinna nobilis</i> Linnaeus, 1758	*	*	*	*	*	*	*
<i>Sepia officinalis</i> Linnaeus, 1758	*	*	*	*	*	*	*
<i>Spondylus gaederopus</i> Linnaeus, 1758	*	*	*	*	*	*	*

TABLE 1

List of megabenthic species recorded in the study area.

Species	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7
Decapoda							
<i>Dardanus calidus</i> (Risso, 1827)				*			
<i>Dromia personata</i> (Linnaeus, 1758)	*	*	*	*		*	
<i>Gallathea strigosa</i> (Linnaeus, 1767)	*	*	*	*	*	*	*
<i>Homarus gammarus</i> (Linnaeus, 1758)	*						
<i>Palinurus elephas</i> (Fabricius, 1787)	*	*	*	*			
Echinodermata							
<i>Antedon mediterraneum</i> (DeLamarck, 1816)	*	*	*	*		*	*
<i>Centrostephanus longispinus</i> (Philippi, 1845)	*		*	*			
<i>Echinaster sepositus</i> (Retzius, 1783)	*	*	*	*	*	*	*
<i>Hacelia attenuata</i> Gray, 1840	*	*	*	*	*	*	*
<i>Holothuria forskali</i> DelleChiaje, 1823	*	*	*	*			
<i>Marthasterias glacialis</i> (Linnaeus, 1758)	*	*	*	*	*	*	*
<i>Ophidiaster ophidianus</i> (DeLamarck, 1816)	*		*	*			
<i>Ophiothrix fragilis</i> (Abildgaard, in O.F. Muller, 1789)	*	*	*	*	*	*	*
<i>Sphaerechinus granularis</i> (DeLamarck, 1816)	*	*	*	*		*	*
<i>Paracentrotus lividus</i> DeLamarck, 1816	*	*	*	*	*	*	*
<i>Peltaster placenta</i> (J.Muller & Troschel, 1842)	*			*			
Tunicata							
<i>Clavelina lepadiformis</i> Muller, 1776	*		*				
<i>Halocynthia papillosa</i> (Linnaeus, 1767)	*	*	*	*	*	*	*
<i>Microcosmus sabatieri</i> Roule, 1885	*	*	*	*			*

TABLE 2

One-way ANOVA values (F, p) testing for differences among sites.

Species	Spatial	
	F	P
<i>Agelas oroides</i>	28.79	0.000
<i>Axinella verrucosa</i>	10.41	0.000
<i>Axinella cannabina</i>	10.26	0.000
<i>Chondrosia reniformis</i>	45.22	0.000
<i>Diplastrella bistellata</i>	12.14	0.000
<i>Dysidea fragilis</i>	7.60	0.000
<i>Ircinia variabilis</i>	23.39	0.000
<i>Petrosia ficiformis</i>	23.39	0.000
<i>Leptopsammia pruvoti</i>	1.74	0.200
<i>Pentapora fascialis</i>	45.01	0.000
<i>Halocynthia papillosa</i>	5.69	0.000
<i>Microcosmus sabatieri</i>	2.32	0.070

TABLE 3

Spatial pattern of dispersion of megabenthic species; χ is the mean, σ the variance, N the number of frames required, D the acceptable error, I Morisita's index, x^2 and d are parameters from a chi-square test, at 95% confidence level.

Station	χ	σ	N	D	I	x^2	d	Pattern of Dispersion
<i>Agelas oroides</i>								
St.1	3,40	2,28	72	10	1,48	108,550	2,81	clumped
St.2	2,80	2,25	64	10	1,35	113,900	3,91	clumped
St.3	2,94	2,28	78	10	1,26	136,150	4,14	clumped
St.4	2,92	2,37	66	10	1,28	125,030	4,46	clumped
St.5	2,48	1,01	20	10	1,07	7,720	-	even
St.6	3,08	2,44	66	10	1,32	125,640	4,49	clumped
St.7	2,28	0,68	10	10	1,14	1,850	-	even
<i>Axinella cannabina</i>								
St.1	1,14	0,37	10	10	1,12	1,200	-	even
St.2	1,25	0,34	7	10	1,15	0,647	-	even
St.3	1,10	0,90	16	20	1,22	11,780	-	random
St.4	1,42	0,87	17	15	1,34	8,520	-	random
St.5	1,33	0,33	10	10	1,21	0,736	-	even
St.6	1,44	0,27	6	10	1,25	0,253	-	even
St.7	2,78	2,26	23	15	1,28	40,690	-	clumped
<i>Axinella verrucosa</i>								
St.1	1,86	0,90	38	15	1,23	16,110	-	random
St.3	1,26	0,68	23	15	1,29	8,070	-	random
St.5	1,30	0,23	12	10	0,99	0,447	-	even
St.7	1,37	0,26	4	10	1,15	0,156	-	random

TABLE 3

Spatial pattern of dispersion of megabenthic species; χ is the mean, σ the variance, N the number of frames required, D the acceptable error, I Morisita's index, χ^2 and d are parameters from a chi-square test, at 95% confidence level.

Station	χ	σ	N	D	I	χ^2	d	Pattern of Dispersion
<i>Diplastrella bistellata</i>								
St.1	2,92	1,43	42	10	1,24	32,780	0,54	random
St.2	1,26	0,69	23	15	1,29	8,110	-	random
St.3	2,55	1,43	81	10	1,31	89,720	0,73	random
St.4	2,10	0,87	18	10	1,02	6,127	-	even
St.5	2,23	1,12	30	10	1,25	16,370	-	random
St.6	3,28	2,98	82	10	1,25	219,300	8,26	clumped
St.7	3,00	1,75	15	15	1,22	14,290	-	random
<i>Dysidea fragilis</i>								
St.1	1,83	0,93	35	15	1,26	16,910	2,60	random
St.3	1,55	0,82	30	15	1,28	8,250	-	random
<i>Chondrosia reniformis</i>								
St.1	3,03	1,62	12	15	1,28	71,020	0,83	random
St.2	3,88	2,11	13	15	1,11	13,700	-	random
St.3	1,79	0,90	37	15	1,22	15,900	2,86	random
St.7	3,34	1,45	47	10	1,24	32,890	1,53	random
<i>Ircinia variabilis</i>								
St.1	1,42	0,45	12	10	1,24	1,136	-	even
St.5	1,75	0,59	12	10	1,16	2,188	-	even
<i>Petrosia ficiformis</i>								
St.1	1,60	0,80	25	10	1,21	10,000	-	random
St.2	1,55	0,91	15	15	1,27	8,010	-	random
St.3	1,03	0,69	20	15	1,19	8,970	-	random
St.4	1,47	0,93	40	10	1,32	22,900	-	random
St.5	4,25	4,14	43	15	1,22	169,370	9,29	clumped
St.6	1,60	0,48	9	10	1,13	1,152	-	even
St.7	1,33	0,25	4	10	1,14	0,140	-	even
<i>Leptosammia pruvoti</i>								
St.1	5,95	3,57	44	10	1,35	92,100	4,24	clumped
St.3	9,54	6,58	71	10	1,47	317,680	13,30	clumped
<i>Pentapora fascialis</i>								
St.1	2,89	1,74	47	10	1,36	48,190	0,17	random
St.2	1,73	0,64	14	10	1,16	3,154	-	even
St.3	1,98	1,07	54	10	1,29	30,640	-2,51	random
<i>Halocynthia papillosa</i>								
St.1	1,34	0,47	12	10	1,17	1,970	-	even
St.2	1,80	0,70	15	10	1,21	-	-	even
St.3	1,14	0,37	10	10	1,10	1,200	-	even
St.4	1,42	0,41	8	10	1,19	0,830	-	even
St.5	1,33	0,26	6	10	1,14	0,254	-	even
St.6	1,25	0,31	7	10	1,23	0,462	-	even
St.7	2,78	2,26	23	15	1,28	40,690	-	clumped
<i>Microcosmus sabatieri</i>								
St.1	1,13	0,35	10	10	1,21	1,081	-	even
St.2	1,61	0,59	13	10	1,23	2,801	-	even
St.3	1,30	0,48	13	10	1,13	2,126	-	even
St.4	1,54	0,60	11	10	1,20	2,330	-	even
St.7	1,25	1,25	8	10	1,31	0,256	-	even

II. Temporal Analysis

Most species showed small-scale fluctuations in temporal variability in population density values (Fig. 3), with the exception of the anthozoan *L. pruvoti* and in a lesser degree the sponge *A. oroides*. Non-metric MDS (Fig. 6) indicated the grouping of autumn, winter and spring samples, while summer was separated at a similarity level of about 60%. One-way ANOSIM gave global R : 1 at a significance level of $p < 0.1\%$, thus confirming the above discrimination. SIMPER analysis showed that the average similarity of the 3-seasons group reached 86.8%, while 3 species (*L. pruvoti*, *A. oroides*, *P. fascialis*)

contributed 85% to it. Alike, the average dissimilarity between the 3-seasons group and summer reached 32.2%, while the same three species contributed 85% to the dissimilarity.

The dispersion of megabenthic species per season is given in Table 4. Most species did not show seasonal changes in the pattern of dispersion, with the exception of *A. cannabina*, which showed an even dispersion during winter. This change was related to a decrease in variance value, while population density was practically stable throughout the year.

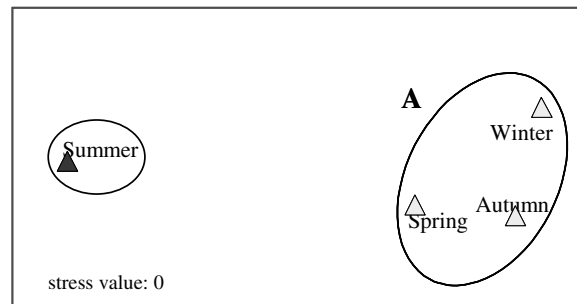


Fig. 6. – Temporal non-metric multidimensional scaling, calculated from numerical abundance data for station 3.

TABLE 4

Seasonal pattern of dispersion of megabenthic species at St.3; χ is the mean, σ the variance, N the number of frames required, D the acceptable error, I Morisita's index, χ^2 and d are parameters from a chi square test, at 95% confidence level.

Station	χ	σ	N	D	I	χ^2	d	Pattern of Dispersion
<i>Agelas oroides</i>								
Winter 1998	4,85	4,82	70	10	1,20	330,52	14	clumped
Spring 1998	3,20	3,17	106	10	1,33	329,70	11,20	clumped
Summer 1998	2,94	2,28	78	10	1,26	136,15	4,14	clumped
Autumn 1998	3,84	5,73	120	10	1,34	1017,4	29,70	clumped
<i>Axinella cannabina</i>								
Winter 1998	1,1	0,45	18	10	1,12	3,31	-	even
Spring 1998	1,1	0,85	23	15	1,21	15,10	-	random
Summer 1998	1,1	0,90	16	20	1,22	11,78	-	random
Autumn 1998	1,1	1,06	23	20	1,26	23,40	-	random
<i>Axinella verucosa</i>								
Winter 1998	1,86	0,90	38	15	1,23	16,113	2,87	random
Spring 1998	1,78	0,95	47	15	1,28	23,32	2,70	random
Summer 1998	1,26	0,68	23	15	1,29	8,07	-	random
Autumn 1998	1,41	0,59	39	15	1,17	9,38	4,44	random
<i>Diplastrella bistellata</i>								
Winter 1998	2,69	1,70	115	10	1,39	122,4	0,52	random
Spring 1998	2,94	1,45	47	10	1,25	32,89	1,53	random
Summer 1998	2,55	1,43	81	10	1,31	89,72	0,73	random
Autumn 1998	3,34	1,45	62	10	1,18	38,39	2,33	random
<i>Dysidea fragilis</i>								
Winter 1998	1,83	0,94	36	15	1,26	16,89	2,61	random
Spring 1998	1,86	1,08	37	15	1,33	22,57	1,82	random
Summer 1998	1,55	0,82	30	15	1,28	8,25	-	random
Autumn 1998	1,81	0,89	32	15	1,24	13,56	2,73	random
<i>Chondrosia reniformis</i>								
Winter 1998	1,55	0,82	20	15	1,28	8,25	-	random
Spring 1998	1,86	0,90	38	15	1,23	16,12	2,87	random
Summer 1998	1,79	0,90	37	15	1,22	15,9	2,86	random
Autumn 1998	1,78	0,95	47	15	1,28	23,32	2,70	random
<i>Petrosia ficiformis</i>								
Winter 1998	1,26	0,68	23	15	1,29	8,07	-	random
Spring 1998	1,41	0,59	39	15	1,17	9,38	4,44	random
Summer 1998	1,03	0,69	20	15	1,19	8,97	-	random
Autumn 1998	1,55	0,81	20	15	1,28	8,25	-	random
<i>Leptosammia pruvoti</i>								
Winter 1998	16,9	12,70	119	10	1,55	1120,8	31,90	clumped
Spring 1998	11,5	6,58	32	10	1,51	120,47	3,17	clumped
Summer 1998	9,54	6,58	71	10	1,47	317,68	13,30	clumped
Autumn 1998	14,1	10,00	103	10	1,49	723,4	23,70	clumped
<i>Pentapora fascialis</i>								
Winter 1998	3,03	1,63	82	10	1,28	71,026	0,84	random
Spring 1998	2,94	1,63	90	10	1,3	80,43	0,69	random
Summer 1998	1,98	1,07	54	10	1,29	30,64	-2,51	random
Autumn 1998	2,89	1,74	47	10	1,36	48,19	0,174	random

TABLE 4

Seasonal pattern of dispersion of megabenthic species at St.3; χ is the mean, σ the variance, N the number of frames required, D the acceptable error, I Morisita's index, x^2 and d are parameters from a chi square test, at 95% confidence level.

Station	χ	σ	N	D	I	x^2	d	Pattern of Dispersion
<i>Halocynthia papillosa</i>								
Winter 1998	1,37	0,42	12	10	1,21	1,54	-	even
Spring 1998	1,30	0,48	13	10	1,13	2,304	-	even
Summer 1998	1,14	0,37	10	10	1,10	1,20	-	even
Autumn 1998	1,23	0,53	18	10	1,19	4,11	-	even
<i>Microcosmus sabatieri</i>								
Winter 1998	1,12	0,48	18	10	1,19	3,70	-	even
Spring 1998	1,08	0,46	17	10	1,16	3,33	-	even
Summer 1998	1,30	0,48	13	10	1,13	2,12	-	even
Autumn 1998	1,22	0,62	10	15	1,22	3,15	-	even

DISCUSSION

The eight sponges studied in the present work are all common Mediterranean species, previously reported from the Aegean Sea (PÉRÈS & PICARD, 1958; KOUKOURAS et al., 1985, 1998; PANSINI et al., 2000; VOULTSIADOU, 2005). Most of them have been characterized as sciaphilic species inhabiting the sciaphilic algae, the coralligenous and the semi-dark cave communities (PÉRÈS & PICARD, 1958; BIBILONI et al., 1989; URIZ et al., 1992; GARRABOU et al., 2002). The species *C. reniformis*, *P. ficiformis* and *I. variabilis* have been found also in the community of photophilic algae (URIZ et al., 1992), while *A. cannabina* was also found in *Posidonia oceanica* meadows (KOUKOURAS et al., 1996). The scleractinian *L. pruvoti* is a solitary species, widespread throughout the Mediterranean, vertically distributed to the lower sublittoral zone and showing a preference to shaded conditions (VAFIDIS et al., 1997). The bryozoan *P. fascialis* is well distributed in the Mediterranean (SALA et al., 1996) and seems to prefer the depth range of 30 - 60 m in the Eastern basin. The friable structure of its colonies governs its ecological niche (MOISETTE, 1988), limiting its presence in relatively sheltered areas, where food for this suspension-feeding organism is provided by the moderate water flow. Finally, the two ascidians, *H. papillosa* and *M. sabatieri*, are considered as Mediterranean endemics (KOUKOURAS et al., 1995). Both are solitary and prefer the most exposed sites. Their strong rhizoids help them withstand strong water currents, which facilitate their nutrition (MONNIOT, 1965).

The diversity of the megabenthos increased in vertical cliffs, especially for sponges and anthozoans. This result is in accordance to the reported positive influence of reduced light conditions and also to the detrimental effects of intense sedimentation, which is much heavier in horizontal surfaces (GLASBY, 1999; PANSINI et al., 2000; BELL & SMITH, 2004).

The faunistic similarity among the three cliff profile groups was high, since in all sites the sponges *A. oroides* and *D. bistellata* dominated. However, the quantitative analyses of the megabenthic species at each site revealed a considerable spatial variation. Three discernible facies were documented in relation to the cliff profile, which has been considered as one of the determining factors for the range of distribution of the megabenthos on hard sub-

strates (PANSINI et al., 2000; BELL & SMITH, 2004). The first facies was recorded on vertical cliffs, the second one on a shallow bio-constructed, gently sloping cliff (dead colonies of the scleractinian *Cladocora caespitosa*) and the third on moderately inclined cliffs. The population density for the two dominant sponge species was found to be higher at the steeper cliffs. Furthermore, increased abundances of the sponge *C. reniformis*, the scleractinian *L. pruvoti* and the bryozoan *P. fascialis* were noted in the first facies, of the sponge *P. ficiformis* in the second, and of the sponge *A. cannabina* and the tunicate *H. papillosa* in the third one.

The dispersion pattern of sessile megabenthic species appeared to be random in most cases, but with certain exceptions. For one, the specific ecological needs of some species, e.g. the sciaphilic nature of *A. oroides* and *L. pruvoti*, led to a clumped dispersion. At shaded conditions clumped dispersions seemed to prevail, as the percentage of clumped species was positively correlated to decreasing levels of shading (MARTI et al., 2004a). For the two ascidians, *H. papillosa* and *M. sabatieri*, the even distribution that was observed may be the result of a territorial behaviour, commonly observed among solitary tunicates (MONNIOT et al., 1991). Another behavioral factor that may influence the dispersion of adults in many sponge, bryozoan and ascidian species may be the selectivity towards settlement surfaces that the larval stages of these organisms show (FROMONT, 1994; WIECZOREK & TODD, 1997; BHAUD, 2000). Furthermore, spatial competition among sessile species also plays a decisive role in their final distribution, as do other biotic interactions such as trophic relations, predation and physical disturbances (GARRABOU et al., 1998, 2002; GARRABOU & ZABALA, 2001; BELL et al., 2003; BELL & SMITH, 2004; MARTI et al., 2004b).

Some authors have reported a seasonality in algal-dominated communities from the lower sublittoral zone, which is weak compared to the one of the upper sublittoral, e.g. above 15 m (GARRABOU et al., 2002; MARTI et al., 2004a, 2004b; ANTONIADOU et al., 2004c). Temporal variations observed in the present work were limited to the discrimination of summer samples, when a significant decline in population density of the scleractinian *Leptop-sammia pruvoti* (species responsible for the seasonal differentiation) was observed. This decline did not affect the

annual pattern of dispersion of the species, which remained clumped, or its abundance in deeper waters, which remained increased (personal observations). Population density of the sponge *Agelas oroides* decreased slightly in summer, although the clumped pattern of dispersion was left unaffected. This algal-dominated community, in contrast to the animal dominated one (coralligenous) of deeper waters (below 50 m in the study area), is generally characterized by a seasonal growth of algae in late spring and summer, which overgrow several animal species (GARRABOU et al., 2002). Therefore, the recorded decrease in population density of *L. pruvoti* and *A. oroides* could possibly be a sampling artefact due to algal overgrowth (PEREZ et al., 2000), a known limitation of visual sampling. However, the dominant (in terms of percent cover) algal species, i.e. the rhodomelacea *Womersleyella setacea* (Hollenberg) R.E. Norris, showed a rather stable coverage throughout the year (ANTONIADOU et al., 2004c), as this species is capable of a continuous asexual reproduction (ATHANASSIADIS, 1997). Algal growth can easily obscure smaller animal species like *L. pruvoti*, a fact not necessarily detrimental for the animal, as its population upturns in autumn. As a result, *L. pruvoti* is probably not completely overgrown by algae, but instead masked enough to be visually missed (GARRABOU et al., 2002). Another explanation could be the well documented increased “fall out” of several sessile species (mainly sponges in summer) occurring in temperate sublittoral cliffs (BELL et al., 2003). This holds true mostly for *A. oroides*, which due to its large massive form is more likely to be damaged by the activities of free-living motile species, such as wrasses (BELL et al., 2003), which are a major part of the fish population in the study area (unpublished data). Additionally, SCUBA diving activities significantly increase in the area in summer, resulting in many animal species being detached, especially those with a 3-D morphology (SALA et al., 1996; GARRABOU et al., 1998; BELL et al., 2003).

The studied algal-dominated community hosted a large number of megabenthic species and had variability more apparent in the spatial than in the temporal scale. Cliff profile was the greater factor influencing spatial variability, with vertical cliffs being the most diverse. Taking into account the fragility of these habitats and the potential damage that diving activities can cause to them (SALA et al., 1996; GARRABOU et al., 1998; BELL et al., 2003), a detailed study of these communities would provide us with much needed information in order to come up with an efficient and viable management plan.

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