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Polychaetes associated with the sciaphilic alga community in the northern Aegean Sea: spatial and temporal variability

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Abstract Polychaete biodiversity has received little attention despite its importance in biomonitoring. This study describes polychaete diversity, and its spatial and temporal variability in infralittoral, hard substrate assemblages. Seven stations were chosen in the central area of the northern Aegean Sea. At each station, one to three depth levels were set (15, 30 and 40 m). Five replicates were collected by scuba diving with a quadrat sampler (400 cm^2) from each station and depth level during summer for the spatial analysis, and seasonally for the study of temporal changes. Common biocoenotic methods were employed (estimation of numerical abundance, mean dominance, frequency, Margalef's richness, Shannon-Weaver index and Pielou's evenness). A total of 5,494 individuals, belonging to 79 species, were counted and classified. Diversity indices were always high. Clustering and multidimensional scaling techniques indicated a high heterogeneity of the stations, although these were all characterized by the sciaphilic alga community. A clear seasonal pattern was not detectable. Summer and autumn samples discriminate, while winter and spring form an even group. The abundance/biomass comparison indicated a dominance of k-strategy patterns, characteristic of stable communities.

Keywords Polychaeta · Infralittoral · Aegean Sea · Hard substrate · Biodiversity

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Introduction

There is a growing interest in biodiversity, defined as the collection of genomes, species and ecosystems occurring in a geographical region (CBDMS 1995). The most fundamental meaning of this term is expressed at species level by the concept of species richness (Bianchi and Morri 2000). Species richness does not simply refer to the number of species, but includes species variety, i.e. composition, which is an important indicator of diversity across spatial scales (Costello 1998). According to the Convention of Biological Diversity definition, biodiversity concerns variability within species (individual/population level), between species (community level), and at the ecosystem level (functional level). The value of biodiversity as an indicator of environment health, and for the functioning of ecosystems, is now largely recognized (Gaston and Spicer 1996; Bianchi and Morri 2000).

Polychaetes are among the most frequent and speciesrich taxa in marine benthic environments (Fauchald and Jumars 1979; Costello et al. 1996). Many authors have suggested a key role of polychaetes in biomonitoring studies (Reish 1978; Bellan 1980; Wenner 1988; Warwick 1986, 1993; Damianidis and Chintiroglou 2000). Before data from polychaete assemblages can be used to identify disturbances, as demanded by international directives and conventions, it is necessary to provide a database on the composition of natural assemblages (Pocklington and Wells 1992; Gaston and Spicer 1996; Ergen and Cinar 1997).

The distribution of polychaetes in hard-bottomed sites is commonly related to algal structure and zonation (Giangrande 1988; Somaschini 1988; Sardà 1991). However, the distribution of polychaetes depends on algal cover and epiphytes more than on the presence of particular macroalgal species (Abbiati et al. 1987; Sardà 1987; Giangrande 1988; Fraschetti et al. 2002). There is a large amount of literature on polychaetes in midlittoral and infralittoral zones of the western Mediterranean (Retiere and Richoux 1973; Cardell and Gili 1988; reviewed by Sardà 1991), yet much less information on the



Table 1 Physical and biotic characteristics of the sampling sites

Station	Slope (°)	Maximum depth (m)	Prevailing winds	Depth level (m)	Pilot algal species
1 Kakia Skala	90	65	N, NE, SE	15	Polysiphonia sp.
				30	Polysiphonia sp., Lithophyllum sp.
				40	Lithophyllum sp., Peyssonnelia sp.
2 Kelyfos	70	35	S, SW, SE, NW	15	Padina pavonica, Polysiphonia sp.
				30	Womersleyella setacea, Padina pavonica
3 Porto Koufo	90	50	SW	15	Womersleyella setacea
				30	Womersleyella setacea
				40	Lithophyllum sp., Peyssonnelia sp.
4 Armenistis	50-60	35	NE	15	Womersleyella setacea, Padina pavonica
				30	Womerslevella setacea
5 Vourvourou	55	18	N, SE	15	Pseudolithophyllum expansum, Gelidium
					pectinatum
6 Eleftheronissos	70	30	NE. SE. N. S	30	Lithothamnion sp., Polysiphonia sp.
7 N. Iraklitsa	65	35	NE, NW, SE	15	Cutleria multifida. Gelidium pectinatum
			· , · · · , · · ·	30	Cutleria multifida, Gelidium pectinatum

situation in the eastern Mediterranean (Nicolaidou et al. 1986; Bellan-Santini et al. 1994; Chintiroglou 1996; Ergen and Cinar 1997; Damianidis and Chintiroglou 2000).

Methods

Sampling sites

According to Marinopoulos (1988), the infralittoral zone can be divided into three ecologically different belts. This study was restricted to the lowest belt (below 15 m), where the sciaphilic alga community occurs (Laubier 1966; Margalef 1984; Antoniadou et al. 2004). Its aim was to reveal the spatial and temporal variability of the polychaete fauna associated with the sciaphilic alga community.

Seven coastal stations were selected in the northern part of the Aegean Sea (Fig. 1). These sites share some common physical characteristics, such as hard substrate down to a depth of 30-40 m and an inclination of more than 50° (for details see Antoniadou et al. 2004), which lead to the establishment of the sciaphilic alga community in the lower infralittoral zone (15–40 m). According to the vertical extension of the hard substrate, one to three depth levels (15, 30 and 40 m) were set at each station, covering the depth range of the local sciaphilic alga community. The main physical characteristics of the sampling sites are given in Table 1. For the spatial analysis, the sites were sampled during summer 1998 (stations 1–6) or summer 1997 to summer 1998) due to its geomorphology

protecting it from the N, NE and NW winds that usually occur in this area during winter.

Physico-chemical factors

Measurements of the main abiotic factors (temperature, salinity, conductivity, dissolved O_2 and pH) were carried out along the water column using a WTW salinity-conductivity- O_2 meter and Lovibond Checkit (pH meter) micro-electronic equipment. Water clarity was determined using a Secchi disc. The inclination of the hard substratum was calculated using a clinometer; currents (speed and direction) were recorded using the autographic current meter Sensordata SD-4 in May 2000.

Data collection

Sampling was carried out by scuba diving using a quadrat sampler (Bellan-Santini 1969) covering a surface of 400 cm² (Weinberg 1978; Karalis et al. 2003). Following Marinopoulos (1988), five replicates were collected at each depth level and site (see Table 1). A total of 75 and 65 samples were available for the study of spatial and seasonal variations, respectively. All samples were sieved (0.5 mm mesh size) and preserved in a 10% formalin solution. After sorting, all polychaetes were counted, weighted (wet weight) and identified to species level. Furthermore, the algae collected were identified, and the dominant species (in terms of percentage cover) were estimated.

Statistics

Common biocoenotic methods were employed to analyze the data (Hong 1982; Marinopoulos 1988; Antoniadou et al. 2004). Thus, the numerical abundance per square meter (A/m²), the mean dominance (mD), the frequency (F), and a variety of diversity indices (Margalef's richness, Shannon-Weaver H' and Pielou's evenness J' based on \log_2) were calculated.

In order to check the null hypothesis (no significant variations in polychaete abundance), a two-way mANOVA test was used to examine the effects of two different factors: depth, and space or time. A logarithmic transformation (logx+1) was used in order to normalize the variance of numerical abundance data in both cases (Zar 1984; Clarke and Green 1988).

The data obtained from each sampling site were analyzed using cluster and multidimensional scaling (MDS) techniques, based on the Bray-Curtis similarity and log-transformed numerical abundances, using the PRIMER package (Clarke and Warwick 1994). The significance of the multivariate results was assessed using the ANOSIM test. SIMPER analysis was applied in order to identify the percentage contribution of each species to the overall similarity within a site, and to the dissimilarity among sites (Clarke and Warwick 1994). Moreover, an abundance-biomass comparison (ABC curves) was performed for each site in order to detect any kind of disturbance in the examined assemblages (Warwick 1986). All the above techniques were employed in both the spatial and temporal analysis.

Results

Spatial variation

Abiotic factors

The main abiotic parameters showed slight variations in relation to depth and sampling site (Table 2). A detailed analysis is given by Antoniadou et al. (2004). Water currents follow the general pattern of cyclonic circulation in the northern Aegean Sea (Stergiou et al. 1997; Somarakis et al. 2002).

Community description

All sites can be classified to the sciaphilic alga community (Augier 1982; Pérès and Picard 1964; Bellan-Santini et al. 1994). However, according to the dominant algae, four facies could be distinguished:

- 1. A facies of the red alga *Polysiphonia* sp. or *Womersleyella setacea*;
- 2. A facies of the red alga *Gelidium pectinatum* and the brown alga *Cutleria multifida*;
- 3. A facies of the red algae *Lithophyllum* sp., *Lithothamnion* sp. and *Peyssonnelia* sp.; and
- 4. A facies with the mixed occurrence of the red algae *Pseudolithophyllum expansum*, *Gelidium pectinatum*, *Lithophyllum* sp. and *Polysiphonia* sp. (see Antoniadou et al. 2004).

The main biocoenotic parameters are presented in Table 3. Overall, 4,361 individuals were counted, belonging to 79 species. Twenty-four species were the most dominant: only *Syllis hyalina* and *Nereis rava* were present at all sites.

Table 2 Mean values of the main abiotic factors in the water column (0–40 m) for stations 1–7 (summer) and for seasons (station 3). *T* temperature, *S* salinity, *C* conductivity, *WC* water clarity, *CV* water current velocity, *CD* water current direction

Station	$T(^{\circ}C)$	S (psu)	C (μ S/cm)	$O_2 (mg/l)$	pН	WC (m)	CV (cm/s)	CD
1	23.1	35.4	48.2	6.98	8.6	21	2.69	NE
2	23.1	35.3	48.1	7.42	8.2	22	1.93	Ν
3	21.6	36.1	49.0	7.22	8.2	20	1.80	SW
4	26.2	34.6	47.0	8.18	7.5	20	3.10	E
5	25.9	34.9	47.3	7.64	8.2	12	2.74	SE
6	23.1	34.8	47.5	7.73	8.1	21	11.40	Ν
7	25.7	33.2	45.5	7.75	8.7	18	1.58	NW
Seasons								
Summer	21.6	36.1	49.0	7.22	8.2	20		
Autumn	19.3	36.8	50.2	6.72	8.2	23		
Winter	12.9	37.4	51.3	6.84	8.2	18		
Spring	14.1	36.9	50.8	8.25	8.2	16		

frequency, d Margalef richi	iess, H'																
Species	Station 1				Station 2			Station 4			Station 5		Station 6		Station 7		
	A			F	A		F	V		F	A	F	A	F	A		F
	15 m	30 m	40 m	1	15 m	30 m	-	15 m	30 m		15 m	-	30 m	-	15 m	30 m	
Laetmonice hystrix (Savignyi, 1820) Harmothoe areolata (Grube, 1860) Harmothoe ljungmani (Malmgren,		10 5		14 7											5 10	5	10 20
1901) Harmothoe spinifera (Ehlers, 1864) Chrysopetalum debile (Grube, 1855) Euphrosine foliosa Audouin & Milne	5	10	2	20 7	Ω.	ŝ	10 10	20	10	50	10	40	10	40	10	5	20 10
Edwards, 1833 Phyllodoce madeirensis (Langerhans,					ŝ		10										
2000) Kefersteinia cirrata (Keferstein, 1862) Syllidia armata Quatrefages, 1865 Pionosyllis lamelligera Saint-Joseph,	5	ŝ		L L	ŝ	10 10	30 10	ŝ	5	10 10	v v	20 20					
1856 Exogone naidina Orsted, 1845 Grubeosyllis limbata (Claparede,	30	10 15	S	35 14	15		20		5	10							
1868) Sphaerosyllis pirifera Claparede, 1868 Spermosyllis torulosa Claparede, 1864	95 5	105 5	10	74 41	30	50	60				20	40	10	40	15	5	40
Eusyus piomstranar Matingren, 1600 Prerosyllis formosa Claparede, 1863 Haplosyllis spongicola (Grube, 1855)	10		10	14 /	ה יהי	10 15	30 IO	10	2	20	20	80	10	20	15	5	40
<i>Syllis amica</i> Quatretages, 1865 <i>Syllis armillaris</i> Muller, 1771 <i>Syllis cornuta</i> Rathke, 1843	35	35	20	54	01	64 55	50 f0	55	95	80	10	40	10	40	15	15	40
Syllis gracilis Grube, 1840 Syllis hyalina Grube, 1863	170	170	50	80	40	25	80	5 160	70	$^{100}_{100}$	09	80	45	09	$10 \\ 30$	10 55	30 70
Syllis krohnii Ehlers, 1864 Syllis prolifera Krohn, 1852 6-112 - 2000 - 2000	80	30	10	46	120	45 10	100 100 100	70	40	80	30	09	25	80		νin	10
Synts virtuad Orube, 1040 Trypanosyllis coeliaca Claparede, 1868		57	10	20	00	35	50						5	20	10	10	30
Trypanosyllis zebra (Grube, 1860) Vanocultic scalare (Ehlare, 1864)	35	10	5	35	15	40	50	5		10	45	60	10	20	35	10	60
Aenosynas scarva (Lincis, 1004) Neersi rava Ehlers, 1867 Nereis zonata Malmgren, 1867 Milne Edwards, Miline Edwards,	155 20 60	60 35 35	30 5 15	67 27 60	65 40 10	250 85 110	100 70 70	270 55 150	165 25 85	100 40 100	55 30	80 80	55 10 15	100 20 40	120 10 15	25 25 20	50 60 60 60 60 60 60 60 60 60 60 60 60 60
1833) Nereididae Heteronereis stage Glycera tesselata Grube, 1863 Glycinde nordmanni (Malmgren,	$10 \\ 105$	65	10	14 67	95	06	06	175	440	100			15	40			
1860) Goniada maculata Ortsed, 1843 Arabella iricolor (Montagu, 1804) Dorvillea rubrovittata (Grube, 1855) Eunice oerstedii Stimpson, 1854			-	:	ъ,	35	10 10 10 10		S.	10			10	40	10 15	10	10 50
Eunice torquata Quatretages, 1805 Eunice vittata (Delle Chiaje, 1929) Lysidice ninetta (Audouin & Milne	110 20	95 25	10 25 15	14 80 60		30 6 5	50 <u>3</u> 20	15 45	180	60 40	10 35	40 80	10	40	30 20	40 45	70 80
Edwards, 1655) Marphysa fallax Marion & Bobretzky,			5	Т		15	20										
Nematonereis unicornis (Grube, 1840) Palola siciliensis (Grube, 1840)	15	15		14	15	50	70	20 5	5	30 10	15	40			20		10
Lumbrineris coccinea (Renier, 1804) Scoletoma funchalensis (Kinberg,	10			14	ŝ	15	30		50	40					10	ŝ	10
Aponuphis bilineata (Baird, 1870) Onuphis sp.		S		7													
Laonice cirrata (Sars, 1851) Polydara cacea (Osted, 1843) Dodecaceria concharum Otsed, 1843 Capitella capitata (Fabricus, 1780) Heteromastus filiformis (Claparede, 1864)					15		10		5 15	10 30						40	10

Species	Station 1				Station 2			Station 4			Station 5		Station 6		Station 7		
	A			н	A		F	A		Ь	A	н	A	н	A		Ь
	15 m	30 m	40 m	I	15 m	30 m		15 m	30 m		15 m		30 m		15 m	30 m	1
Euclymene oerstedii (Claparede, 1836)	S			7													
Polyopthalmus pictus (Dujardin, 1820)		5		7				75		40	10	40					
Sclerocheilus minutus Grube, 1863 Amphitrite variabilis (Risso, 1826)	10	5		14	5	S	10	5	10	30							
Theostoma oerstedi (Claparede, 1864) Polycirrus aurianticus Grube, 1860 Terebella lapidaria Linneaus, 1767						in in	10								S		10
Terebellides stroemi Sars, 1835 Amphiglena mediterranea (Leyding,	70	5 15		7 40	105	50	80	50	20	70			5	20	20	5	50
1851) Branchionma bombyx (Dalyell, 1853) Scholla tehnicii Version 1856	10	5	5	27		9	00	S	10	30					5	5	20
Sabella pavonina Savignyi, 1820 Taminina na Savignyi, 1820		10		L		P 4	07 01	¢,		00							
Jasminerra canaeta (Orube, 1803) Janita fimbriata (Delle Chiaje, 1822) Ficopomatus enigmaticus (Fauvel,			10	14		o	10	07	S	10			5	20			
1923) Hydroides pseudouncinata Zibrowius,						S	10				5	20				5	10
1968 Placostegus crystallinus Zibrowius,						10	20										
1968 Pomatoceros triqueter (Linnaeus,					5	20	40								15	30	60
Serpula concharum Langerhans, 1880	ŝ	-		r- 1		15	10						5	20	20	35	50
Serputa vermicutaris Linnaeus, 1/0/ Vermiliopsis infundibulum (Gmelin,	S	10	5	14		35	40	25	50	50	35	100	30	40	45	25	80 0
Veros) Promiliopsis labiata (Costa, 1861) Promula sp. Spirorbidae	2			L	9,380	5 910	00 00 00	725	ŝ	10 10 40	-	č				w w	10
Polygordidae N A	26 217 1,085 4.64	29 143 715 5.64	21 54 270 5.01		27 27 2,010 10,050	36 250 2,160	10 5.11	23 394 1,970 6.33	$^{24}_{1,310}$	3.68	15 18 83 415 4.13	07	18 57 285 3.85		26 105 525 4.21	28 101 505	5.37
68.6 ,H	3.87	4.04	4.01				3.81	4.39		3.21	3.28		3.81		3.74		4.18
J ^{+ +.21} 0.87	0.82	0.83	0.92				0.81	0.85		0.71	0.71		0.91		0.90		0.89

Table 3 (continued)



Fig. 2 Biocoenotic parameters (*above*) and diversity indices (*below*) for each depth level (15, 30, 40 m) and stations in summer. *d* Margalef richness, H' Shannon-Weaver index, J' Pielou's evenness, S number of species, N number of individuals

Abundance of polychaete fauna

Concerning the spatial distribution, mANOVA showed that both depth and site had a significant effect (F=15.94, P=0.001 and F=13.30 P=0.001, respectively). The Fisher PLSD test indicated that differences exist between the three depth levels (15, 30 and 40 m) and between stations 2 and 4 on the one hand, and the rest of the stations on the other. Stations 2 and 4 are discriminated mainly due to the presence of high numbers of spirorbids. The decrease in polychaete abundance with depth is probably related to the algal vertical zonation: filamentous algae dominate in shallow waters, and encrusting algae in deep.

Composition and diversity of polychaete fauna

The spatial fluctuation of the diversity indices and of the total number of individuals (*N*) and species (*S*) at each depth level is shown in Fig. 2. Richness values (*D*) ranged from 3.80 to 6.60, *H*' values from 3.28 to 4.35 and *J*' values from 0.72 to 0.91. These indices are a function of the number of species and individuals: high *N* and low *S* values result in low diversity indices. Spirorbids were excluded from the above calculation. They occurred at high numbers at stations 2 (15 and 30 m) and 4 (15 m), reaching abundances of 9,380, 910 and 725 individuals/ m², respectively, thus altering the diversity values.

Affinity analysis

The affinity of the samples (station, depth) is given in Fig. 3. Both analyses (cluster and non-metric MDS) in-



Fig. 3 Affinity of summer samples from different sites (stations 1–7) and depths (15, 30, 40 m). Results of cluster (*above*) and MDS (*below*) analysis based on Bray-Curtis similarity index

dicate a separation of the samples into four main groups at about 55% similarity degree. The stress value for the twodimensional MDS configuration is 0.16. The one-way ANOSIM test gave global R=0.87, at a significance level of P<0.1, indicating a good discrimination between the four basic groups. Further examination in order to localize the differences among the groups by means of a pairwise test did not reveal any significant variation in R values, yet did show higher similarities between groups A and B, and between C and D.

SIMPER analysis identified 6-9 (13–19) species as responsible for 60% (90%) of the average similarity of groups, and 16–20 (38–46) species as responsible for 60% (90%) of the average dissimilarity of groups (Table 4).

The ABC curves (Fig. 4) show that, for most sites, the biomass curve was above that of abundance. Accordingly, the k-dominance pattern was produced. For station 2, however, the situation was reverse, and for station 4 the two curves coincide. This is due to the extremely high number of spirorbids, species with very small body size and thus negligible biomass.

Temporal variation

Abiotic factors

The seasonal pattern of the main abiotic parameters is summarized in Table 2. A seasonal thermocline was detected at about 20 m depth (end of July), while salinity and conductivity gained lower values during summer.

Table 4 Percentage contribution	of species to	60% similari	ty (S) within g	groups and /or	c dissimilarity (DS) among grou	ps, according to	the spatial mu	ltivariate analys	IS
Species	A	В	С	D	A:B	A:C	A:D	B:C	B:D	C:D
	S=59.9	S=63.2	S=56.9	S=67.7	DS=48.1	DS=53.6	DS=54.5	DS=49.4	DS=51.7	DS=48.1
Harmothoe ljungmani Harmothoe sninifera									2.24	3.03 1.87
Grubeosyllis limbata					2.23			3.50	2.83	
Exogone naidina					3.36			4.09	3.75	
Sphaerosyllis pirifera		6.70	8.35		3.19	2.40	2.25	4.48	4.15	
Haplosyllis spongicola					20 0		1 00			
Sylus amica		L0 3		2 61	00.7	7.20	1.30	20 0		
Syllis cornuta Syllis pracilis		10.0		10.0		C0.7		07.0	2.75	3.73
Syllis hvalina	6.20	10.87	16.81	7.87	1.85					
Syllis prolifera	7.83	6.01	9.25		2.02	3.00	5.04		4.04	4.08
Syllis vittata					2.04	2.22	1.89			
Trypanosyllis coeliaca					1.88					
Trypanosyllis zebra								2.54	2.06	3.12
Nereis rava	9.68		9.94	10.95	3.91	3.85		4.66	3.47	3.60
Nereis zonata	7.29				3.49	3.40	2.18			2.00
Platynereis dumerilii		4.58		5.61	3.07	4.61	2.68	4.21	2.23	2.68
Glycera tesselata	9.45	10.90				4.88	6.61	6.16	7.96	4.03
Eunice vittata		8.53		7.87	3.63	2.29	2.14	5.51		4.02
Palola siciliensis										2.70
Lysidice ninetta			9.54	6.51	2.40	2.33	1.94	2.73	2.45	
Nematonereis unicornis					2.15	3.45	3.64	2.31		
Dorvillea rubrovittata							2.58		3.11	4.21
Scoletoma funchalensis					2.04			3.80	2.38	1.85
Polyopthalmus pictus					2.25	2.56	2.01			
Polydora caeca							2.30		2.78	3.77
Amphitrite variabilis								2.66	2.59	
Amphiglena mediterranea	7.83	6.40			1.84	5.18	3.12	4.69	2.35	2.70
Branchiomma bombyx					2.26			3.34		
Serpula concharum					6.51		3.01		3.51	5.66
Pomatoceros triqueter				5.61			2.11		3.70	4.73
Vermiliopsis infundibulum			7.98	7.25	2.33	2.16	1.88	2.28	2.02	2.15
Spirorbidae	16.12				13.42	14.59	12.41			

Fig. 4 ABC curves for stations 1–7 (summer)



Community description

The main biocoenotic parameters are presented at Table 5. Overall 1,133 individuals were counted, belonging to 66 species. 24 species, largely the same as those reported in the spatial survey, were dominant in the seasonal samples. *Syllis hyalina, Sphaerosyllis pirifera, Glycera tesselata* and *Vermiliopsis infundibulum* were dominant in all seasons.

Abundance of polychaete fauna

Only depth had a significant effect (mANOVA: F=6.58, P=0.002). The Fisher PLSD procedure revealed that this effect was restricted to 40 m versus 15 and 30 m. No direct seasonal effect on polychaete abundance was detectable (F=2.30, P=0.06).

Composition and diversity of polychaete fauna

The temporal fluctuation of the diversity indices, the total number of individuals (N) and the number of species (S) at each depth level is shown in Fig. 5. Richness values (D) ranged from 3.91 to 6.48, H' values from 3.45 to 4.41, and evenness values (J') from 0.80 to 0.97. In general, diversity indices varied among seasons.

Affinity analysis

The seasonal discrimination of samples is given in Fig. 6. Five groups (A–E) can be distinguished at about 50% similarity level. The stress value for the two-dimensional configuration is 0.12, indicating a good ordination (Clarke and Warwick 1994). The ANOSIM test confirms the results of the discriminative techniques (R=0.88, P<0.1). The pairwise test showed that the variations were significant in all cases (R ranging from 0.75 to 1).

SIMPER analysis identified 5-7 (10–17) species as responsible for 60% (90%) of the average similarity of groups, and 12–20 (22–38) species as responsible for 60% (90%) of the average dissimilarity of groups (Table 6).

The ABC curves for different seasons show biomass curves being always above those of abundance (Fig. 7). Therefore, the k-strategy pattern dominated throughout the year.

Discussion

According to Pérès and Picard (1964), the Mediterranean infralittoral zone comprises two distinct communities: the photophilic alga community (at the upper level) and the sciaphilic alga community (at the lower level, often mentioned as precoralligenous and coralligenous). These two communities share some common characteristics: they both depend on the presence of different algal forms (Bellan-Santini et al. 1994) and are influenced by the hydrodynamism and light (Hong 1982; Marinopoulos 1988).

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individuals,	
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1865) Pomatoceros triqueter (Linnaeus,	30			10	30	5			Ζ	5	5		14	25	5		20
1865) Jasmineira candela (Grube, 1863)				ŝ	ŝ			ŝ	L	S			7				
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<i>Frotuta</i> sp. S	37	27	19	21	ŋ	ر 18 ر	18	27	70	29	19	23		21	29	16	
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A	6.61 6.61	610 5.41	400 4.1	340 4.74		200 4.37	320 4.12	330 6.28		0.05 6.04	282	5.25		010 4.41	405 6.25	5.1	
J^{\prime}	4.36 0.84	4.01 0.84	$3.73 \\ 0.88$	$3.59 \\ 0.82$		3.64 0.87	$3.46 \\ 0.83$	4.41 0.93		4.29 0.88	$3.72 \\ 0.87$	$4.15 \\ 0.92$		3.82 0.87	4.12 0.85	$3.73 \\ 0.97$	



Fig. 5 Biocoenotic parameters (*above*) and diversity indices (*below*) over an annual cycle at station 3 (15, 30, 40 m depth). *S* summer, *A* autumn, *W* winter, *Sp* spring, *d* Margalef richness, *H'* Shannon-Weaver index, *J'* Pielou's evenness, *S* number of species, *N* number of individuals

Bellan (1964, 1969) studied the photophilic alga community and found 128 species of Polychaeta which were classified, according to their ecological preferences, to 11 discrete "stocks". Cardell and Gili (1988) studied the facies of Lithophyllum tortuosum and recorded 71 species. They concluded that this assemblage is very homogeneous, both spatially and temporally. However, Sphaerosyllis pirifera and Platynereis dumerilii showed an increase in numerical abundance in summer. Most species were common in the hard substrate stock (Bellan 1969), and especially within the photophilic alga community: some species were characteristic of the concretioned substrate (Laubier 1966; Sardà 1991). Fraschetti et al. (2002) studied the facies of Cystoseira amentacea and found 59 species of Polychaeta, most of which were common species among sublittoral photophilic algae (Sardà 1991). The same authors did not find any noticeable seasonal changes, with the exception of the large numbers of *Platynereis dumerilii* in summer. Chintiroglou (1996) reported 87 species associated with Cladocora caespitosa colonies at 5-18 m depth, and Damianidis and Chintiroglou (2000) recognized 48 species associated with *Mytilus galloprovincialis* assemblages in the upper infralittoral zone. Sardà (1991), in a study of hard substrate communities from 1 to 40 m depth, found 220 species and discriminated five distinct communities: the Lithophyllum lichenoides (with the lowest diversity), the shallow photophilic, the deeper photophilic, the *Posido*nia oceanica rhizomes and the infralittoral sciaphilous community. The contributions of the different ecological



Fig. 6 Affinity of seasonal samples from different depths at station 3. Results of cluster (*above*) and MDS (*below*) analysis based on Bray-Curtis similarity index

stocks (Bellan 1969) to these communities change according to habitat complexity. In our study, we found 79 species of polychaetes in the sciaphilic alga community (15-40 m), while Marinopoulos (1988) found 36 (21)common) at similar depths. Most of these species are members of the photophilic alga community, but there is also a significant contribution of cryptic, hard substrate, soft substrate and coralligenous (concretioned substrate) species. It seems that polychaetes have a large ecological tolerance and that their occurrence is largely dependent on substrate availability and complexity (Bellan 1964, 1969; Hong 1982). We found clear spatial differences in polychaete distribution, while temporal differences were less apparent. The spatial distribution of polychaetes largely corresponds with the occurrence of different algal facies. We have noted a high affinity between stations 1 and 3 at all depth levels. This could be expected, since these two sites share some common characteristics such as the high inclination ($\sim 90^{\circ}$) and large bathymetrical extension of the rocky substrate. Station 7 is separated, probably due to abiotic parameters (low salinity). Its relatively moderate inclination sets station 7 near to stations 5 and 6, while the sharpest slope ranks stations 2 and 4 closer to stations 1 and 3. The depth level of 40 m (stations 1 and 3) shows high affinity with stations 5 and 6, as it hosts a fairly low number of polychaete species and individuals. SIMPER analysis showed that both the similarities within groups and the dissimilarities between groups were the result of small contributions of a large number of species, indicating a diverse community with a

Fig. 7 ABC curves for different seasons (station 3). *S* summer, *A* autumn, *W* winter, *Sp* spring



highly complex structure (Dahl and Dahl 2002). This heterogeneity may result from the presence of several algal species of different architecture (Chemello and Milazzo 2002). Fan-shaped structures and filamentous forms dominate group A, filamentous forms group B, encrusting forms group C, and filamentous bush-like encrusting forms group D. Many authors have stated that polychaetes are not related to specific algal species, but to specific algal architectures (Naim and Amoureux 1982; Sardà 1988; Gambi et al. 1995; Fraschetti et al. 2002). Groups A and B are characterized by high diversity and abundance in comparison to groups C and D. It should be noted that the high abundance in group A is mainly due to the presence of high numbers of spirorbids attached to the thalli of Padina pavonica. Spirorbids are capable of settling immediately after release from parental tubes and are typically multiannual in the sense of Fauchald (1983), living in unstable environments. They probably perish when the thalli of *Padina pavonica* decay after mid-September (Diapoulis and Koussouris 1988). Spirorbids strongly influence the discrimination of group A, the ABC analysis and the diversity indices. Another difference was found in the polychaete fauna associated with the two filamentous Rhodomelacea, Womersleyella setacea and Polysiphonia sp. An abundant and diversified polychaete is associated only with the former. Womerslevella setacea is an introduced and probably invasive species (Boudouresque and Verlague 2002) which has spread over the Mediterranean (Verlaque 1989; Airoldi et al. 1995) and the northern Aegean Sea (Athanassiadis 1997). It forms paucispecific populations with increasing turf development. These turfs trap sediment, forming a stratum that prevents the development of other algal species on the rocky substrate (Piazzi and Cinelli 2000). However, the entrapped sediment increases the complexity of the system, offering suitable microhabitats for the settlement of many soft-sediment polychaete species.

The study of temporal changes in polychaete distribution revealed that summer is distinct from the other three seasons. Winter and spring form an even group, while autumn branches out according to depth. This is the case for the upper depth levels (15 and 30 m), where *Womersleyella setacea* dominated throughout the year. This species is capable of continuous vegetative reproduction (Athanassiadis 1997), creating a very stable and homogenous habitat which may contribute to the lack of seasonality. The image is much more complicated at the 40-mdepth level, where the dominant algae were represented by various species of Corallinacea and Peyssonneliacea. Here, summer samples were similar to winter ones, while autumn and spring samples discriminated.

According to the relevant literature, there is no distinct seasonality in the lower infralittoral zone, in contrast to the upper one (Hong 1982; Marinopoulos 1988). However, a discrimination of summer is frequently observed (Damianidis and Chintiroglou 2000) and may be due mainly to the massive recruitment of a few species, e.g. *Platynereis dumerilii* (Cardell and Gili 1988; Fraschetti et al. 2002). In our study, the bathymetric distribution of polychaetes changed with season, while the species in-

Table 6 Percentage contribution	of species t	o 60% simi	larity (S) with	nin groups a	nd/or dissimi	ilarity (DS) a	among group	s, accordin	g to the tem	poral multiva	ariate analysi	S
Species	С	Е	A:B	A:C	A:D	A:E	B:C	B:D	B:E	C:D	C:E	D:E
	S=51.5	S=58.9	DS=71.4	DS=57.8	DS=67.7	DS=67.8	DS=57.8	DS=53	DS=57.1	DS=54.5	DS=50.2	DS=49.9
Harmothoe spinifera Phyllodoce madeirensis Syllidia armata Grubeosyllis limbata			6.02 5.40		4.97	2.54 2.54	2.21 4.54 3.04	6.08	3.00 3.93 2.21	2.96	2.37 2.70	2.93
Exogone naidina Haplosyllis spongicola Syllis amica		10.34	3.69	6.68	6.27	7.54	4.24		3.24	5.34	2.41 4.73	2.61 3.22
Syllis cirropunctata Syllis cirropunctata Syllis cormuta			5.40	C7.C			5.12 2.21	6.08	4.33			
Syllis hyalina Syllis krohni		11.46	3.69	4.12	5.67	6.29	3.01	L	3.97 2.60	4.50	3.74 6.26	5.35 3.02
Trypanosyllıs coelıaca Trypanosyllis zebra Pionosyllis lamelligera		0.98	4.66	3.25	4.97	2.80 2.98	3.3/ 4.41	5.24	4.45 2.16	4.46	3.07 2.47	
Nereis rava Nereis zonata			6.98	5.22	9.41	4.80	2.21 3.03	2.62	2.79	3.89	3.60	3.76
Ceratonerets costae Platynereis dumerilii Heteronereis stage Nereididae	8.54 15.12		4.66	5.15 6.41	8.11	2.64	2.33	5.24 4.15	2.23 2.95	2.81 4.46	cc.2 5.47	2.36 7.63
Goniada maculata Emice vittata	17.08	13	6.53 3.60	11.59	3.14	8.94	3 50		010	7.21		7.68
Lumbrineris unicornis Lumbrineris coccinea	16.16	6.04 6.47	60.0	6.50		3.39 3.18	3.12	2.62 4.15	2.26 2.26	2.81 8.44	3.52 2.45	5.78 6.34
Polydora caeca Polycirrus aurianticus Terebellides stroemi			2.33			2.48	2.21	2.62	2.10 2.13	2.84	2.44	2.64 2.85
Amphiglena mediterranea Branchiomma bombyx Scholla ramoning	10.77	6.92		3.25	3.14	3.42	4.41	2.62 4.15	4.95		L3 C	78 C
Serpula concharum Serpula vermicularis				3.25	3.14			2.62 2.62		2.81	10.7	2.64
Placostegus crystallinus Pomatoceros lamarckii Vermiliopsis infundibulum Hydroides pseudouncinata			3.69 4.66		3.14 3.14 6.27	2.80 4.54	3.50 3.58	2.62	2.38	2.81 2.81 4.55	2.94 3.78 2.35	3.78 2.35

ventory at the stations remained unchanged throughout the year. Marinopoulos (1988) also found seasonal changes in the abundance of polychaetes at different depths, with the same species (*Syllis hyalina*, *Syllis prolifera*, *Syllis vittata*, *Platynereis dumerilii* and *Sphaerosyllis pirifera*) being abundant at low depth during summer and in deeper waters during winter. It seems that the seasonality of the sciaphilic alga community is mainly achieved by a vertical rearrangement of the abundances of different polychaete species.

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