Journal of the Marine Biological Association of the United Kingdom, 2008, 88(5), 873–881.
doi:10.1017/S0025315408001823 Printed in the United Kingdom

Spatio-temporal variability of zoobenthic communities in a tectonic lagoon (Lake Vouliagmeni, Attika, Greece)

CHARITON CHINTIROGLOU, CHRYSSANTHI ANTONIADOU AND PANAGIOTIS DAMIANIDIS
Aristotle University, School of Biology, Department of Zoology, Thessaloniki, Greece, Gr 54 124

Lake Vouliagmeni (Attica, Greece) is a lagoon of great scientific interest due to its endemic fauna, widely used for recreational activities. Understanding the dynamics of this peculiar ecosystem is essential for its conservation. An ecological survey of the benthic communities was carried out, in both spatial and temporal scales. Material was collected with SCUBA diving, by taking off samples from the principal habitats of the lagoon, i.e. meadows, soft and hard substrata. The identification of the collected 61,975 living specimens revealed the presence of 12 floral and 20 faunal species. Multivariate analyses separated the sampling sites according to the four different habitats of the lagoon, whereas no temporal patterns came up. Micrograzers were the dominant trophic group, followed by deposit feeders regardless of the habitat studied. Lake Vouliagmeni is among the less diverse Mediterranean lagoons, mostly due to its isolation from the sea that hinders the entrance of marine species.

Keywords: spatio-temporal variabilty, zoobenthic communities, tectonic lagoon, Lake Vouliagmeni, Attika, Greece

Submitted 8 November 2007; accepted 14 March 2008

INTRODUCTION

Coastal lagoons are dynamic, rapidly changing ecosystems, characterized by the instability of the abiotic environment (Barnes, 1980; Guelorget & Perthuisot, 1992) and the limited biodiversity in terms of species richness, as few organisms, mainly of marine origin, are found (Arias & Drake, 1994; Cognetti & Maltagliatti, 2000). These brackish habitats are valuable due to their high productivity (Barnes, 1980; Guelorget & Perthuisot, 1992; Baizari *et al*, 2003; Mogias & Kevrekidis, 2005). They are also ideal systems for biological and evolutionary studies mostly because of the increased presence of sibling species (Cognetti & Maltagliatti, 2000; Virgilio & Abbiati, 2004).

Lake Vouliagmeni is the common name of a lagoon located in Attica, Greece, of high biological importance (Chintiroglou *et al.*, 1996). It is a 'tectonic laguna' (Guelorget & Perthuisot, 1992), that was formed 2000 years ago (Papapetrou-Zamanis, 1969) and has been exploited as a spa area since the end of the 19th Century (Chrystomanos, 1889). The area still attracts large numbers of bathers and has been declared a natural monument by the Greek State (Chintiroglou *et al.*, 2004), though the on-going development of tourist facilities have raised serious concerns over the viability of this closed micro-ecosystem (Gontikaki *et al.*, 2003).

The biological research of Lake Vouliagmeni started when Doumenc *et al.* (1987) described *Paranemonia vouliagmeniensis*, a new species of sea anemone, which is endemic in the lagoon. Afterwards, few works were published about the life cycle and the ecology of *P. vouliagmeniensis* (Chintiroglou *et al.*, 1996, 2000) and the population structure of the two bivalves, *Abra segmentum* and *Cerastoderma edule*, of the lagoon (Gontikaki *et al.*, 2003). Recent research showed the presence of several genera of taxonomic interest, i.e. *Cliona* and *Manayunkia* (Chintiroglou *et al.*, 2004). It seems therefore relevant to acquire original datasets, focusing on structural and functional aspects of its biocoenoses.

Taking into account all the above, the present work aims at assessing: (1) the structure of hard and soft substrata benthic biocoenoses, including a trophic group analysis; and (2) the distribution of benthic biodiversity and its comparison with other Mediterranean lagoons.

MATERIALS AND METHODS

Study area and sampling sites

Lake Vouliagmeni, situated 25 km south-east of the centre of Athens, was formed when the roof of an underground cave collapsed and flooded, after an earthquake occurred 2000 years ago (Chintiroglou *et al.*, 1996). The lagoon covers a surface area of 4000 m^2 with a maximum depth of 13 m (Gontikaki *et al.*, 2003). The 'western' part of the lake is a 30 m high rocky cliff. The lagoon is 260 m long and 145 m wide with an extensive underwater channel network, that reaches depths of 100 m. The surface water temperature varies from 19–21°C. The lagoon has no direct communication with the adjacent sea. It is supplied with warm seawater (28–35°C) via an underground channel, which spreads longer than 3 km through a network of flooded caves. On the eastern side of the lagoon a small supply of freshwater exists making its water brackish, with salinities that vary from 14.5–17 psu. Lake Vouliagmeni is a popular spa, which attracts a large

Corresponding author:
C. Chintiroglou
Email: chintigl@bio.auth.gr

number of swimmers throughout the year, who want to benefit from the hydrogen sulphide containing waters. The source of hydrogen sulphide is believed to be several de-oxidized organic salts (Chrystomanos, 1889), whereas the presence of sulpho-bacteria is still under discussion (Papapetrou-Zamanis, 1969).

After preliminary sampling, four types of habitats were identified at the lagoon: (1) typical hard substratum of calcareous rocks (0–13 m); (2) soft substratum of mixed calcareous deposits and gravels with sand and silt at the upper sublittoral zone (until 0.5 m); (3) soft substratum of silt and sandy-silt in deeper (>1.5 m); and (4) meadows of the species *Ruppia cirrhosa* and *Scyrpus maritimus* (3–6 m). Seven sampling sites were set dispersed at the lagoon (Figure 1) according to the habitat type and the degree of the anthropogenic pressure, which is tenser on the southern coast of the lagoon and is shallow, mainly due to bathers' activities. Thus, three sites were set at the upper sublittoral zone (A, B and C, ranked as B > A > C in terms of disturbance), one at the lower sublittoral (D), one at meadow (F) and two at the hard substratum (E and Z).

Sampling techniques

Seasonal sampling (July 1997, October 1997, January 1998 and April 1998) was carried out with SCUBA diving at the seven sites. Regarding soft substrata (sites A, B, C and D) three replicates were collected at each site, with the use of an 18 × 25 cm corer sampler (Stirn, 1981; Antoniadou *et al.*, 2004; Kourelea *et al.*, 2004). Three replicates were collected from hard substrata (sites E and Z) with the use of a 400 cm^2 quadrate sampler, by totally scraping off the substrate to include both sessile and motile species (Antoniadou & Chintiroglou, 2005). Three replicates (5 l each) were also collected from meadows at site F (Gontikaki *et al.*, 2003). Overall, 84 samples were obtained, sieved (mesh opening 0.5 mm) and fixed in 9% formaldehyde. After sorting, all living specimens were identified at species level and counted.

Temperature, salinity, conductivity, dissolved O_2 and pH were measured in the water column with a WTW salinity–conductivity O_2-meter and Lovibond Checkit (pH meter) micro-electronic equipment. Water clarity was measured with the Secchi disc, while the inclination of the hard substrate was calculated with a clinometer. Sediment analysis (granulometric composition) was carried out and Folk's system of classification was applied (Folk *et al.*, 1970). Two substrate samples were collected with SCUBA diving and use of 1 l corer sampler at each sampling period (Gee & Bauder, 1986; Antoniadou *et al.*, 2004).

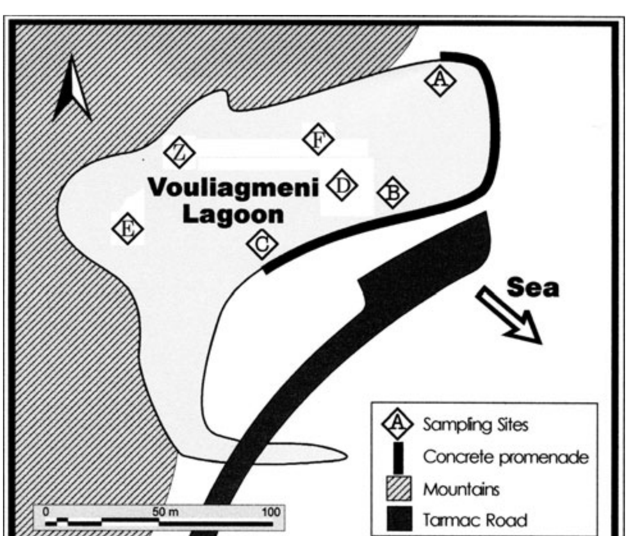

Fig. 1. Map of Lake Vouliagmeni indicating sampling sites.

Data analyses

The collected material (flora and fauna) was identified at species level. Zoobenthos was counted and classified in trophic groups, according to the nature and origin of food: (1) herbivores (H), feeding on macroalgae and/or phanerogams; (2) carnivores (C), feeding on various sessile or motile invertebrates; (3) suspension feeders (S), feeding on suspended organic particles in the water column; (4) deposit feeders (D), feeding on deposit particles at the bottom of the lagoon; and (5) micrograzers (M), feeding on living micro-organisms and biofilm (Fauchald & Jumars, 1979; Hily & Bouteille, 1999; Bazairi *et al.*, 2003). Then, it was analysed with common biocoenotic methods (Karalis *et al.*, 2003; Antoniadou & Chintiroglou, 2005), including the estimation of abundance as population density (N/m^2) and the calculation of diversity indices (i.e. Margalef's richness, Shannon–Wiener and Pielou's evenness, based on $\log_2$).

Analysis of variance (two-way ANOVA) was used to check the null hypothesis of no significant differences in the abundance of the dominant taxa or trophic groups between sites and seasons. Prior to the analyses, the homogeneity of variance was tested by Cohran's test and, when necessary, data were log-transformed (Zar, 1984; Clarke & Green, 1988). The Fisher LSD test was used for post hoc comparisons.

Non-metric multidimensional scaling (nMDS) via Bray–Curtis distances on log-transformed numerical abundances data was used to visualize spatial and seasonal changes in the composition of the fauna. Analysis of similarity (ANOSIM) was used to assess the significance of the multivariate results. Similarity of percentages (SIMPER) was used to identify the species which were responsible for any spatial or seasonal pattern found in the composition of the fauna. All multivariate analyses were performed with the PRIMER software package (Clarke & Warwick, 1994).

RESULTS

Abiotic factors

The values of the physical and chemical parameters recorded in the water column showed a similar spatial pattern with slight seasonal differences. Temperature ranged from 21–28°C (March and June values, respectively), salinity from 16–18 psu, dissolved oxygen from 6.5–8.5 mg/l and pH varied around 7.2. Water clarity overpassed 7 m in all cases. The inclination of hard substratum was around 60° at both sites (E and Z), while the sediment was silt at site D, and sandy with gravels at sites A, B and C.

Table 1. Population density of the zoobenthic species recorded at Lake Vouliagmeni (SS, soft substratum, sites A, B, C and D; M, meadow, site F; HS, hard substratum, sites E and Z).

Taxa	Summer 1997							Autumn 1997							Winter 1998							Spring 1998						
	SS				M	HS		SS				M	HS		SS				M	HS		SS				M	HS	
	A	B	C	D	F	E	Z	A	B	C	D	F	E	Z	A	B	C	D	F	E	Z	A	B	C	D	F	E	Z
Foraminifera		11	133			258		11	344			16	25	25					416	8	67	178	44		300	48	558	1217
Porifera																												
Cliona sp.							42																					
Cnidaria																												
Paranemonia vouliagmeniensis	11	22	278	56	132	150	300	78	67	22	67	164	83	325	122	67	211	22	560	283	208	178	44	111	22	452	108	83
Nematoda				22		558	2608												68	142	33	22				12	33	
Platyhelminthes		22	11				25		22							11												
Polychaeta																												
Capitella capitata	133	389	800	56	16	208	200	411	2644	222	22	292			133	167	733		124		17	156	522	389			100	58
Hediste diversicolor	344	100	144	22	16			544		111	22	28			256	1356	211	411	116			311	67	389	344	28	8	
Manayunkia sp.				11		358	158								44	67	200	89	216	667	542			22		256	67	
Spio sp.	11							478		156				50							17							
Oligochaeta																												
Limnodrilus sp.	56		511	44		25	175		1167	356		4			300	789	922	11	20			333	389	278				
Gastropoda																												
Acteum sp.	11			33	4		17								11		67						11	178				
Caecum sp.																				58								
Hydrobia acuta	5500	11856	6222	4756	2976	5908	12242	11678	27644	778	2600	2062	1667	1250	1856	3078	1100	1078	4600	4675	4275	6233	4589	13833	1711	3668	2917	5117
Bivalvia																												
Abra segmentum	1767	1778	1833	1156	12			3044	1989	511	256	40			1456	7578	3200		8			1444	878	967	11			
Cerastoderma glaucum		11				25	842	1533	89	144	800	1894	50	100	189	522	678	22	108	258	50	56	33	222	22	44	17	
Ostracoda	122	222	556	244	60	8		144	556	22	133	4			389	189	133	44	48		17	411	278		311	104		
Copepoda						92	17						317	142					4	50	67					8	108	358
Cirripedia																												
Balanus amphitrite						8																						
Isopoda																												
Lekanosphaera hookeri	800	478	2300	56	898	3775	1345	1133	444	878	544	1580	2083	3508	1356	533	1822	89	2788	425	808	2611	1311	1856	100	1972	1050	1675
Amphipoda																												
Gammarus aequicauda	78	78	567	278	924	1867	525			44	11	1012	1450	2367	122		44	11	3200	1542	2300	89	89	111		1652	1283	1533
Microdeutopus anomalus	789	133	756	289	288	558	958	856	1122	622	11	128	25	358	1244	467	1789	322	600	150	175	433	222	556	33	116	133	108
Insecta																												
Chironomus sp.	44	44	233	289	72	8	192	78	189	300	100	36	58	67	78	56	267	444	756	167	1042	44	67	167	22	292	42	142

Biocoenosis structure

Twelve phytobenthic and 17 zoobenthic species (five higher taxa, namely Foraminifera, Nematoda, Platyhelminthes, Copepoda and Ostracoda were not identified at species level) were identified (Table 1). The highest species richness of the fauna was recorded on hard substratum (21 taxa), followed by soft substratum (18 taxa) and *Ruppia cirrhosa* meadow (17 taxa). Overall, 61,975 individuals were counted, showing increased abundance at the latter habitat. Generally the same species were recorded at the different habitats studied, but with large fluctuations in terms of abundance.

The dominant species in soft substratum sites (A, B, C and D) were *Hydrobia acuta*, *Abra segmentum*, *Lekanosphaera hookeri* and *Microdeutopus anomalus*, whereas *Cerastoderma glaucum* showed occasionally high abundance too. In hard substratum sites (E and Z), and also in *Ruppia cirrhosa* meadow (F) the species *H. acuta*, *L. hookeri* and *Gammarus aequicauda* dominated, while the species *Paranemonia vouliagmeniensis* and the taxon of Annelida showed increased abundance at times. The abundance of the above species showed significant differences among the studied habitats (ANOVA results; Table 2). Accordingly, they all showed increased abundance in *Ruppia cirrhosa* meadow, with two exceptions: (1) the annelid *Limnodrilus* sp. and the bivalve *A. segmentum*, whose densities were higher at the upper sublittoral soft substratum sites; and (2) the polychaete *Capitela capitata*, whose density varied among the four habitats, apart from the hard substratum and the lower sublittoral soft substratum sites, where similar values were recorded. In contrast, only the bivalve *C. glaucum* and the polychaetes *C. capitata* and *Manayunkia* sp. showed significant seasonal variations in abundance (ANOVA results; Table 2), with increased density recorded in autumn for the former two species and in winter and in spring for the later one.

Richness values (d) ranged from 0.93 to 1.57, H′ values from 1.23 to 3.14 and J′ values from 0.33 to 0.85 (Figure 2).These values were rather low, as a limited number of species was recorded, among which several dominated.

The study of the similarity of the sites was based on zoobenthos. Non-metric MDS indicated the separation of the sites in four main groups, which represented the four different habitats of the lagoon: (1) Group I, hard substratum samples; (2) Group II, meadow samples; (3) Group III, upper sublittoral soft substratum samples; and (4) Group IV, lower sublittoral soft substratum samples (Figure 3). SIMPER analysis showed that 8–10 species contributed to 90% of the average similarity of groups, while 13–15 species contributed to 90% of the average dissimilarity of groups (Table 3). The spatial discrimination of these groups was confirmed by one-way ANOSIM (global R = 0.852 $P < 0.1$), whereas the pairwise test showed significant variations in all cases (R = 0.767–0.926). In contrast, the seasonal discrimination of samples was not significant (ANOSIM results R = 0.039 $P = 23.8$). However, focusing at each community level, some trends came up. In the photophilic algae community, developed on hard substratum, the samples from both sites (E and Z) matched according to season, with the exception of the summer, when they discriminated. In the *Ruppia cirrhosa* meadow (site F) and in the silty sublittoral soft substratum (site D) two seasonal subgroups were apparent: (1) summer and spring; and (2) autumn and winter. Finally, in the community of fine sands with gravels, from the upper sublittoral zone (sites A, B and C), no seasonal trends were recorded.

Table 2. Two-way ANOVA results (significant differences in bold).

Species/taxon	Spatial dispersion		Seasonal dispersion	
	F	*P*	F	*P*
Abra segmentum	11.01	**<0.05**	2.25	0.089
Capitella capitata	6.90	**<0.05**	3.97	**<0.05**
Cerastoderma glaucum	6.20	**<0.05**	3.25	**<0.05**
Gammarus aequicauda	41.55	**<0.05**	2.21	0.938
Hediste diversicolor	3.16	**<0.05**	2.52	0.069
Hydrobia acuta	30.19	**<0.05**	30.19	0.877
Lekanosphaera hookeri	47.33	**<0.05**	0.76	0.519
Limnodrilus sp.	10.08	**<0.05**	1.62	0.197
Microdeutopus anomalus	10.88	**<0.05**	2.53	0.063
Manayunkia sp.	11.83	**<0.05**	3.98	**<0.05**
Paranemonia vouliagmeniensis	37.89	**<0.05**	2.20	0.095

Trophic group analysis

Micrograzers was the dominant trophic group at all habitats of the lagoon, followed by deposit feeders and herbivores, while suspensivores and carnivores made a small contribution (Figure 4). The temporal dispersion of the above trophic groups was not significant, while significant spatial differences were only detected with respect to deposit feeders and herbivores (ANOVA results; Table 4). Deposit feeders showed increased abundance at the upper sublittoral soft substratum sites and herbivores at hard substratum sites and at *Ruppia cirrhosa* meadow.

Biodiversity comparisons

The biodiversity of Lake Vouliagmeni, in terms of species richness, was compared with relevant data from other Mediterranean lagoons (Table 5) and accordingly the Lake was classified among the less diverse temperate lagoons. Comparing the morphological characteristics of these lagoons, showed that it is also among the smaller and deeper lagoons with no direct communication to the sea, characterized by the stability of temperature and salinity. Therefore, Lake Vouliagmeni constitutes a unique environment that could explain the presence of endemic species, as well as the absence of species of marine origin that increase the biodiversity in most Mediterranean lagoons.

DISCUSSION

Lake Vouliagmeni hosts a total of 32 species: 12 floristic, 17 invertebrates and 3 vertebrates (pisces). With the exception of the sea anemone *Paranemonia vouliagmeniensis*, which is endemic to the Lake, all these species have been previously reported from other Mediterranean lagoons (Nicolaidou *et al.*, 1988; Barnes, 1994; Millet & Guelorget, 1994; Reizopoulou *et al.*, 1996; Koutsoubas *et al.*, 2000; Marchini *et al.*, 2004; Virgillio & Abbiati, 2004) and considered as common brackish water species with high ecological adaptability (Cognetti & Maltagliatti, 2000). Particularly strange is the occurrence of *Mollienisia* sp., a South American aquarium

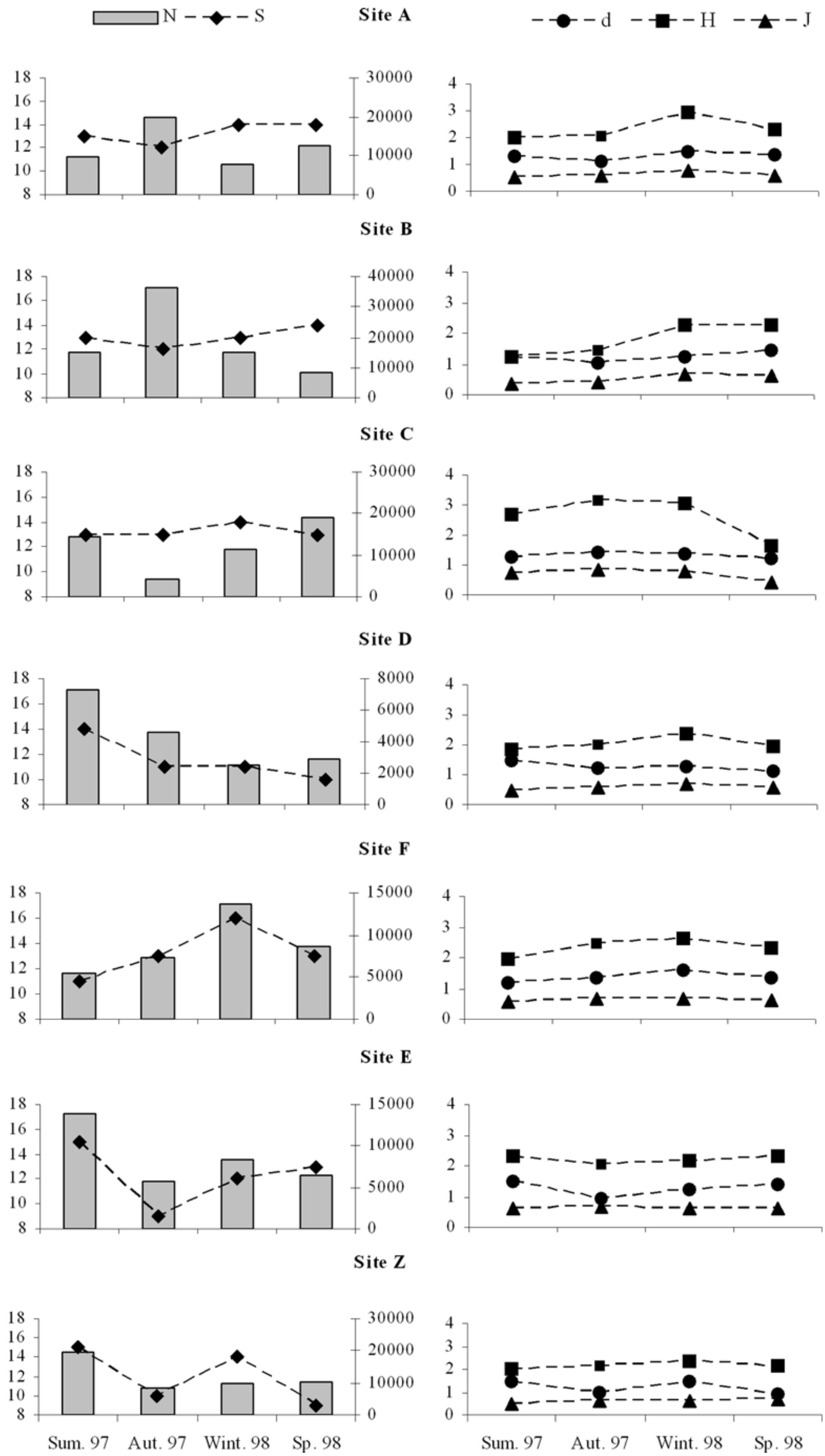

Fig. 2. Seasonal variation of the biocoenotic parameters (above) and diversity indices (below) at each sampling site (A–Z) of Lake Vouliagmeni (N, number of individuals; S, number of species; d, Margalef richness; H, Shannon–Wiener index; J, Pielou's evenness).

https://doi.org/10.1017/S0025315408001823 Published online by Cambridge University Press

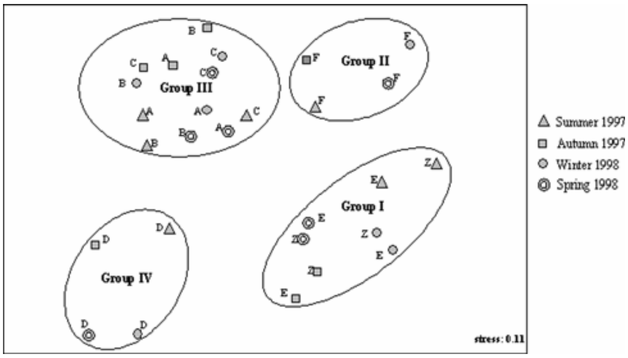

Fig. 3. Non-metric multidimensional scaling showing the spatial and seasonal patterns according to the zoobenthic structure at Lake Vouliagmeni.

fish (Vogel *et al.*, 1965), which seems to have been transferred to the lagoon and has, somehow, successfully settled (Chintiroglou *et al.*, 2004).

Most of the macrobenthic species recorded in Lake Vouliagmeni had a large spatial distribution and were not characteristic of a single habitat. Still, the different habitats provided in the lagoon were separated according to their faunistic abundance. Nearly all species showed increased density in *Ruppia cirrhosa* meadows, where others dominated at specific habitats. The bivalve *Abra segmentum*, the polychaete *Capitella capitata* and the oligochaete *Limnodrilus* sp. prevailed at soft substratum sites; the bivalve *Cerastoderma glaucum* and the amphipod *Gammarus aequicauda* prevailed at both hard substratum and *Ruppia cirrhosa* meadow, while foraminiferans were mostly found on hard substratum.

All the recorded benthic species showed significant spatial differences to their abundance, while seasonal differences were scarcely detected. The seasonal differences should be the result of biological processes, since the abiotic environment was stable throughout the year. Thus, the increased density of the bivalve *C. glaucum* in autumn could be attributed to the life cycle of the species. Its life span in Lake Vouliagmeni is around 1 year, with recruitment in autumn and disappearance of the population in summer (Gontikaki *et al.*, 2003). The polychaete *C. capitata*, a known opportunistic species (Pearson & Rosenberg, 1978; Borja *et al.*, 2000), can quickly exploit the increased organic load, which accumulates in the sediment by the decay of the flora, after summer (Malea *et al.*, 2004). *Manayunkia* sp. is a sessile species that probably utilizes the space offered by the elimination of the various epiphytes in the cold season of the year (Diapoulis & Koussouris, 1988).

The structure of the zoobenthic communities in Lake Vouliagmeni showed insignificant temporal trends. This is a quite unusual feature, since most of the Mediterranean coastal lagoons experience strong seasonal fluctuations, in both species richness and population densities (Millet & Guelorget, 1994; Koutsoubas *et al.*, 2000; Sfriso *et al.*, 2001; Arvanitidis *et al.*, 2005; Mogias & Kevrekidis, 2005). This is probably the result of the combined effect of three major factors: the stability of the abiotic environment, the relatively great depth of the lagoon and the lack of migration, due to the remoteness from the bordering sea.

Micrograzers was the dominant trophic group at all habitats of the lagoon, due to the increased abundance of *Hydrobia acuta*, which feeds on benthic diatoms and bacteria (Graham, 1988). Deposit feeders follow, represented by *A. segmentum* and *Lekanosphaera hookeri*, with the former exclusively found on soft substrata and meadow. The trophic structure analysis revealed that soft substratum communities were functionally different from both hard substratum and *Ruppia cirrhosa* meadow, mostly due to the increased presence of herbivores at the latter two. This result coincides with a previously published scheme for the Lake (Chintiroglou *et al.*, 1996).

Lake Vouliagmeni was classified among the less diverse Mediterranean lagoons, considering the reported number of species. Most Mediterranean lagoons retain a direct connection with open sea, facilitating the migration of marine species and the distribution of the fauna in zones (I–V) according to the degree of confinement (Guelorget & Perthuisot, 1992; Barnes, 1994). In contrast, Palude del Capitano and Lake Vouliagmeni communicate through

Table 3. SIMPER results. Percentage contribution of species to 90% within group similarity (S) and/or among group dissimilarity (DS).

Taxa	Within group similarity (S)				Among group dissimilarity (DS)					
	I 74.28	II 76.75	III 77.67	IV 62.21	I–II 35.35	I–III 38.92	I–IV 42.80	II–III 36.94	II–IV 47.68	III–IV 36.61
Abra segmentum			13.86	4.12	5.85	15.65	7.08	7.30	4.43	11.89
Capitella capitata		3.44	8.98		7.05	6.66	4.69	4.90	6.72	10.95
Cerastoderma glaucum	4.24	3.79			8.19	5.10	5.94	7.44	7.37	7.30
Chironomus sp.	6.41	8.32	4.81	10.72	6.76	3.58	4.35	7.04	5.44	4.59
Foraminifera	4.30				6.34	6.13	7.57	6.45	6.02	5.21
Gammarus aequicauda	16.85	13.94			5.59	9.71	14.46	13.03	14.11	6.59
Hediste diversicolor		6.19	6.62	9.13	9.29	8.70	8.06		3.30	5.53
Hydrobia acuta	19.20	15.75	16.34	28.72	5.32	3.06	3.43	4.88	6.38	4.66
Lekanosphaera hookeri	16.12	14.25	12.60	11.99	5.95	2.73	9.23	7.00	11.04	7.91
Limnodrilus sp.			6.24			8.25		5.85		10.06
Manayunkia sp.					7.27	6.14	6.76	6.42	5.82	3.66
Microdeutopus anomalus	8.56	9.92	9.83	7.84	6.10	3.70	5.15	4.00	7.39	7.16
Nematoda					5.53	5.70	6.22	3.85	3.48	
Ostracoda	7.19	5.56	6.28	12.75	4.02	3.37	3.10	3.74		3.95
Paranemonia vouliagmeniensis	9.20	10.31	4.51	7.08	6.82	3.59	5.49	8.92	9.34	3.18
Total	92.09	91.48	90.05	92.35	90.07	92.07	91.54	90.84	90.85	92.64

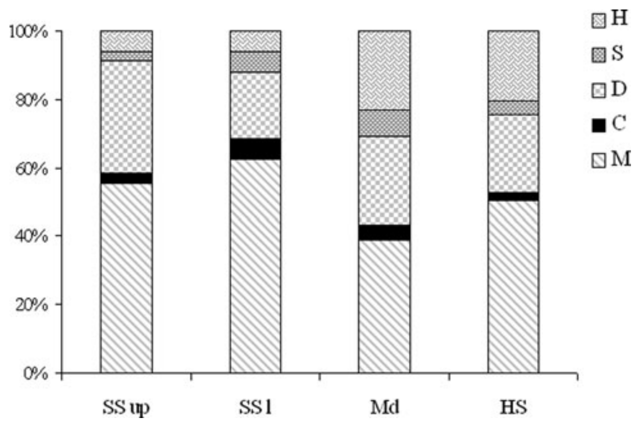

Fig. 4. Contribution of the trophic groups at each community (HS, hard substratum; Md, *Ruppia cirrhosa* meadow; SS up, soft substratum upper sublittoral; SS l, soft substratum lower sublittoral; H, herbivores, S, suspensivores; D, deposit feeders; C, carnivores; and M, micrograzers).

Table 4. Two-way ANOVA results (significant differences in bold).

Trophic group	Spatial dispersion		Seasonal dispersion	
	F	*P*	F	*P*
Micrograzers	1.34	0.287	0.79	0.510
Suspension feeders	0.56	0.640	2.11	0.129
Deposit feeders	7.83	**<0.05**	0.86	0.472
Herbivores	11.24	**<0.05**	2.33	0.103
Carnivores	1.52	0.239	2.65	0.075

underground channels (Bianchi *et al.*, 1994; Chintiroglou *et al.*, 1996). The isolation from the adjacent sea through a continuous calcareous rocky barrier hinders the entrance of marine species and their fauna is typically paralic (zones IV and V). This fact combined with the stability of the abiotic environment of Lake Vouliagmeni, seems to play a key role in the maintenance of a rather stable and limited fauna, including the presence of an endemic sea anemone. This fact stimulates the scientific interest for further research and justifies the declaration of this special system as a natural monument.

ACKNOWLEDGEMENTS

This work was supported by the Greek Ministry of Development (General Secretariat for Research and Technology) over the period 1997–1999. We are grateful to the Managerial Board of Lake Vouliagmeni for their help during samplings and to both anonymous referees for providing useful comments which improved our manuscript.

REFERENCES

Antoniadou C. and Chintiroglou C. (2005) Biodiversity of zoobenthic hard-substrate sublittoral communities in the Eastern Mediterranean (North Aegean Sea). *Estuarine, Coastal and Shelf Science* 62, 637–653.

Antoniadou C., Krestenitis Y. and Chintiroglou C. (2004) Structure of the 'Amphioxus sand' community in Thermaikos Bay (Eastern Mediterranean). *Fresenius Environmental Bulletin* 13, 1122–1128.

Arias A.M. and Drake P. (1994) Structure and production of the benthic macroinvertebrate community in a shallow lagoon in the Bay of Cádiz. *Marine Ecology Progress Series* 115, 151–167.

Arvanitidis C., Chatzigeorgiou G., Koutsoubas D., Kevrekidis T., Dounas C., Eleftheriou A., Koulouri P. and Mogias A. (2005) Estimating lagoonal biodiversity in Greece: comparison of rapid assessment techniques. *Helgoland Marine Research* 59, 177–186.

Barnes R.S.K. (1980) *Coastal lagoons. The natural history of a neglected habitat.* Cambridge: Cambridge University Press. Cambridge Studies in Modern Biology, No. 1.

Barnes R.S.K. (1994) Macrofaunal community structure and life histories in coastal lagoons. In Kjerfve B. (ed.) *Coastal lagoon processes.* Amsterdam: Elsevier Oceanography Series No. 60, pp. 311–362.

Bazairi H., Bayed A., Glemarec M. and Hily C. (2003) Spatial organisation of macrozoobenthic communities in response to environmental factors in a coastal lagoon of the NW African coast (Merja Zerga, Morocco). *Oceanologica Acta* 26, 457–471.

Table 5. Biodiversity of Mediterranean lagoons (T, annual range of temperature; Sal, annual range of salinity; S, number of animal species).

Lagoon	Surface (km²)	Depth (m)	Sea connection	T (°C)	Sal (psu)	S	References
Palude del Capitano	0.2	3	Indirect			14	Bianchi *et al.* (1994)
Gialova	2.50	0.7	Direct		13–60	87	Dounas *et al.* (1998)
Tsopeli	1.00	1.0	Direct	8–29	21–35	26	Reizopoulou *et al.* (1996)
Vivari	0.50		Direct	12–34	31.5–40	17	Reizopoulou *et al.* (1996)
Fogliano	4.04	0.9	Direct		18–45	63	Dounas *et al.* (1998)
Monaci	0.95	0.8	Direct			43	Dounas *et al.* (1998)
Caprolace	2.26	1.3	Direct			145	Dounas *et al.* (1998)
Fondi	38.00	9.1	Direct		13–33	34	Dounas *et al.* (1998)
Lungo	47.00	4.5	Direct		13–33	39	Dounas *et al.* (1998)
Prevost	38.00	1.0	Direct		17–40	63	Dounas *et al.* (1998)
Goro	25.00	1.5	Direct	–27	8–26	33	Marchini *et al.* (2004)
Ghar El Melh	30.00		Direct			83	Dounas *et al.* (1998)
Burollus	500.00	1.0	Direct			9	Dounas *et al.* (1998)
Bardawill	1440.00	2.5	Direct		33.1–93.5	45	Dounas *et al.* (1998)
Venice			Direct	10–27.4		97	Sfriso *et al.* (2001)
Cadiz			Direct	11.5–24.3	16–65	29	Arias & Drake (1994)
Valli di Comacchio	100.00	1.0	Direct	4–26.1	17.3–35.3	46	Mistri (2002)
Vouliagmeni	0.40	7.0	Indirect	21–28	16–18	20	Present study

Bianchi C.N., Boero F., Forti S. and Morri C. (1994) La Pallude del Capitano: un ambiente salmastro costiero della peninsola salentina di interesse idrobiologico e speleologico. *Istituto Italiano di Speleologia Memoria* 6, 99–106.

Borja A., Franco J. and Perez V. (2000) A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin* 40, 1100–1114.

Chintiroglou C.C., Valkouma T. and Culley M. (1996) Biological studies in Athens Lake Vouliagmeni. I. The allometry of feeding and body size in a population of the sea anemone *Paranemonia vouliagmeniensis* Doumenc *et al.* 1987 (Actiniaria: Anthozoa). *Journal of the Marine Biological Association of the United Kingdom* 76, 603–616.

Chintiroglou C.C., Antoniadou C. and Damianidis P. (2000) Spatial dispersion and density of the *Paranemonia vouliagmeniensis* population in Vouliagmeni Lagoon. *Journal of the Marine Biological Association of the United Kingdom* 80, 941–942.

Chintiroglou C.C., Antoniadou C., Damianidis P. and Diapoulis A. (2004) Contribution to the knowledge of the macrobenthic biodiversity of Vouliagmeni Lagoon (Attica, Greece). *Rapport de la Commission International pour l'Exploration de la Mer Méditerranée* 37, 506–506.

Chrystomanos A. (1889) *Chemical analysis of the curing waters of Vouliagmeni lake*. Athens: University of Athens.

Clarke K.R. and Green R.H. (1988) Statistical design and analysis for biological effects study. *Marine Ecology Progress Series* 46, 213–226.

Clarke K.R. and Warwick R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation.* Plymouth: Plymouth Marine Laboratory.

Cognetti G. and Maltagliatti F. (2000) Biodiversity and adaptive mechanisms in brackish water fauna. *Marine Pollution Bulletin* 40, 7–14.

Diapoulis A. and Koussouris T. (1988) Classification and biogeographical affinities of marine algae in the Ionian Sea. *Rapport de la Commission International pour l'Exploration de la Mer Méditerranée* 31, 9–11.

Doumenc D., England K.W. and Chintiroglou C. (1987) A new species of sea-anemone in the genus *Paranemonia* Carlgren (Anthozoa, Actiniaria) from the Aegean Sea. *Zoologica Scripta* 16, 271–275.

Dounas C., Koutsoubas D., Arvanitidis C., Petihakis G., Drummond L. and Eleftheriou A. (1998) Biodiversity and the impact of anthropogenic activities in Mediterranean lagoons: the case of Gialova Lagoon, SW Greece. *Oebalia* 24, 77–91.

Fauchald K. and Jumars P. (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: an Annual Review* 17, 193–284.

Folk R.L., Andrews P.B. and Lewis D.W. (1970) Detrital sedimentary rock classification and nomenclature for use in N. Zealand. *New Zealand Journal of Geology and Geophysics* 13, 937–968.

Gee G.W. and Bauder J.W. (1986) Particle-size analysis. In Klute A. (ed.) *Methods of soil analysis. Part 1* Madison, USA: American Society of Agronomy, Agronomy Monographs 9, pp. 383–411.

Gontikaki E., Antoniadou C. and Chintiroglou C.C. (2003) Population structure of *Cerastoderma glaucum* and *Abra ovata* in Vouliagmeni Lagoon (Attiki). *Journal of the Marine Biological Association of the United Kingdom* 83, 1095–1097.

Graham A. 1988. *Molluscs: prosobranch and pyramidellid gastropods. Synopses of the British fauna (New Series)*, 2nd edition. Leiden: Brill/Backhuys.

Guelorget O. and Perthuisot J.P. (1992) Paralic ecosystems biological organization and functioning. *Vie et Milieu* 42, 215–251.

Hily C. and Bouteille M. (1999) Modifications of the specific and feeding guild diversity in an intertidal sediment colonised by an eelgrass meadow (*Zostera marina*) (Brittany, France). *C.R. Académie de Science Paris. Sciences de la vie/Life Sciences* 322, 1121–1131.

Karalis P., Antoniadou C. and Chintiroglou C. (2003) Structure of the artificial hard substrate assemblages in ports in Thermaikos Gulf (North Aegean Sea). *Oceanologica Acta* 26, 215–224.

Kourelea E., Vafidis D., Chintiroglou C.C., Trontsios G. and Chicharo L. (2004) Temporal variations in fine sand assemblages in the North Aegean Sea (Eastern Mediterranean). *International Review of Hydrobiology* 89, 175–187.

Koutsoubas D., Arvanitidis C., Dounas C. and Drummond L. (2000) Community structure and dynamics of the molluscan fauna in a Mediterranean lagoon (Gialova lagoon, SW Greece). *Belgian Journal of Zoology* 130, 135–142.

Malea P., Kevrekidis T. and Mogias A. (2004) Annual versus perennial growth cycle in *Ruppia maritima* L.: temporal variation in population characteristics in Mediterranean lagoons (Monolimni and Drana Lagoons, Northern Aegean Sea). *Botanica Marina* 47, 357–366.

Marchini A., Gauzer K. and Occhipinti-Ambrogi A. (2004) Spatial and temporal variability of hard-bottom macrofauna in a disturbed coastal lagoon (Sacca di Goro, Po River Delta, Northwestern Adriatic Sea). *Marine Pollution Bulletin* 48, 1084–1095.

Millet B. and Guelorget O. (1994) Spatial and seasonal variability in the relationships between benthic communities and physical environment in a lagoon ecosystem. *Marine Ecology Progress Series* 108, 161–74.

Mistri M. (2002) Persistence of benthic communities: a case study from the Valli di Comacchio, a Northern Adriatic lagoonal ecosystem (Italy). *ICES Journal of Marine Science* 59, 314–322.

Mogias A. and Kevrekidis T. (2005) Macrozoobenthic community structure in a poikilohaline Mediterranean lagoon (Laki Lagoon, northern Aegean). *Helgoland Marine Research* 59, 167–176.

Nicolaidou A., Bourgoutzani F., Zenetos A., Guelorget O. and Perthuisot J.P. (1988) Distribution of molluscs and polychaetes in coastal lagoons in Greece. *Estuarine, Coastal and Shelf Science* 26, 337–350.

Papapetrou-Zamanis A. (1969) Le lac de Vouliagmeni (Attiki). *Annales Géologiques des Pays Helléniques* 21, 210–216.

Pearson T.H. and Rosenberg R. (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review* 16, 229–311.

Reizopoulou S., Thessalou-Legaki M. and Nicolaidou A. (1996) Assessment of disturbance in Mediterranean lagoons: an evaluation of methods. *Marine Biology* 125, 189–197.

Sfriso A., Birkemeyer T. and Ghetti P.F. (2001) Benthic macrofauna changes in areas of Venice lagoon populated by seagrasses or seaweeds. *Marine Environmental Research* 52, 323–349.

Stirn J. (1981) *Manual of methods in aquatic environment research. Part 8. Ecological assessment of pollution effects (Guidelines for the F.A.O. (GFCM)/UNEP Joint Coordinated Project on Pollution in Mediterranean).* FAO Fisheries Technical Paper, No. 209, 190 pp.

Virgilio M. and Abbiati M. (2004) Habitat discontinuity and genetic structure in populations of the estuarine species *Hediste diversicolor* (Polychaeta: Nereididae). *Estuarine, Coastal and Shelf Science* 61, 361–367.

Vogel Z., Brazda V. and Brazda P. (1965) *Poissons d'aquarium. Atlas illustré*. Paris: Gründ.

and

Zar J.H. (1984) *Biostatistical analysis*. 2nd edition. New Jersey: Prentice-Hall Inc.

Correspondence should be addressed to:
Chariton Chintiroglou
Aristotle University, School of Biology
Department of Zoology, Thessaloniki, Greece, Gr 54 124
email: chintigl@bio.auth.gr

https://doi.org/10.1017/S0025315408001823 Published online by Cambridge University Press