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Seasonal Variation of the Macrozoobenthic Community Structure at Low Salinities in a Mediterranean Lagoon (Monolimni Lagoon, Northern Aegean)

key words: macrozoobenthos, community structure, salinity, lagoon, Mediterranean Sea

Abstract

The macrozoobenthic community structure and dynamics at low salinities (0.3–6 psu) in a Mediterranean lagoon (Monolimni lagoon) were investigated. Samples were collected monthly from February 1998 to February 1999 at two sampling stations. Community structure was analyzed by means of uni- and multivariate methods. 21 taxa were collected; the amphipod *Corophium orientale* and the gastropod *Ventrosia maritima* dominated the assemblages. Total abundance peaked (50,000–60,000 individuals m^{-2}) in mid or late autumn. Community structure showed an almost even seasonal periodicity; seasonal changes were mainly derived from the intense variation in abundance of most species and the non–occurrence of a few ones (*e.g. Corophium insidiosum, Polydora ciliata*) in spring and summer. Non–occurrence, which led to a depression of the most diversity indices, was possibly the only direct impact of the extremely low salinities (~0.3 psu) on community structure. The main structuring factors of the community in the deeper outer part of the lagoon were water temperature and depth, and in the innermost part, where a *Ruppia maritima* meadow occurred, were water temperature and predation pressure by crabs (*Carcinus aestuarii*) and gobies (*Knipowitchia caucasica*). A temporary decline in total abundance in summer followed an increase in abundance of these predators.

1. Introduction

Coastal brackish habitats have been the subject of extensive studies. Nevertheless, the factors determining the pattern of distribution and seasonal dynamics of the macrobenthic fauna in these habitats are not yet sufficiently known. GUELORGET and PERTHUISOT (1992) introduced the concept of "paralic ecosystem" and "confinement" and applied these concepts mainly to the study of the coastal brackish habitats of the microtidal Mediterranean Sea. The authors proposed that "confinement", which represents the turnover time of marine water, is the main factor determining the horizontal zonation of benthic assemblages in the coastal brackish ecosystems ("paralic" ecosystems); they also stated that the populations in these ecosystems remain stable despite frequent considerable environmental variations (*e.g.* in salinity); even more, summer dystrophic crises do not destroy the ecosystem which recovers quickly once the crisis is over.

Useful information on the seasonal dynamics of the macrozoobenthic assemblages in Mediterranean coastal brackish habitats was given in some mainly recent publications (*e.g.* REIZOPOULOU *et al.*, 1996; LARDICCI *et al.*, 1997; TAGLIAPIETRA *et al.*, 1998; KOUTSOUBAS *et al.*, 2000); several of these studies were carried out in lagoons, which suffer from summer dystrophic crises. However, the monthly variation in macrobenthic community structure and the associated environmental factors at very low salinities in Mediterranean brackish habitats have not substantially been investigated.

Monolimni lagoon, which is located in the Evros Delta (Northern Aegean), is a poikilohaline, relatively enclosed Mediterranean brackish system. Although a significant scientific effort has been spent on macrobenthic fauna of several other areas of Evros Delta (*e.g.* GOUVIS and KOUKOURAS, 1993; GOUVIS *et al.*, 1997; KEVREKIDIS, 1997), the composition of the macrozoobenthic assemblages in Monolimni lagoon remains practically unknown.

We describe the monthly variation in the macrozoobenthic community structure and dynamics at very low salinities in a Mediterranean lagoon (Monolimni lagoon), and investigate the key abiotic and biotic variables affecting community structure. Several variables (*e.g.* temperature, salinity, oxygen concentration, sediment characteristics, biomass of macrophytes, density of epibenthic predators, *etc.*) are examined. Our hypothesis was that the macrozoobenthic community would show a rather homogeneous composition throughout the annual cycle; the seasonal dynamics of the community would mainly be governed by temperature, which strongly affects the life cycle of the species.

2. Methods

2.1. Study Area

Evros Delta is located at the N.E. end of the Aegean Sea (Fig. 1). Fresh water flows in the delta area primarily through the eastern branch of Evros river; additional fresh water inflows enter in the delta area through the western branch of Evros River and the streams Mikri Maritsa and Loutron, usually from late autumn to early summer. Three islets and some lagoons have been formed in the delta area. Monolimni (or Paloukia) lagoon occupying an area of about 112 ha communicates with the sea mainly

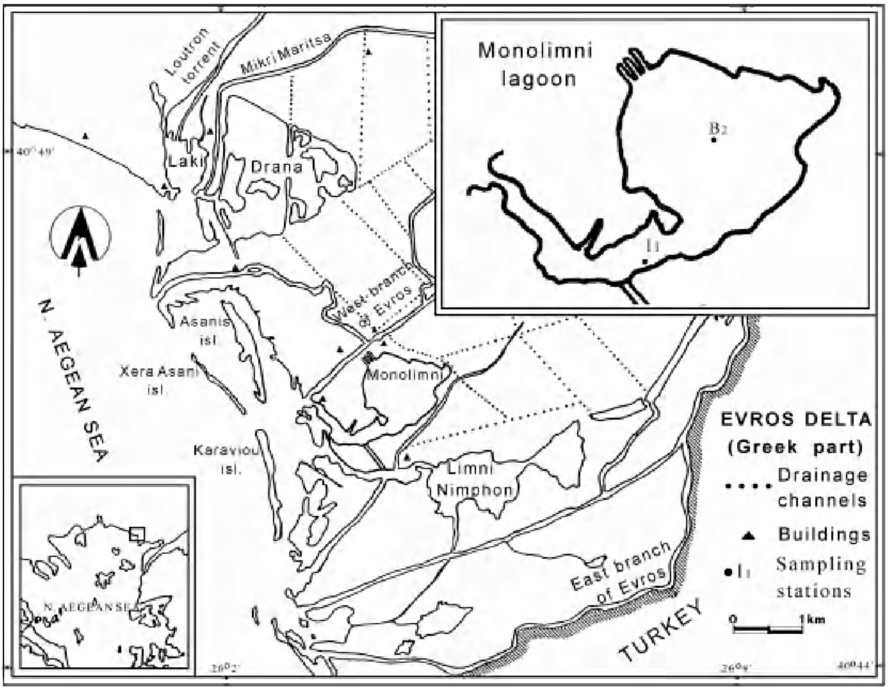

Figure 1. Geographical location of the study site, (B) map of Evros Delta and map of Monolimni lagoon showing the sampling stations.

through an opening 15 m wide at its N.W. end (Fig. 1). The maximum depth at the outer southern part of Monolimni lagoon is about 2.5 m and at the innermost northern part about 60 cm. An extensive macrophyte meadow (*Ruppia maritima* L.) covers almost completely the bottom of the northern part. Extensive culture of various species of mullet is the main exploitation pattern occurring in the lagoon. An annual fishing production of 11 100 kg was recorded in Monolimni lagoon in 1998 according to the local Fishery Service.

2.2. Sampling and Laboratory Techniques

Monthly samples were collected during February 1998 – February 1999 at station I_1 located in the southern part of the lagoon and at station B_2 located at the northern part (Fig. 1). Each time at each station, 4 random sampling units were taken with a modified van Veen grab (LARIMORE, 1970); the grab covered a surface of 400 cm^2 (20 × 20 cm) and penetrated to a depth of 20 cm. The samples were sieved immediately through a 0.5 mm screen. Sediment samples were taken with a small corer for particle size analysis and estimation of the amount of organic matter. Depth and salinity, temperature, dissolved O_2, O_2 saturation and pH of the water near the bottom, as well as temperature of the sediment at depths of 1 cm and 5 cm were also measured. Additionally, two samples of epibenthic decapods and small fishes were taken using a special net (with a square opening having a side of 40 cm) which was pulled on the sediment along a 10 m distance.

Sediment analysis and estimation of organic matter were made according to the methods described by BUCHANAN (1984). All animals were identified to the lowest possible taxon and counted.

2.3. Data Analysis

Macrobenthic community structure was analyzed by total number of individuals (N), number of species (S) and species richness Margalef's (d), Shannon – Wiener species diversity (H´) (natural logarithm) and evenness (J) indices calculated for each sampling unit.

Cluster analysis (Bray–Curtis similarity index, group average clustering) and non – metric multidimensional scaling (MDS) were used to investigate faunal similarities among monthly samples in each station separately (data transformed to fourth root). The significance of differences between clusters of monthly samples was tested using the Analysis of Similarities – ANOSIM. Species responsible for similarities and for differences between clusters of monthly samples were investigated using the similarity percentages procedure – SIMPER (CLARKE, 1993). Environmental variables best correlated with the multivariate pattern of the macrobenthic community were identified by means of harmonic Spearman coefficient, ϱw (BIO – ENV analyses) (CLARKE and AINSWORTH, 1993). In order to apply BIO –ENV analysis, several matrices including combinations of non-highly correlated environmental variables were used; Spearman's rank correlation coefficient was applied to identify these correlations between the environmental variables. The PRIMER package developed at Plymouth Marine Laboratory was used.

3. Results

3.1. The Environment

3.1.1. Abiotic Variables

The monthly variation in abiotic factors of water and sediment throughout the sampling period in stations I_1 and B_2 is shown in Table 1. In station I_1 depth varied between 50 cm and 70 cm almost throughout the sampling period; it showed a higher value in April (85 cm). In station B_2 depth fluctuated between 30 cm and 55 cm. Water temperature near the bottom showed lower values in December (1.8 °C in st. I_1, 4.2 °C in st. B_2) and higher ones in July (26.7 °C in st. I_1, 28.5 °C in st. B_2); sediment temperature at a 1 cm or 5 cm depth showed a seasonal variation correlated with water temperature (Table 1). Salinity near the

Table 1. Monthly variation in physicochemical parameters of water and sediment in stations I_1 and B_2, as well as in dry weight biomass of leaves and sheaths of *Ruppia maritima* L. in station B_2 (after MALEA *et al.*, in preparation), during the sampling period.

			F'98	M	A	M	J	J	A	S	O	N	D	J'99	F
st. I_1	**Water**	**Depth (cm)**	50	50	85	55	70	60	50	60	55	60	50	55	70
		Salinity (psu)	0.8	0.3	0.4	0.3	1.2	3.4	5.6	4.2	4.2	3.0	1.6	0.7	0.5
		Dissolved O_2 (mg/l)	13.5	13.5		8.4	6.05	6.1	7.5	7.2	8.7	10.39		14.7	14.32
		O_2 saturation (%)	114.6	110.2		85	74.0	76.5	85.6	82.0	83.5	95.3		122.0	116.5
		pH	8.1	8.33	8.25	7.6	8.12	8.3	7.5	7.4	8.1	7.96	8.13	9.10	8.85
		Temp. (°C)	9.4	5.8	16.1	16.0	25.8	26.7	24.6	20.9	14.2	9.3	1.8	6.4	5.9
	Sediment	**Temp. at 1 cm (°C)**	10.0	6.1	16.3	16.0	24.7	26.6	22.1	22.4	14.5	10.3	2.1	7.7	6.1
		Temp. at 5 cm (°C)	9.4	5.9	16.1	16.0	25.6	26.5	22.0	22.2	14.4	10.3	1.9	7.1	5.9
		Median diameter (Md) (μm)	164	170	153	159	159	170	159	170	143	159	170	176	164
		QD (phi)	0.35	0.35	0.25	0.35	0.30	0.35	0.35	0.35	0.30	0.35	0.35	0.35	0.35
		Organic matter (%)	0.43	0.45	0.15	0.45	0.36	1.73	0.92	1.12	0.94	1.09	0.27	0.88	0.75
st. B_2	**Water**	**Depth (cm)**		30	40		45	35	30	40	35	50	30	35	55
		Salinity (psu)	0.8	0.3	0.3	1.2	1.3	2.8	5.6	5.7	4.6	3.0	1.7	0.7	0.5
		Dissolved O_2 (mg/l)	11.5	14.65		11.42	13.98	18.0	14.5	9.78	15.05	13.02		14.3	13.35
		O_2 saturation (%)	101.0	127.2		117.0	173.5	220.0	175.0	116.6	161.3	122.0		125.0	105.0
		pH	7.45	8.66	8.65	8.15	9.32	9.2	8.68	8.6	8.8	8.11	8.3	9.15	8.8
		Temp. (°C)	9.2	8.2	17.4	16.7	26.6	28.5	26.5	23.1	17.8	10.2	4.2	8.6	5.0
	Sediment	**Temp. at 1 cm (°C)**	8.5	8.2	16.7	16.7	27.0	26.7	24.5	24.0	17.2	11.4	3.7	8.5	5.1
		Temp. at 5 cm (°C)	8.1	7.6	16.0	16.7	26.0	28.6	23.5	21.9	16.4	11.2	3.5	8.1	5.2
		Median diameter (Md) (μm)	125	120	125	105	108	108	94	112	125	129	116	108	101
		QD (phi)	0.90	0.65	0.65	0.60	0.65	0.55	0.75	0.60	0.80	0.80	0.70	0.60	0.85
		Organic matter (%)	0.48	0.93	0.75	0.90	2.20	1.0	1.09	1.36	1.43	0.98	0.84	0.82	1.31
	Biomass of	**leaves and sheaths of *Ruppia maritima* L. (g DW m^{-2})**	0.856	1.493	2.719	29.306	67.659	66.834	87.961	108.602	114.917	30.253	18.420	8.175	

bottom varied between 0.3 and 5.6 or 5.7 psu throughout the sampling period in both stations (Table 1). In July 1997, water salinity near the bottom varied between 30 and 31.5 psu overall the lagoon (unpublished data). An increased freshwater inflow during winter and spring of 1998 following a period of intense rainfall on the Evros river catchment area resulted in a sharp decline in salinity values in Monolimni lagoon.

Dissolved O_2 and O_2 saturation showed high values throughout the sampling period (minimum values 6.05 mg/l, 74% in station I_1, 9.8 mg/l, 101% in station B_2); oxygen concentrations were higher in station B_2 than in station I_1 almost throughout the study period and particularly during the period of the maximum growth of *Ruppia maritima* (Table 1). Values of pH ranged from 7.4 to 8.3 during the most of the sampling period in station I_1 and scored (~9) in winter; they varied between 7.45 and 9.32 in station B_2 (Table 1). The sediment was fine sand in station I_1 and very fine sand in station B_2; the median diameter (Md) of the sediment showed a low monthly fluctuation in both stations (Table 1). The values of the organic matter of the sediment were lower in station I_1 (0.15–1.73%) than in station B_2 (0.48–2.2%) and much lower in both stations than those reported for several Mediterranean lagoons (*e.g.* Reizopoulou *et al.*, 1996; Lardicci *et al.*, 1997; Tagliapietra *et al.*, 1998).

3.1.2. Biotic Variables

Macroalgae were occasionally observed in both parts of the lagoon throughout the study period. In the innermost northern part the biomass of the leaves of *Ruppia maritima* gradually increased from spring to August and October (Malea *et al.*, in preparation) (see also Table 1).

Two decapods (*Carcinus aestuarii*, *Crangon crangon*) and two small fishes (*Knipowitschia caucasica*, *Syngnathus acus*) were found in the monthly samples taken with the special net in station I_1 (Table 2). The aforementioned species along with the small fish *Aphanius fasciatus* were also collected in station B_2 (Table 2). *Carcinus aestuarii* was mainly found from May to October in both stations having higher abundance in May – June in station B_2. The

Table 2. Monthly variation in the number of individuals/10 m^2 of the epibenthic decapods and the small fishes collected using a special net in stations I_1 and B_2 during the sampling period.

Species		F' 98	M	A	M	J	J	A	S	O	N	D	J' 99	F
Station I_1	*Crangon crangon* (Linnaeus, 1758)	1.3			76.3	10	3.8	76.3	40	61.3	10			
	Carcinus aestuarii Nardo, 1847			1.3	3.8	2.5	11.3	6.3	1.3	5	1.3		1.3	1.3
	Knipowitschia caucasica Kawrajsky, in Berg, 1916		1.3			1.3	15	62.5	6.3	28.8	3.8	1.3	1.3	2.5
	Syngnathus acus Linnaeus, 1758					15	20	10	15	6.3	2.5			
Station B_2	*Crangon crangon* (Linnaeus, 1758)				6.3	6.3		1.3	8.8	20	18.8	3.8		
	Carcinus aestuarii Nardo, 1847				20	11.3	2.5	1.3	1.3	3.8				
	Knipowitschia caucasica Kawrajsky, in Berg, 1916	3.8	2.5		468.8	152.5	15	22.5	60	91.3	55	16.3	21.3	6.3
	Syngnathus acus Linnaeus, 1758				1.3	6.3	13.8	2.3	51.3	38.8	25		1.3	1.3
	Aphanius fasciatus Nardo, 1827							1.3	1.3			1.3		

Table 3. The taxa of the assemblages in stations I_1 and B_2 showing the highest values of presence (P) and mean monthly dominance (D) during the sampling period.

Taxa	Station I_1		Station B_2	
	P	D (%)	P	D (%)
Ventrosia maritima (MILASCHEWITCH, 1916)	13	37.9	13	51.3
Corophium orientale SCHELLENBERG, 1928	13	39.8	13	14.9
Abra ovata (PHILIPPI, 1836)	12	1.3	13	12.1
Streblospio shrubsolii (BUCHANAN, 1890)	13	5.1	13	6.2
Hediste diversicolor (O. F. MULLER, 1776)	13	3.2	13	3.1
Gammarus aequicauda (MARTYNOV, 1931)	13	1.3	13	3.8
Cerastoderma glaucum (POIRET, 1789)	8	1.6	13	0.3
Microprotopus maculatus NORMAN, 1867	9	1.8	7	0.5
Corophium insidiosum CRAWFORD, 1937	8	6.3	5	0.03
Polydora ciliata (JOHNSTON, 1838)	4	0.4	5	0.05
Cumacea	12	1.2	4	0.1
Tubificidae	8	0.06	12	0.7
Chironomidae larvae			12	6.9

goby *Knipowitschia caucasica* was found almost throughout the sampling period in both stations having higher abundance in station B_2 especially during May – June (Table 2). It is known that the diet of both *C. aestuarii* and *K. caucasica* includes macrobenthic invertebrates (*e.g. Corophium*, *Gammarus*, *Cerastoderma*, *Abra*, *Hediste*, Diptera larvae) (*e.g.* COTIGLIA *et al.*, 1983a; 1983b; KEVREKIDIS *et al.*, 1990; CARRER and OPITZ, 1999).

3.2. *Macrozoobenthic Assemblage*

Twenty one taxa were collected in Monolimni lagoon throughout the sampling period. Nineteen taxa were identified in the monthly samples in station I_1 and twenty ones in station B_2. The species composition was similar in both stations. In station I_1 seven taxa were constantly found throughout the study period (at 13 or 12 months) (Table 3). The amphipod *Corophium orientale* and the gastropod *Ventrosia maritima* dominated the assemblage showing a cumulative mean monthly dominance of 77.7% (Table 3). Five taxa were less frequently found (Table 3); three of these taxa (*Cerastoderma glaucum*, *Microprotopus maculatus*, *Corophium insidiosum*) showed a more or less remarkable mean monthly dominance (Table 3). Nine taxa were constant in the innermost station B_2 (Table 3). Lagoonal taxa of freshwater ancestry (larvae of Chironomidae, Tubificidae) were included in these taxa (Table 3). The gastropod *V. maritima*, the amphipod *C. orientale* and the bivalve *Abra ovata* were the dominants; these species showed a cumulative mean monthly dominance of 78.3% (Table 3). Two of the constant taxa (*C. glaucum*, Tubificidae) had a low mean monthly dominance, while four taxa (*M. maculatus*, *C. insidiosum*, *Polydora ciliata*, Cumacea) were less frequently collected having a very low mean monthly dominance (Table 3).

3.3. *Structural Analysis*

3.3.1. Univariate Analysis

The total number of individuals of the macrobenthic fauna in station I_1 gradually increased from spring (mean value 2,640–4,740 individuals m^{-2}) to October (50,420 individuals m^{-2})

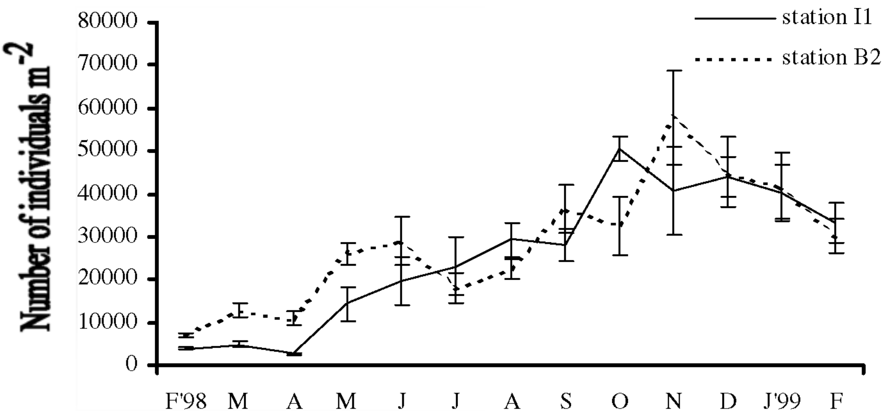

Figure 2. Monthly variation in the total number of individuals of the macrobenthic fauna in stations I_1 and B_2 during the sampling period; dots = mean; bar lines = standard error.

and then gradually decreased until the last sampling (33,340 individuals m^{-2}) (Fig. 2). Number of species (S) and species richness (d) varied between 5.75 and 11.25, and 0.49 and 1.21, respectively (Fig. 3). Species diversity (H′) and evenness (J) varied between 0.67 and 2.23, and between 0.39 and 0.92, respectively (Fig. 4). Community indices showed a decrease from February 1998 to June; most of them displayed an abrupt decline in April (Figs. 3, 4). From June onwards they gradually increased (Figs. 3, 4).

Total macrobenthic density in station B_2 gradually increased from February 1998 (mean value 6,960 individuals m^{-2}) to November (57,680 individuals m^{-2}); that increase was temporarily interrupted in July (Fig. 2). From November onwards, total density gradually decreased until February 1999 (30,140 individuals m^{-2}) (Fig. 2). S and d ranged from 8 to 11.8, and from 0.70 to 1.14, correspondingly; their values decreased from spring to June, while their gradual increase from June onwards was temporarily interrupted in August (Fig. 3). H′ and J fluctuated between 1.20 and 1.82, and between 0.53 and 0.79, respectively, showing their lowest values in autumn and winter (Fig. 4).

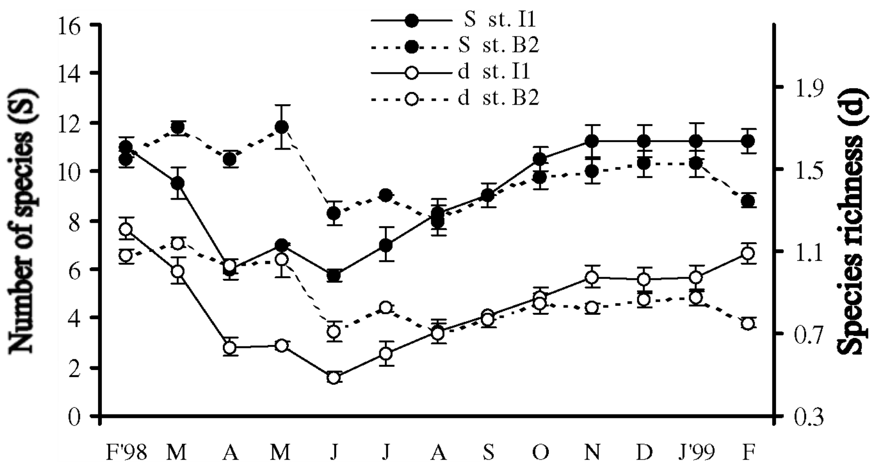

Figure 3. Monthly variation in the number of species and species richness in stations I_1 and B_2 during the sampling period; dots = mean; bar lines = standard error.

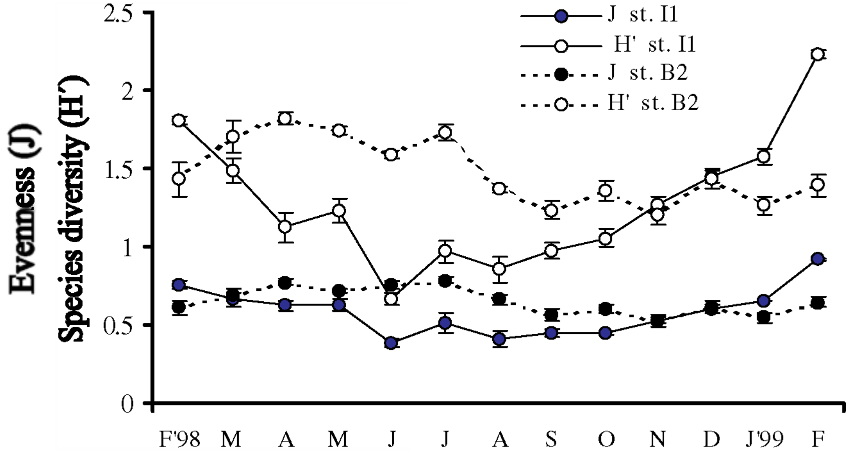

Figure 4. Monthly variation in species diversity and evenness in stations I_1 and B_2 during the sampling period; dots = mean; bar lines = standard error.

3.3.2. Multivariate Analysis

The similarity dendrogram and multidimensional scaling (MDS) ordination plot of the monthly samples in station I_1 are shown in Figures 5 and 6, respectively, and those corresponding to station B_2 in Figures 7 and 8, respectively. The similarity among monthly samples was very high in both stations (Figs. 5, 7).

In station I_1, at a 80.21% similarity level, six significantly distinct sample groups were formed (ANOSIM, global $R = 0.93$, $p < 0.001$) corresponding to different periods of the year

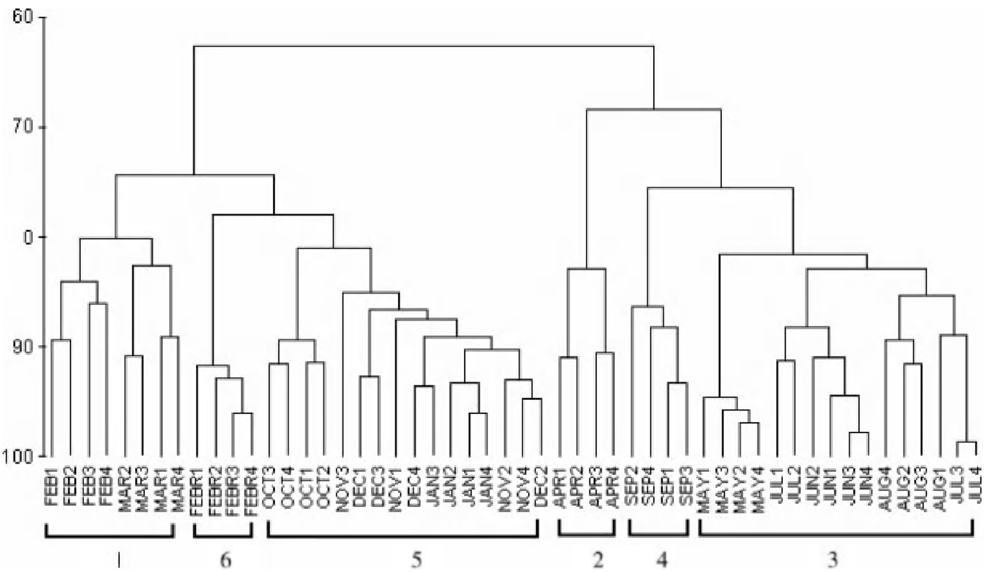

Figure 5. Dendrogram of hierarchical classification of the monthly sampling units on the basis of similarity in the faunal composition in station I_1. FEB: February 1998; FEBR: February 1999.

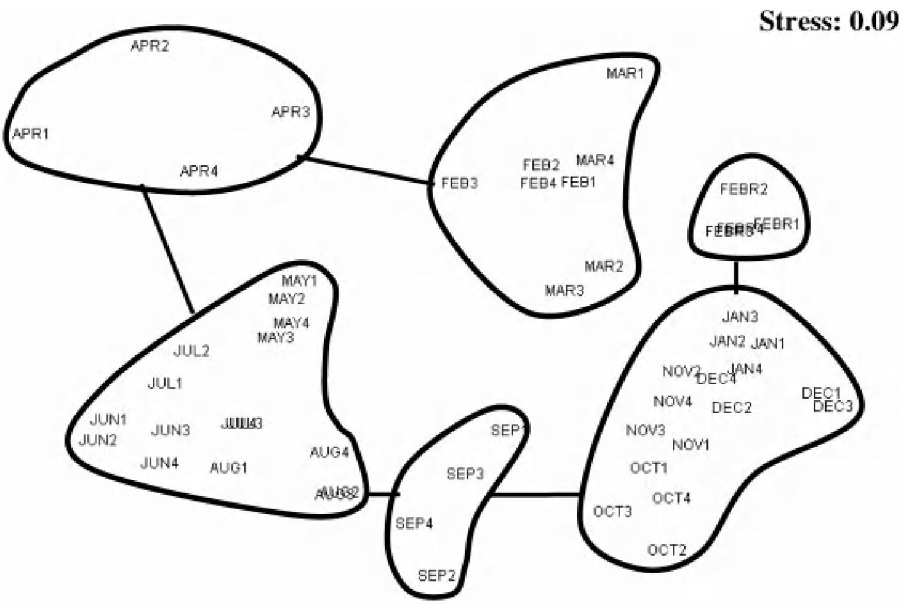

Figure 6. Multidimensional scaling (MDS) ordination plot of the monthly sampling units in station I_1. FEB: February 1998; FEBR: February 1999.

(Figs. 5, 6). The variation in community structure showed a seasonal trend: it changed evenly from late winter – early spring to late spring – summer, autumn – winter and late winter (Fig. 6). The samples of September had a transitional position between those of May –

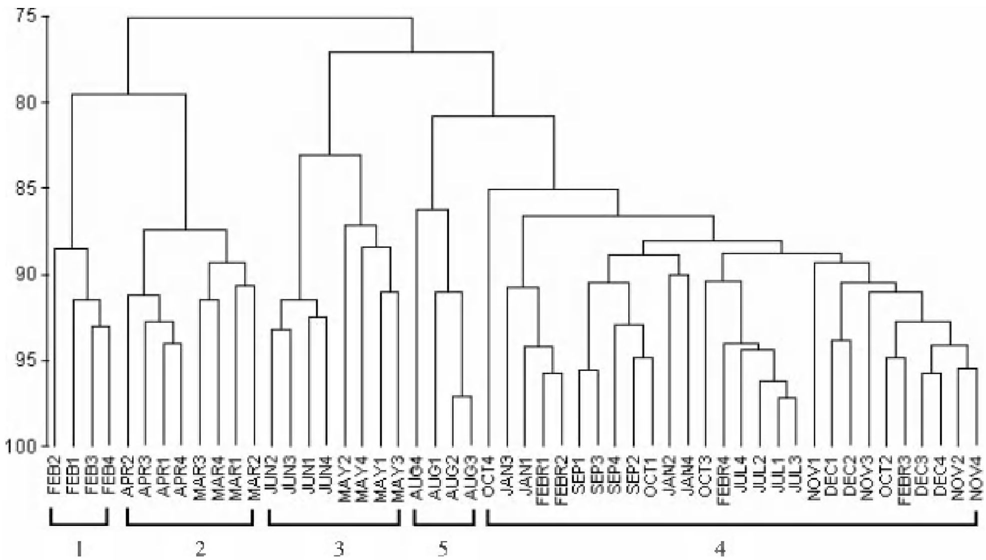

Figure 7. Dendrogram of hierarchical classification of the monthly sampling units on the basis of similarity in the faunal composition in station B_2. FEB: February 1998; FEBR: February 1999.

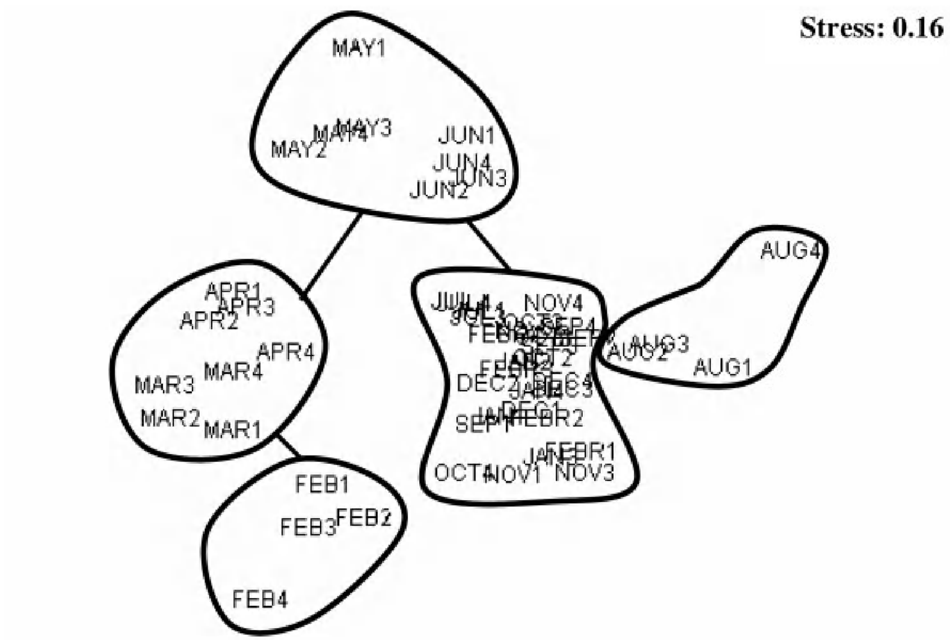

Figure 8. Multidimensional scaling (MDS) ordination plot of the monthly sampling units in station B_2. FEB: February 1998; FEBR: February 1999.

August and October–January, as well as the samples of February 1999 between those of October–January and February 1998–March, while the position of April samples indicates that a temporal abrupt change in community structure occurred in mid spring (Fig. 6).

In station B_2, at a 83.07% similarity level, five sample groups were distinguished (ANOSIM, global $R = 0.95$, $p < 0.001$) (Figs. 7, 8). The first group included the samples of February 1998, the second those of March and April, the third those of May and June, the fourth those of July and September – February 1999, and the fifth those of August (Figs. 7, 8). Community structure changed evenly from late winter to early – mid spring, late spring–early summer and mid summer–autumn– winter, but August samples separated from those of July–February 1999 (Fig. 8).

The average densities of the species contributed >70% to similarity in each main sample group in station I_1 and in each sample group in station B_2 (SIMPER) are given in Table 4. The average densities of the species which were responsible for the differences between the successive sample groups in station I_1 and in station B_2 (cut – off 70%) (SIMPER) are given in Tables 5 and 6, respectively. These analyses indicate that the grouping of the monthly samples was mainly derived from: a) the intense seasonal variation in density of the same species (*e.g. Ventrosia maritima*, *Corophium orientale*, *Streblospio shrubsolii*, *Hediste diversicolor*, *Gammarus aequicauda*); b) the absence of few taxa during some periods (*Abra ovata*, *Cerastoderma glaucum*, *Corophium insidiosum*, *Polydora ciliata* in station I_1, *C. insidiosum*, *P. ciliata*, Cumacea in station B_2).

In station I_1, *C. orientale* reached its highest abundances during summer, *V. maritima* during autumn–winter, *S. shrubsolii* in May–August, *G. aequicauda* in April, *H. diversicolor* during summer, autumn and winter, Cumacea and *A. ovata* during autumn–winter (Tables 4, 5). In station I_1, a faunistic impoverishment occurred in April characterized by the disappearance of the bivalves (*A. ovata* and *C. glaucum*) and the decreased abundances of the most of the other

Table 4. Average densities (individuals m^{-2}) of taxa contributed >70% to similarity in each main sample group in station I_1 and in each sample group in station B_2 during the sampling period (SIMPER).

	Station I_1				Station B_2				
Taxa	**FEB' 98–MAR**	**APR**	**MAY–AUG**	**OCT–JAN**	**FEB' 98**	**MAR–APR**	**MAY–JUN**	**JUL–FEB' 99**	**AUG**
Ventrosia maritima	1525.0	300.0	1893.75	21748.44	3706.25	4637.50	7115.63	21879.46	9062.5
Corophium orientale	496.88		15637.50	12673.44		778.13	6796.88	5643.75	
Abra ovata	418.75				1362.50	1506.25	4981.25	3923.21	2925.0
Streblospio shrubsolii	1159.38	1025.0	2431.25		943.75	2084.38	4950.0		
Hediste diversicolor	256.25	106.25	1020.31	1023.44	312.50	1140.63			
Gammarus aequicauda		1112.50					1984.38	1056.25	1856.25
Cerastoderma glaucum				1034.38					
Microprotopus maculatus				1157.81	106.25	706.25			
Corophium insidiosum	140.63			3995.31					
Chironomidae larvae					150.0			2517.86	7437.50

Table 5. Differences (< or >) in average densities (individuals m^{-2}) of taxa contributed >70% to dissimilarity between the successive main sample groups in station I_1 (SIMPER).

Taxa	FEB' 98–MAR		APR		MAY–AUG		OCT–JAN		FEB' 98–MAR
Abra ovata	418.75	>	0	<	68.75		596.88	>	418.75
Gammarus aequicauda	84.38	<	1112.5	>	353.13		340.63	>	84.38
Cerastoderma glaucum	56.25	>	0		0	<	1034.38		
Corophium insidiosum	140.63	>	12.5		0	<	3995.31		
Cumacea	125.0	>	12.5	<	154.69	<	493.75	>	125.0
Corophium orientale	496.88	>	68.75	<	15637.5		12673.44	>	496.88
Streblospio shrubsolii			1025.0	<	2431.25	>	496.88	<	1159.38
Microprotopus maculatus					4.69	<	1157.81	>	15.63
Ventrosia maritima					1893.75	<	21748.44		
Polydora ciliata					0	<	301.56	>	0
Tubificidae							28.13		28.13

Table 6. Differences (< or >) in average densities (individuals m^{-2}) of taxa contributed >70% to dissimilarity between the successive sample groups in station B_2 (SIMPER).

Taxa	FEB' 98		MAR–APR		MAY–JUN		JUL–FEB' 99		FEB' 98	JUL–FEB' 99		AUG
Polydora ciliata	112.50	>	0				9.82	<	112.50			
Cumacea	0	<	93.75	<	140.63	>	0.89					
Tubificidae	37.50	>	6.25	<	171.88	<	329.46			329.46	>	37.50
Gammarus aequicauda	43.75	<	371.88		1984.38	>	1056.25	>	43.75	1056.25	<	1856.25
Corophium orientale	93.75	<	778.13	<	6796.88	>	5643.75	>	93.75	5643.75	>	193.75
Corophium insidiosum	0	<	21.88	>	0							
Microprotopus maculatus	106.25	<	706.25	>	9.38		40.18	<	106.25			
Chironomidae larvae			293.75	>	15.63	<	2517.86			2517.86	<	7437.50
Streblospio shrubsolii					4950.0	>	1086.61	>	943.75	1086.61	>	81.25
Ventrosia maritima					7115.63	<	21879.46					
Hediste diversicolor			1140.63	>	1087.50							
Cerastoderma glaucum			184.38	>	100.0	>	41.96	<	93.75			

Table 7. Summary of the combinations of the environmental variables showed the five higher values of the harmonic Spearman rank coefficient (ϱw) with macrobenthic community structure in stations I_1 and B_2 during the sampling period.

	Variable combinations	ϱw
Station I_1	Water Temperature, Depth	0.620
	Water Temperature	0.614
	Sediment Temperature at 5 cm depth, Depth	0.605
	Sediment Temperature at 1 cm depth, Depth	0.602
	Water Temperature, Depth, pH	0.597
Station B_2	Water Temperature, *Carcinus aestuarii*	0.521
	Water Temperature, *Carcinus aestuarii*, *Knipowitschia caucasica*	0.516
	Sediment Temperature at 1 cm depth, *Carcinus aestuarii*, *Knipowitschia caucasica*	0.513
	Sediment Temperature at 5 cm depth, *Carcinus aestuarii*, *Knipowitschia caucasica*	0.509
	Sediment Temperature at 1 cm depth, *Carcinus aestuarii*	

species (Table 5). In station B_2, the differences between August samples and those of July–February 1999 were mainly caused by the remarkably lower densities of *C. orientale*, Tubificidae and *S. shrubsolii* and the higher ones of Chironomidae larvae and *G. aequicauda* in August (Table 6).

Taking the data of both stations into account (Tables 4, 5, 6) we can state that: a) *Corophium insidiosum* was found with noteworthy abundances only in station I_1 in February 1998–March and mainly in October–January; b) *Polydora ciliata* was mostly collected in February 1998 in station B_2 and mainly from October to January in station I_1. These species were not essentially collected in Monolimni lagoon from early or mid spring to October.

3.3.3. Associated Environmental Variables

The five highest values of the harmonic Spearman rank coefficient (ϱ_w) deriving from the performance of the BIO – ENV analysis in each one station are given in Table 7. In station I_1 water temperature and adding over and above the combination of water temperature with depth, are best correlated with the seasonal variation in the macrobenthic community structure (Table 7). The combinations of sediment temperature at 5 cm or 1 cm depth and depth, and of water temperature, depth and pH showed the next highest values of ϱ_w (Table 7). The set of water temperature, depth and salinity showed a value of 0.59. The combination of water temperature and abundance of *Carcinus aestuarii* best correlated with the macrobenthic community structure in station B_2 (Table 7). The sets of water or sediment temperature with the abundances of *Carcinus aestuarii* and *Knipowitschia caucasica* showed the next high values of the harmonic Spearman rank coefficient (Table 7). The highest values of ϱ_w in station B_2 were lower than those in station I_1 (Table 7).

4. Discussion

The macrobenthic fauna in Monolimni lagoon was mainly composed of about 12–13 taxa. Almost all the collected species can be considered as euryhaline and are common and frequently abundant inhabitants of the Mediterranean coastal brackish habitats. However, most of these taxa have never been reported with this high level of density from habitats sustaining such low salinities for long periods (*e.g.* MARAZANOF, 1969; DIVIACCO, 1983; GRAVINA *et al.*, 1988; CUNHA and MOREIRA, 1995). Based on the results of the faunal composition, the whole macrozoobenthic community – can be classified to the "euryhaline and eurythermal biocoenosis in brackish waters" as defined by PERES (1967). Assemblages exhibiting the same set of characters (small number of species, high dominance of a few species, relatively low diversity) have been previously described from several brackish habitats throughout the Mediterranean (*e.g.* REIZOPOULOU *et al.*, 1996; KEVREKIDIS, 1997; MISTRI *et al.*, 2001). Maximal monthly total abundances of macrozoobenthos in Monolimni lagoon were among the highest ones recorded in several Mediterranean lagoons (*e.g.* REIZOPOULOU *et al.*, 1996; TAGLIAPIETRA *et al.*, 1998; BACHELET *et al.*, 2000).

The macrozoobenthic community in Monolimni lagoon showed a rather homogeneous composition throughout the year. Community structure showed an almost even seasonal periodicity. Seasonal changes in the community pattern were caused by the pronounced seasonal fluctuations in densities of the most abundant species and the absence of a few ones mainly in late spring and summer. Similarly, in some other Mediterranean brackish habitats with higher salinities, species composition did not change seasonally but the densities of the same species have been reported to fluctuate widely (*e.g.* NICOLAIDOU *et al.*, 1985; GOUVIS *et al.*, 1997; KEVREKIDIS, 1997).

The seasonal dynamics of the faunal assemblage in the outer, southernmost part of Monolimni lagoon was mainly governed by water temperature and on the more by the synergistic effect of water temperature and water depth. Temperature along with photoperiod provide a seasonal cue for the induction and termination of reproduction of the marine organisms in most temperate latitudes (*e.g.* DE MARCH, 1977; MOORE, 1981) and therefore for community changes (*e.g.* WHITLATCH, 1977). The available information on the reproductive biology and life history of the most abundant species indicates that the observed density fluctuations of these species is expected to be mainly a result of their life cycle (*e.g.* KEVREKIDIS and KOUKOURAS, 1988/89; 1992; SARDA and MARTIN, 1993; ABRANTES *et al.*, 1999).

In the outer, southernmost part of Monolimni lagoon depth showed a low monthly fluctuation (50–70 cm) during most of the sampling period; it had its highest value in April (85 cm) being almost the only environmental variable, which exhibited a comparatively extreme value in that month. The temporal increase in depth was probably due to an increased freshwater inflow, which most probably resulted in a sudden intense sedimentation. That sedimentation was possibly responsible for the temporal impoverishment of the macrobenthic fauna in April which was characterized by the disappearance of bivalves and the decrease in abundances of most of the other taxa and was also reflected as a depression of community indices. The combination of water temperature and depth with pH also showed a positive correlation with community structure. The highest pH values (~9) occurred in mid and late winter coincided with a decline in macrofaunal abundance; in several Mediterranean brackish habitats pH showed values lower than 8.7 throughout the year (*e.g.* KEVREKIDIS and KOUKOURAS, 1989; ARVANITIDIS *et al.*, 1999).

The main structuring factors of the macrobenthic community in the shallower, innermost northern part of Monolimni lagoon were temperature along with predation pressure mostly by crabs (*Carcinus aestuarii*), but as well as by gobies (*Knipowitschia caucasica*). *Carcinus aestuarii*, which is a seasonal migrant, was found from May to October, having higher abundances in May – June, while *K. caucasica* also showed highest abundances in May–June; this goby, which is a sedentary lagoonal species, breeds from the end of April to the end of July (KEVREKIDIS *et al.*, 1990). In addition, high summer temperatures increase the feeding activity of predators (ARIAS and DRAKE, 1994). Therefore, increased predation pressure during early summer probably was responsible for: (a) the temporal decline in total abundance in July, (b) the different grouping of the summer samples in station B_2 in relation to that in station I_1, where water temperature itshelf was the main structuring factor. The role of predation by crabs and small fish in regulating the dynamics of macrobenthic fauna (top – down control), particularly in summer, in brackish water habitats has been stated by many authors (*e.g.* WILTSE *et al.*, 1984; AARNIO and BONSDORFF, 1993; SARDA *et al.*, 1996).

In the shallower, innermost northern part of Monolimni lagoon, no variable correlated with community structure showed an extreme value during August, when a faunistic change was recorded. This change was characterized by a sharp decline in the abundances of *Corophium orientale*, *Streblospio shrubsolii* and Tubificidae and an increase in those of the very resistant Chironomidae larvae and the epibenthic *Gammarus aequicauda*. Extreme values of a non–measured variable, such as low oxygen concentrations at night due to high temperatures and intense respiration rhythm of the large amount of *Ruppia maritima* (see CUNHA and MOREIRA, 1995), could be possibly responsible for that change. Nevertheless, a dystrophic crisis was not observed during late summer in Monolimni lagoon.

A few species of the assemblage (*e.g. Corophium insidiosum*, *Polydora ciliata*) were not found mainly from mid-spring to early autumn in Monolimni lagoon; the disappearance of these species led to a depression of most community indices. The increase in water temperature during spring should not be considered responsible for that disappearance. Extremely low salinities (<1 psu) over a long period (late winter and spring) were probably responsible. *Polydora ciliata* has been previously found in Mediterranean brackish habitats in salinities higher than 3 psu (*e.g.* GRAVINA *et al.*, 1988; NICOLAIDOU and PAPADOPOULOU, 1989). In Biguglia lagoon, Corsica, 95% of the population of *C. insidiosum* disappeared due to a sharp decline in salinity (from 34 to 1.7 psu) and increased current velocity (CASABIANCA, 1972/73). Salinity increase during summer (1–5.5 psu) was followed by the reoccurrence of these species mainly in the outer part of Monolimni lagoon with a time lag; immigration and transportation of larvae from the marine environments surrounding the lagoon probably resulted in the recolonization of the populations of *C. insidiosum* and *P. ciliata*, correspondingly (KARAKIRI and NICOLAIDOU, 1987; LAGADEUC and BRYLINSKI, 1987). This time lag might be responsible for the positive but not strong correlation between salinity and community structure. Salinity increase during summer coincided with an increase in most community indices.

The abundance of the macrobenthic invertebrates in northerly habitats usually increases during the warmest period of the year following the increase in their reproductive activity (*e.g.* ZAJAC and WHITLATCH, 1982). In the Mediterranean brackish habitats, the breeding season widens, but macrofauna usually experiences extreme environmental conditions (*e.g.* high temperature and salinity, low oxygen concentration) and predation pressure during summer (*e.g.* ARIAS and DRAKE, 1994); as a consequence, a reduction in number of species and individuals, even a total disappearance of benthic fauna, usually occurs in late summer (*e.g.* GUELORGET and MICHEL, 1979a; LARDICCI *et al.*, 1997; TAGLIAPIETRA *et al.*, 1998). Macroinvertebrate abundance in Mediterranean brackish habitats frequently displayed a seasonal variation with a peak in winter or spring (*e.g.* GUELORGET and MICHEL, 1979a) and sometimes a second peak in autumn (*e.g.* GUELORGET and MICHEL, 1979a; 1979b; GOUVIS *et al.*, 1997; MISTRI *et al.*, 2001). However, seasonal patterns with a peak in abundance in mid or late autumn have been also observed (*e.g.* GUELORGET and MICHEL, 1979a; KEVREKIDIS, 1997; present study). The increase in total abundance during spring at salinities of about 0.3 psu in Monolimni lagoon indicates that most community species are highly tolerant to extremely low salinities and the assemblages only partly were directly affected by the extremely low salinities.

As hypothesized, the macrozoobenthic community in Monolimni lagoon displayed a rather homogeneous composition throughout the year; seasonal changes in community structure were mainly caused by the pronounced fluctuations in densities of the same species and governed by water temperature. However, community structural changes were also caused by the absence of some, less tolerant, species in spring, after a long period of extremely low salinities; additionally, temporary changes followed an increase in depth, an increase in abundance of epibenthic predators (crabs and gobies) in early summer and possible low oxygen concentrations at night in late summer.

5. Conclusions

To summarize, the following conclusions could be derived:

1. The macrozoobenthic assemblages in Monolimni lagoon were characterized by a small number of species, high dominance of a few species and relatively low diversity. Total abundance showed a seasonal variation with a peak in mid or late autumn; its maximum monthly values were among the highest ones recorded in Mediterranean lagoons.
2. Community structure displayed an almost even seasonal periodicity. Seasonal changes were mainly due to the pronounced fluctuation in abundance of the most species and, additionally, to the non – occurrence of a few ones in spring and summer.
3. Most species showed to be highly tolerant to extremely low salinities. The vanishing of a few species in spring was possibly the only direct impact of the extremely low salinities (~0.3 psu) occurred in late winter and spring on community structure. Salinity increase during summer coincided with an increase in most community indices.
4. The seasonal dynamics of the faunal assemblage in the deeper outer part of the lagoon was mainly governed by water temperature, which strongly affects the life cycle of the species. A temporary increase in depth was possibly responsible for an impoverishment of the fauna in April.
5. The main structuring factors of the community in the innermost part, where a *Ruppia maritima* meadow occurred, were water temperature and predation pressure mostly by crabs but as well as by gobies. That pressure was probably responsible for a decline in total abundance in July.

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