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Zooplankton dynamics in a gypsum karst lake and interrelation with the abiotic environment

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Abstract: Zooplankton species composition and abundance variation was studied in Lake Amvrakia, which is a deep, temperate, gypsum karst lake situated in the western Greece. The two year survey of zooplankton revealed 33 species (23 rotifers, five cladocerans, four copepods and one mollusc larva). The mean integrated abundance of the total zooplankton ranged between 83.6 and 442.7 ind. L^{-1}, with the higher density to be recorded in the surface 0–20 m layer. Small numbers of specimens of almost all species were found also in the hypoxic or anoxic hypolimnion. Copepods and especially the calanoid *Eudiaptomus drieschi* dominated the zooplankton community throughout the sampling period, followed by *Dreissena polymorpha* larvae, rotifers and cladocerans. Seasonal succession among the cladocerans and the most abundant rotifer species was observed. The concentration of chlorophyll-*a* was the most important factor for the variation of total zooplankton, as well as for the rotifers' community. Dissolved oxygen affected copepods and cladocerans, water level correlated mainly with the molluscs larvae of *D. polymorpha*, while temperature influenced the variation of several rotifers, the cladoceran *Diaphanosoma orghidani* and the mollusc larvae. Negative correlation of conductivity with the cladoceran *Daphnia cucullata* and the copepods *E. drieschi* and *Macrocyclops albidus* was found. The differences in species composition found in Lake Amvrakia in comparison to the nearby lakes are probably ought to the geographical isolation and perhaps to its particular chemistry (e.g., elevated conductivity).

Key words: zooplankton; seasonal variation; gypsum lake; abiotic parameters

Introduction

Zooplankton occupies the centre of the aquatic food web, being important as food for almost all freshwater fish at some stage in their life history, while at the same time grazing on algae, bacteria, protozoa and other invertebrates (Lampert & Sommer 1997). Studies of zooplankton communities may be useful in the prediction of long term changes in lake ecosystems (Ferrara et al. 2002; Preston & Rusak 2010), as these communities are highly sensitive to environmental variation. Thus, changes in abundance, species diversity and community composition can provide important indications of environmental change or disturbance.

Although many studies have been conducted in several lakes, multiscale, spatial and temporal relationships between zooplankton variability and environmental heterogeneity are still not satisfactorily understood. The reasons for this lie to the complexity of the different aquatic ecosystems worldwide (considering both biotic and abiotic elements), while this complexity increases when considering global climate change (Preston & Rusak 2010; Huber et al. 2010). Consequently, one is unable to forecast the exact time, place, composition and proportions of different zooplankton species that occur in a given lake. Yet, it is important to investigate the main factors that may govern the biology and ecology of these organisms especially in particular freshwater ecosystems, in order to have a better possibility to predict future changes, which might influence the biodiversity worldwide.

Gypsum karst lakes are characterized as sulphate lakes, being rich in gypsum or calcium sulphate and having elevated conductivity values. These particular ecosystems escape the attention of the investigators mostly because they are man-made, usually a result of surface mining gypsum, and consequently studies of the zooplankton of such areas are scarce (Kuznetsova & Bayanov 2001; Zurek 2006; Stanković et al. 2010). The latter authors found that the gypsum karst lakes are unique ecosystems that can even have different community composition compared to other nearby karstic lakes. Thus, they can represent some of the most interesting biotopes from the biodiversity point of view, though the actual weight of their importance has not been thoroughly evaluated.

Lake Amvrakia (38°45′ N, 21°11′ E) is a warm monomictic lake, located in western Greece having a catchment area of 112 km^2 and maximum depth of about 50 m. The lake belongs to the Sulphate type (Overbeck

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et al. 1982) and is unique among the Greek lakes having the highest concentration of sulphates (Zacharias et al. 2002), which derive from extensive gypsum sediments especially in its western banks. From the hydrological point of view, the lake is supplied by water only from precipitation and surface runoff, while there are strong water level fluctuations due to high evaporation rates especially during the summer and the irrigation of the surrounding agricultural area year-round. These variations usually result in periodic drainage of the shallower northern part of the basin and, consequently, fluctuation of actual surface area of the lake, which on average lies between 1,400 and 2,200 ha. The intense cultivation of tobacco plants in the agricultural areas around Lake Amvrakia during the past years and the extensive land wash by the irrigation drainage waters resulted probably to the increase of the organic loads draining into the lake. The isolation of Lake Amvrakia from the other lakes of the region, along with the existing special physicochemical constants and geomorphology, has resulted to the presence of endemic species of phytoplankton (Spartinou 1992).

The improvement of freshwater ecosystems, such as the gypsum lakes, is one of the aims of the EU Water Framework Directive (WFD) 2006/60/EC. Lake Amvrakia seems to have all the characteristics of an interesting ecosystem, however, there have been only two studies during the last forty years (Overbeck et al. 1982; Danielidis et al. 1996), dealing mainly with the abiotic features and the phytoplankton of the lake, while data on the zooplankton community were scarce and fragmentary (Koussouris 1978; Danielidis et al. 1996). Considering that, the study of the biological components of a water body can produce useful information towards its quality improvement and efficient management, the present study provides novel and comprehensive information on the community structure and spatial and temporal distribution of zooplankton, through an extensive two-year investigation. Moreover, there was an effort to investigate the possible influence of the main environmental forces on the zooplankton variation. Finally, we speculate on what extent the particular environment of a gypsum karst lake, along with its geological isolation, could have affected the community composition and/or other ecological aspects of these organisms.

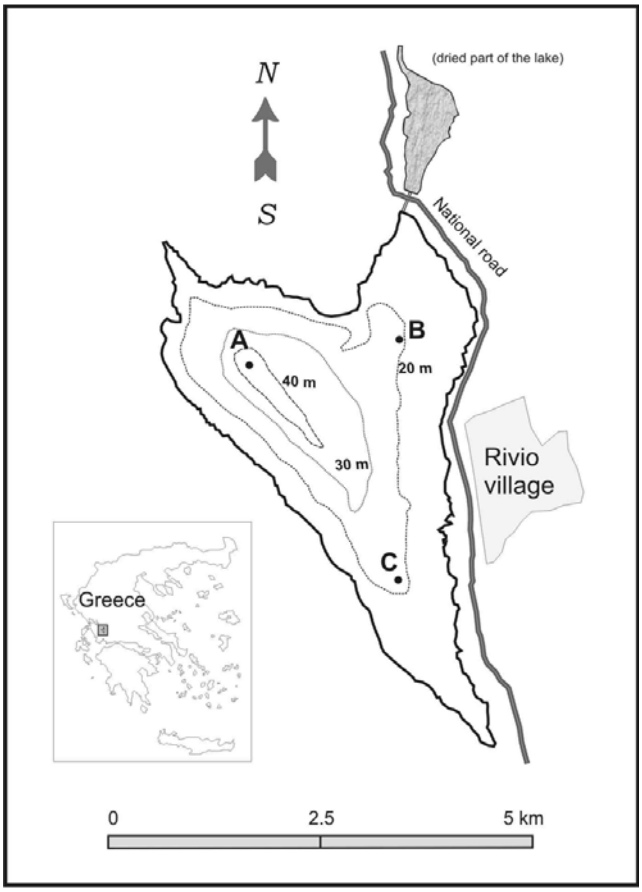

Fig. 1. Amvrakia Lake with the three sampling stations (A, B, C).

Material and methods

Zooplankton samples were collected monthly during a two year period (September 2006 to August 2008) from three stations A, B and C with maximum depths of 50, 22 and 21 m, respectively (Fig. 1). The samples were collected with vertical hauls conducted at 5 m depth intervals from near the bottom (40 m in station A) to the surface for each station using a HYDROBIOS plankton net (20 cm in diameter, 100 cm in length, 50 μm mesh size) with a closing mechanism. The net was towed at a speed of approximately 0.5 m s^{-1}. All samples were taken in the morning and were fixed in 4% formalin. The zooplankton specimens were examined microscopically and were identified to the lowest taxonomic level possible. For the abundance analysis, three counts of 1.5 ml subsamples were made on a Sedwick-Rafter cell from each sample having a total volume of 100 ml (Doulka & Kehayias 2008).

Vertical profiles of water temperature, pH, conductivity and concentration of dissolved oxygen (DO) were taken at all stations using a TROLL 9500 water quality instrument. The water transparency was measured with a Secchi disc. For the estimation of total phosphorus (TP), phosphates (PO_4), nitrates (NO_3), nitrites (NO_2), ammonia (NH_4) and silicates (SiO_2), water samples were collected at the deepest station A from 0, 5, 10, 15, 20, 30 and 40 m with a 5 L HYDROBIOS water sampler. Analyses of all chemical parameters were performed according to APHA, AWWA & WPCF (1998). For the determination of chlorophyll-*a* concentration (chl-*a*), 1500 ml of the water samples taken from the above depths was filtered through a Whatman GF/A glass fiber filter shortly after collection. Pigment extraction was made in 90% acetone and concentrations were determined spectrophotometrically (APHA, AWWA & WPCF 1998). The trophic classification of the lake was estimated using Caslon's trophic state index (TSI) for total phosphorus, chl-*a* and transparency (Carlson 1977).

In order to ascertain the structural features of the zooplankton community the Shannon-Wiever diversity index H' (Maguran 1988), was calculated for each sampling station and date:

$$H' = -\sum_{i=1}^{S} (p_i \ln p_i)$$

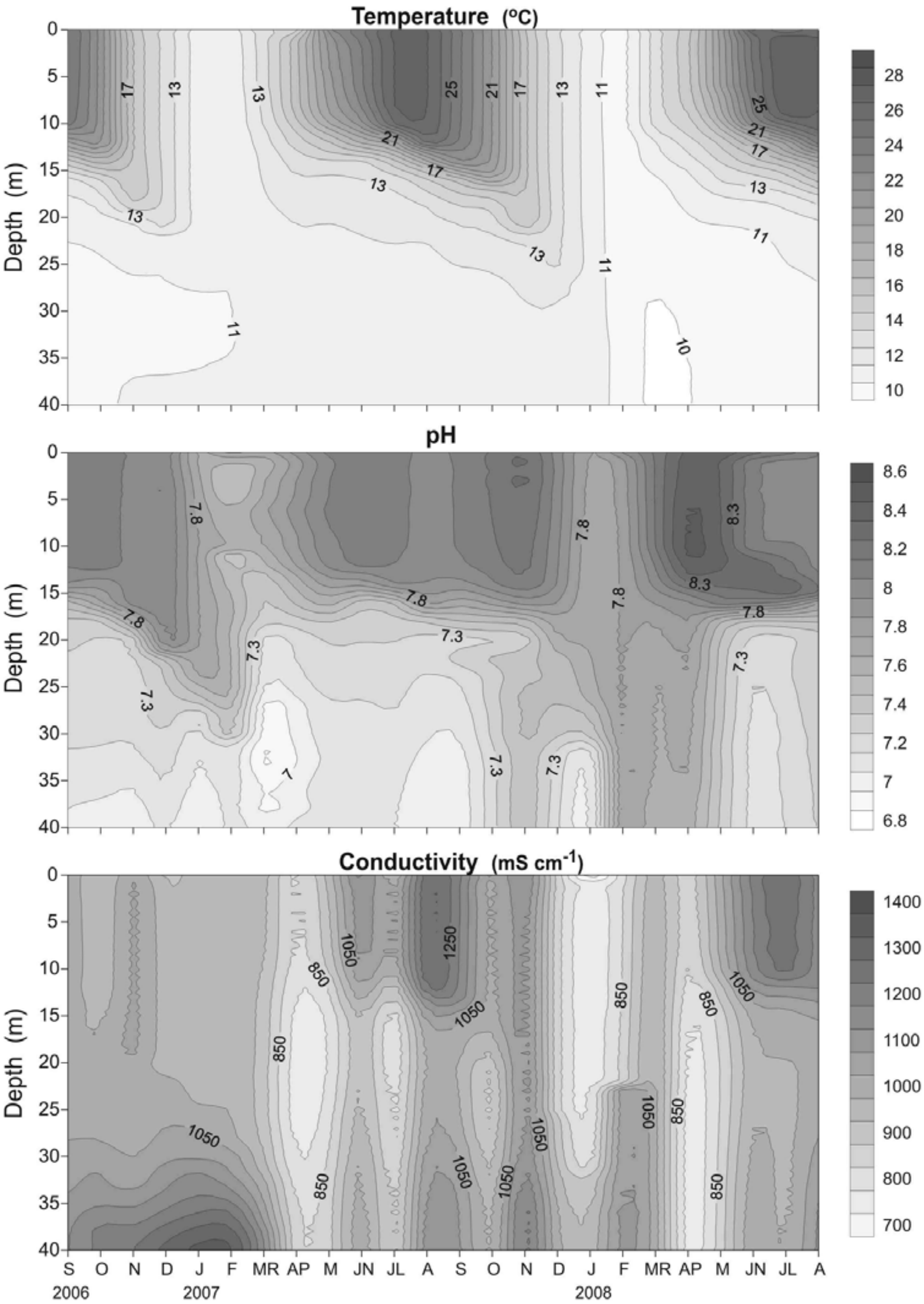

Fig. 2. Seasonal fluctuation of temperature (℃), pH and conductivity (μS cm^{-1}) in the water column of station A during September 2006 to August 2008.

where H' is the diversity index and p_i the relative abundance of each species (i) in a sample.

The non-parametric Kruskal-Wallis and Mann-Whitney U-test were used for investigating differences in the environmental parameters and in the abundance of zooplankton species and groups among the three stations and between the two sampling periods (September 2006 – August 2007 and September 2007 – August 2008). Multiple regression analysis was used to ascertain the influence of the environmental factors on each of the zooplankton species. All data analyses were performed with SPSS 17.0 (SPSS, Inc. 2008) statistical package.

Results

Physicochemical parameters

The temperature in Lake Amvrakia fluctuated between 9.68 and 28.33℃ (February and July 2008, respectively). The annual cycle of thermal stratification showed a monomictic regime for both sampling years, with the establishment of a thermocline layer from April to November within the range of 10–20 m (Fig. 2). During the winter turnover the lake was well oxygenated through almost the entire water column. In contrast, during the stratification period the DO in

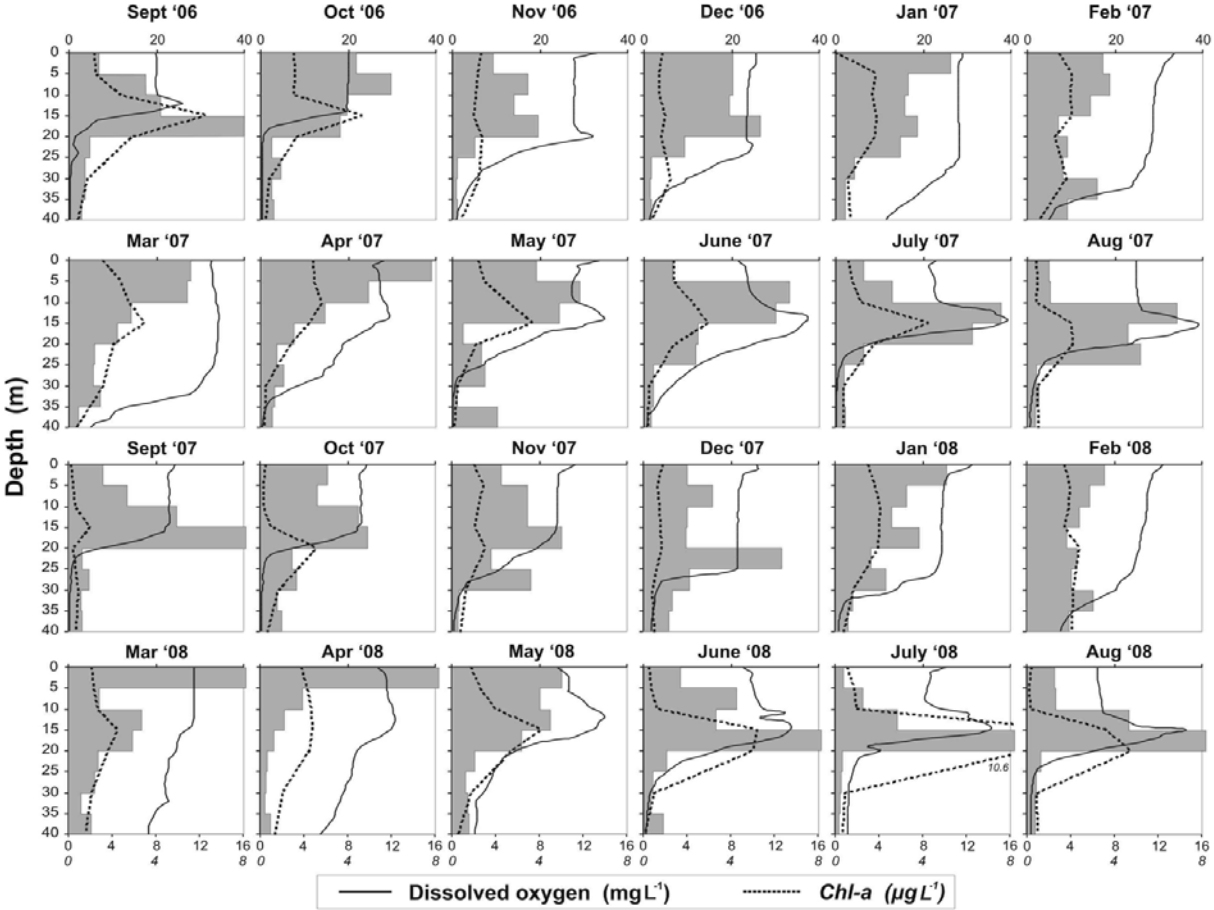

Fig. 3. Vertical profiles of DO (mg L^{-1}) and chl-a (μg L^{-1}) in station A during the sampling period (September 2006 – August 2008). The shadowed area presents the vertical distribution of the total zooplankton in station A as percentages (%) of total caught in water column sampled.

the hypolimnetic layer decreased leading to hypoxic or even anoxic conditions under 30 m, especially in autumn (Fig. 3). The maximum concentration of dissolved oxygen was recorded in July 2007 (15.73 mg L^{-1}) within the metalimnetic layer. The values of pH ranged from 6.87 in the hypolimnion in March 2007, to 8.67 in the surface waters in November 2006. In the vertical axis, higher pH values were recorded in the epilimnion during the stratified period, while they were almost constant in the whole water column during the mixing period (Fig. 2). Conductivity fluctuated between 643.1 μS cm^{-1} in January 2008 (epilimnetic layer) and 1367 μS cm^{-1} in February 2007 in the hypolimnion. During the stratified period, higher values were found in the epilimnion, while during the mixing period there was an increase on conductivity with depth (Fig. 2). The water transparency, as indicated by the Secchi disc depth, ranged from 3.5 m in May and in June 2007 to 10.5 m in June 2008. There was a statistically significant difference between the two sampling years in the water level recorded at station A (U-test, $P = 0.000$), which declined from 49.6 m in December 2006 to 42.9 m in August 2008. For all the above parameters, there were no differences between the three sampling stations (Kruskal-Wallis test, $P > 0.05$).

The chl-a fluctuated between 0.004 μg L^{-1} in January 2007 at the surface to 10.57 μg L^{-1} in July 2008 in the 15 m, always being higher in the metalimnetic layer during the stratification period, while having a uniform distribution during the mixing period (Fig. 3). The concentration of phosphates (PO_4) in the water was greater in winter and in the mid-summer, reaching up to 0.167 mg L^{-1} in December 2006. Nitrates (NO_3) and nitrites (NO_2) showed intense variation and their concentration fluctuated between undetected values to 1.376 and 0.042 mg L^{-1} in January 2008 and in November 2006, respectively. The concentration of ammonia (NH_4) generally presented low values except in April 2008 when the highest value of 0.165 mg L^{-1} was observed in the deepest part of the lake (40 m). The concentration of total phosphorus (TP) presented the highest value of 264.69 μg L^{-1} in October 2006 in 40 m of depth. In the vertical axis, the general trend for all the above chemical parameters was to present lower values in the epilimnion and higher in the meta- and hypolimnion during the stratified period, while their concentration was more uniform during turnover. The concentration of silicates (SiO_2) presented higher values in July for both sampling years with the greatest accumulations recorded always in hypolimnetic depths. There were no statistically significant differences (U-

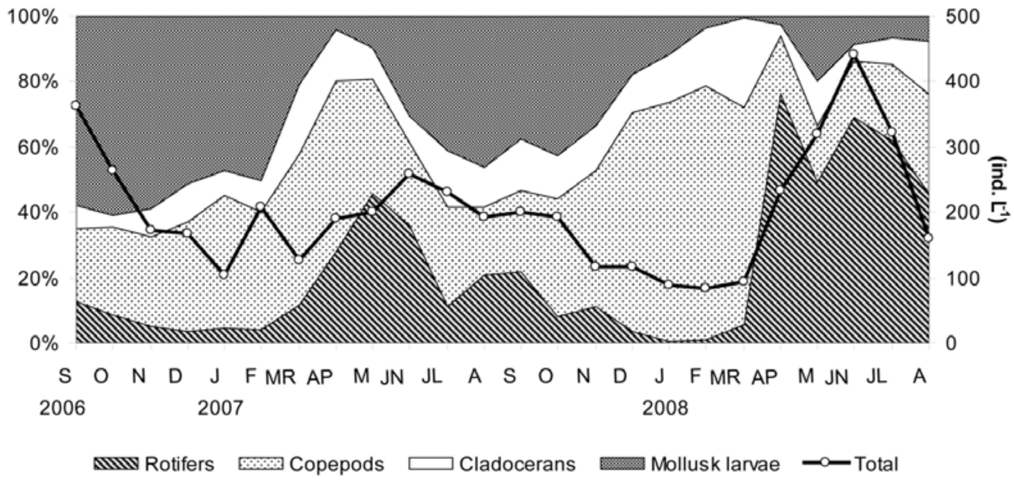

Fig. 4. Seasonal variation of the total zooplankton abundance (ind. L^{-1}) and percentage (%) contribution of the main zooplanktonic groups during September 2006 to August 2008.

test, $P < 0.05$) between the two sampling periods in the concentration of none of the chemical parameters mentioned.

The Carlson index (TSI) for the concentration of total phosphorus (TP), transparency (SD) and chl-*a*, varied between 29.8 to 61.9, 26.1 to 40 and 11 to 39.6, respectively. Between the two sampling periods there were no statistically significant differences apart from TSI (SD) which had higher values in the first sampling period from September 2006 to August 2007 (*U*-test, $P = 0.028$). The values of TSI index classifies Lake Amvrakia between oligotrophic and mesotrophic level.

Zooplankton species composition and variability

The two years of investigation in Lake Amvrakia revealed 33 zooplanktonic invertebrate species which comprised four groups; 23 rotifers, five cladocerans, four copepods and one mollusc larva (Table 1). Shannon diversity index (H') ranged from 0.97 to 2.4 showing generally lower values during autumn and winter and higher during the warm months. There were no statistical differences of this index among the three stations (Kruskal-Wallis test, $P > 0.05$), or among the two years of investigation (*U*-test, $P = 0.525$). The mean integrated abundance of the total zooplankton ranged between 83.6 and 442.7 ind. L^{-1} (Fig. 4). There were no statistically significant differences in the abundance for the total zooplankton and any of the species between the three stations (in the 0–20 m depth layer) during the whole sampling period (Kruskal-Wallis test, $P > 0.05$). The abundance of the total zooplankton showed a decrease after September 2006, remained low during fall and winter and increased at the beginning of spring in both sampling periods (Fig. 4). This seasonal fluctuation followed the monoacmic pattern with a peak in June, which was the result of the increase of rotifers. There were no statistically significant differences in the mean integrated abundance of the zooplankton groups between the two sampling periods, except for the mollusc larvae of *Dreissena polymorpha* (Pallas,

Table 1. List of the zooplankton species found in Lake Amvrakia.

Rotifera
Asplanchna priodonta (Gosse, 1850)
Bdelloida
Brachionus angularis (Gosse, 1851)
B. calyciflorus (Pallas, 1766)
Collotheca sp.
Conochilus unicornis (Rousselet, 1892)
Euchlanis sp.
Fillinia longiseta (Ehrenberg, 1834)
H. mira (Hudson, 1871)
H. intermedia (Wiszniewski, 1929)
Kellicottia longispina (Kellicott, 1879)
Keratella cochlearis (Gosse, 1851)
Keratella tecta (Gosse, 1851)
Keratella tropica (Apstsein, 1907)
Keratella quadrata (Müller, 1786)
Lecane luna (Müller, 1776)
Notholca squamula (Müller, 1786)
Ploesoma hudsoni (Imhof, 1891)
Polyarthra sp.
Pompholyx sulcata (Hudson, 1885)
Synchaeta sp.
Trichocerca sp.
T. similis (Wierzejski, 1893)
Copepoda
Eudiaptomus drieschi (Poppe et Mrazek, 1895)
Harpacticoida
Macrocyclops albidus (Jurine, 1820)
Thermocyclops dybowskii (Landé, 1890)
Cladocera
Alona sp. (Baird, 1843)
Bosmina longirostris (O.F.Muller, 1785)
Ceriodaphnia pulchella (Sars, 1862)
Daphnia cucullata (G.O. Sars, 1862)
Diaphanosoma orghidani (Negrea, 1982)
Mollusca
Dreissena polymorpha (Pallas, 1771)

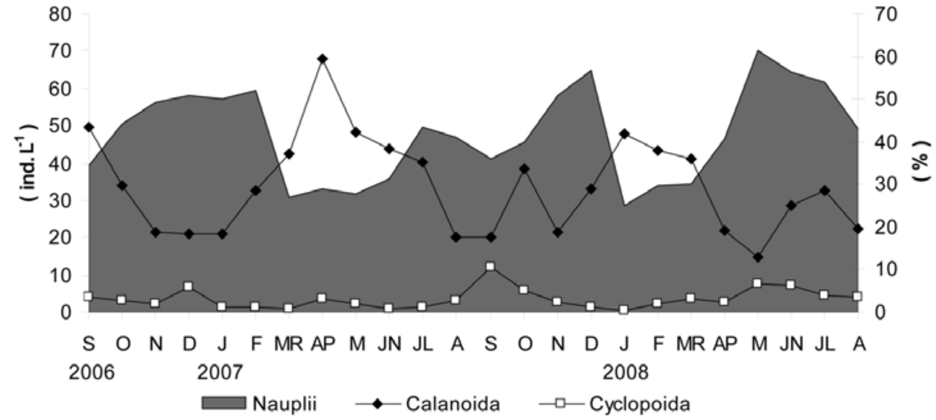

Fig. 5. Seasonal variation of the abundance (ind. L^{-1}) of the calanoid *Eudiaptomus drieschi* and the cyclopoid copepods, and the proportions (%) of nauplii in the copepods community during September 2006 to August 2008.

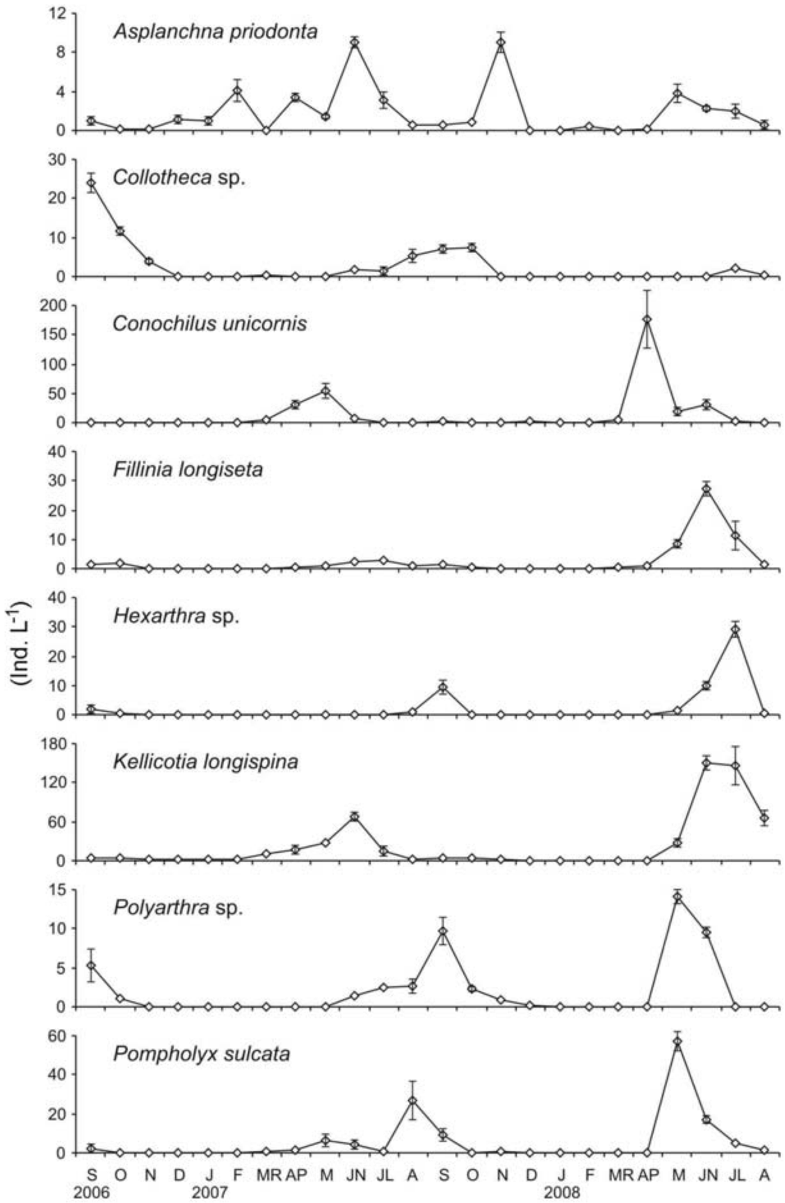

Fig. 6. Seasonal variation of the average abundance (ind. L^{-1}) of the eight most important rotifer species during September 2006 to August 2008. Vertical bars account for the standard error.

1771), which showed higher values in 2006–2007 (*U*-test, $P < 0.05$).

Considering the vertical distribution of the total zooplankton in the deeper station A, higher abundance values were recorded in the surface 0–20 m layer and decreased with depth (Fig. 3). During the stratification period the zooplankton aggregated close to or within the thermocline layer, where chl-*a* and oxygen concentrations were higher, while the vertical distribution of all groups in winter was rather uniform. There were no differences in the vertical distribution of the zooplanktonic groups between the two sampling periods (*U*-test, $P > 0.05$). It is interesting to note that, although the general diminishing of zooplankton abundance with the increase of depth, representatives of most of the species found in the upper layers were also present in the hypoxic (and sometimes anoxic) deeper layers.

Copepods had the highest average proportion within the zooplankton community accounting for 33.1% in 2006–2007 and 41.1% in 2007–2008 (Fig. 4), followed by *D. polymorpha* larvae (39.9 and 16.0% in 2006–2007 and 2007–2008, respectively), rotifers (15.9 and 29.4%, respectively) and cladocerans (11.0 and 13.5%, respectively). The calanoid *Eudiaptomus drieschi* (Poppe et Mrazek, 1895) was the dominant species throughout the sampling period (Fig. 5) accounting on average for 51.4% in the copepod community, while the cyclopoid species *Macrocyclops albidus* (Jurine, 1820) and *Thermocyclops dybowskii* (Landé, 1890) had considerably lower contribution (3.2 and 3.0%, respectively). The maximum abundance for *E. drieschi* was recorded in late winter to early spring in both years, while the peaks of abundance for the two cyclopoid species always coincided with the lowest values of *E. drieschi* (Fig. 5). The nauplii of all species were present in considerable numbers all year round and accounted on average for 42.5%, while always having greater proportions 1–2 months prior to the abundance maximum of *E. drieschi* (Fig. 5). Egg-bearing females of *E. drieschi* were present throughout the sampling period.

The mean abundance of rotifers ranged from 0.1 to 397.5 ind. L^{-1} (January and June 2008, respectively), while there were no statistically significant differences in the abundance between the two sampling periods for the most abundant species (*U*-test, $P < 0.05$). *Kellicotia longispina* (Kellicott, 1879) and *Conochilus unicornis* (Rousselet, 1892) were the numerically most important species accounting for 33.0 and 20.2%, respectively in the rotifer's community. *Asplanchna priodonta* (Gosse, 1850), *Collotheca* sp. and *Pompholyx sulcata* (Hudson, 1885) accounted for 11.0, 10.6 and 8.9%, respectively, while *Fillinia longiseta* (Ehrenberg, 1834), *Polyathra* sp. and *Hexarthra* sp. accounted together for 10.5%. Most of these species showed a distinct pattern of seasonal variation in both sampling periods having higher abundance in spring to early summer, while in late autumn and winter they were present in low numbers. However, the peaks of abundance for most of the species were recorded in different sampling dates presenting a seasonal succession (Fig. 6).

The mean abundance of cladocerans ranged between 3.7 ind. L^{-1} in January 2007 to 71.8 ind. L^{-1} in July 2007. *Diaphanosoma orghidani* (Negrea, 1982) was dominant in the warmer periods and accounted on average for 37.8% in the cladoceran's community, followed by*Bosmina longirostris* (Müller, 1785) and *Daphnia cucullata* (Sars, 1862), which were more abundant in the colder months and accounted for 28.9 and 16.1%, respectively (Fig. 7). *Ceriodaphnia pulchella* (Sars, 1862) accounted for 17.3% and showed three peaks of abundance in December 2006, 2007 and in July 2008, while *Alona* sp. (Baird, 1843) specimens were sporadically found in the samples. Finally, larvae of the mollusc *D. polymorpha* were present in the zooplankton throughout the sampling period (Fig. 4), reaching maximum of abundance in February 2007 (251.2 ind. L^{-1}), while the lowest value in March 2008 (0.09 ind. L^{-1}).

Influence of physicochemical parameters on zooplankton

Among the environmental parameters, chl-*a*, DO, water level and temperature seemed to have the most important influence on the temporal and vertical distribution of most of the zooplankton taxa (Table 2). Chl-*a* was the most important factor for the total zooplankton, as well as for the rotifers' community, affecting *K. longispina*, *Hexarthra* sp. and *Keratella* sp., the copepod *M. albidus* and the cladoceran *C. pulchella.* The concentration of DO was the most important factor for total copepods, especially *E. drieschi*, and also for total cladocerans. There was a strong positive correlation of the water level with *D. polymorpha* larvae and *Collotheca* sp., while it was negatively correlated with several rotifer species and with *B. longirostris.* Temperature affected mostly the rotifers *Collotheca* sp., *Polyarthra* sp. and *T. similis* (Wierzejski, 1893), the cladoceran *D. orghidani* and the mollusk larvae of *D. polymorpha.* Among the other parameters, transparency was the most important factor for several rotifer species, while pH seems to play an important role for *C. unicornis*, *Th. dybowskii* and *D. cucullata.* The nutrients PO_4, NO_3 and NO_2 have always negative effects to various species, while SiO_2, showed positive correlation with the rotifers *K. longispina* and *Hexarthra* sp. (Table 2).

Discussion

Physicochemical parameters

Lake Amvrakia is a deep temperate lake having a short period of turnover from late November to March, as it was previously reported by Overbeck et al. (1982) and Danielidis et al. (1996). The size of the lake and the water circulation (Verginis & Leontaris 1978) probably resulted in the absence of horizontal differences of physiochemical parameters such as, transparency, temperature, DO, pH and conductivity. The main characteristic in the vertical axis was the depletion of oxygen in the deeper hypolimnion, where anoxic conditions prevail, especially at the end of the

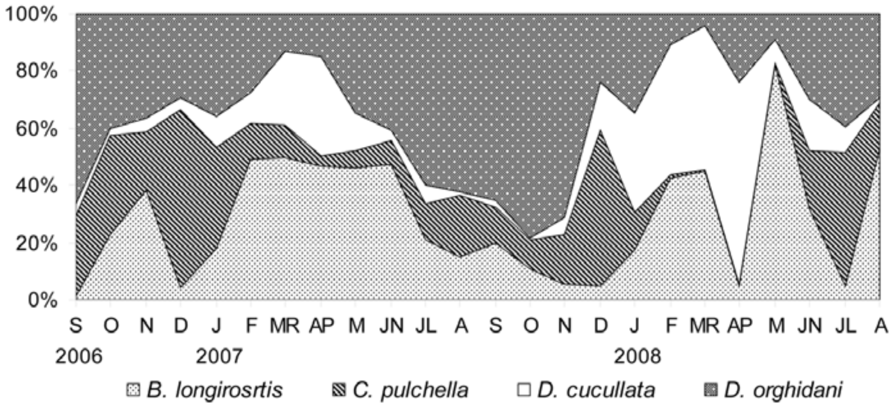

Fig. 7. Seasonal percentage (%) contribution of the cladoceran species *Bosmina longirostris*, *Ceriodaphnia pulchella*, *Daphnia cucullata* and *Diaphanosoma orghidani* to the abundance of the community during September 2006 to August 2008.

Table 2. Multiple regression analysis between the environmental factors (temperature, DO, pH, conductivity, transparency, water level, chl-*a*, NO_3, NO_2, NH_4, PO_4, SiO_2) and the zooplankton species/groups.

Species/Groups	Temp.	DO	pH	Cond.	Trans.	WL	Chl-*a*	NO_3	NO_2	NH_4	PO_4	SiO_2	r^2	df
A. priodonta		0.27**		0.25**									0.122	141
Collotheca sp.	0.68**	–0.38**				0.45**					–0.31**		0.485	139
U. unicornis			0.39**	–0.31**									0.223	141
F. longiseta						–0.26**				–0.22**			0.128	141
Hexartha sp.					0.39**	–0.16*	0.47**					0.21**	0.356	139
K. longispina	0.29**				0.17**		0.68**		–0.22**			0.35**	0.534	138
Keratella sp.					0.49**	–0.19**	0.39**						0.382	140
Polyarthra	0.41**				0.36**								0.326	141
P. sulcata					0.34**	–0.26**	0.24**		0.19*				0.297	139
T. similis	0.25**					0.19*							0.078	141
Rotifera	0.48**			–0.18*	0.20**		0.49**		–0.25**				0.474	138
E. drieschi		0.35**		–0.19**			0.34**	–0.19*					0.529	139
M. albidus			0.18**	–0.21**	0.30**		0.50**		–0.20**				0.428	138
Th. dybowskii		0.31**	–0.51**										0.141	141
Nauplii		0.31**					0.17*			–0.15*	–0.18*		0.358	139
Copepoda		0.34**		–0.18**			0.27**	–0.14*			–0.16*		0.542	138
B. longirostris		0.22**			–0.17*	–0.24**							0.110	140
C. pulchella	0.23**				0.22**	0.25**	0.38**		–0.24**				0.267	138
D. cucullata			0.34**	–0.27**			0.30**						0.344	140
D. orghidani	0.58**				0.17*	0.19**	0.15*						0.402	138
Cladocera	0.29**	0.34**					0.18*	–0.17*					0.450	139
D. polymorpha	0.62**				0.23**	0.53**	0.27**		–0.18**				0.591	138
Total zooplankton	0.23**	0.24**					0.34**	–0.19*		–0.20**			0.578	138

Explanations: * $P < 0.05$, ** $P < 0.01$.

prolonged summer stratification. The anoxic conditions in the deeper layers were accompanied by the presence of hydrogen sulphide (H_2S) produced not only from the decomposition activities, but also from the gypsum substrate (Danielidis et al. 1996). During the stratified period DO was higher within the metalimnion, where also the maximum concentration of chl-*a* was recorded. The high transparency of the water permits the photosynthetic activity in the metalimnion, where the phytoplankton growth is benefited by the high nutrient concentrations released by decomposition processes. As a result, oxygen production increases in this layer, where increased solubility of oxygen due to decreasing temperatures is also expected.

Generally, Lake Amvrakia seems to hold the main physicochemical features observed by Overbeck et al. (1982) and Danielidis et al. (1996), who conducted surveys in the lake about forty and thirty years ago, respectively. However, in comparison to the findings of Danielidis et al. (1996), there was an increase in the values of most of the physicochemical parameters recorded in the present study, although their patterns of variation in the water column were similar. Thus, the maximum values of temperature, DO, conductivity and chl-a have been increased by 9%, 68.3%, 26.7% and 16.3%, respectively. Moreover, there was a considerable increase of the maximum concentration of nutrients, such as phosphates (234%), nitrates (118.4%), ammonia (17.9%), silicates (823%) and TP (212%). These elevated values of nutrients in Lake Amvrakia, were probably related to the inflow of irrigation and drainage waters rich in residual fertilizers, which were used in the extensive tobacco cultivations in the surrounding areas during the past years. The higher values of chl-a found in the present study, and as a by-product, the increased DO in the metalimnetic layer could also be the result of this chronic influx of nutrients to the lake. Nevertheless, although their concentrations have been increased from the past, the trophic level of the lake has not been altered dramatically, being an oligo- to mesotrophic aquatic ecosystem (Overbeck et al. 1982; Danielidis et al. 1996).

The drop of the water level as much as 6.7 meters during the sampling period, verifies that Lake Amvrakia is subjected to intense water volume fluctuations, which are due to the evaporation and to the use of water for irrigation purposes (Danielidis et al. 1996). Still, this water level variation seemed not to have significantly affected the concentrations of the chemical parameters.

Zooplankton species composition and variability

There are two previous reports providing only qualitative data on the zooplankton community of Lake Amvrakia (Koussouris 1978; Danielidis et al. 1996). Among these studies, Koussouris (1978) reported a list of only eight rotifer species, without any descriptive information, and his data came from only one sample. Danielidis et al. (1996) provided a short note on the zooplankton species of the lake without further data on their abundance and seasonal variation. Although most of the species found in the present study have been reported by the previous authors, certain differences exist, while there were 10 new records of rotifer species and of one cladoceran (*Alona* sp.). In particular, the rotifers *Gastropus stylifer* (Imhof, 1891), *Brachionus sessilis* (Varga, 1951) and *Ptygura seminatans* (Edmonson, 1939) reported by Danielidis et al. (1996), were not found in the present study, while the cladoceran *Diaphanosoma orghidani* was probably misidentified as *D. brachyurum* (Liévin, 1848) and the larvae of *Dreissena polymorpha* as *Corbicula* sp. (von Mühlfeld, 1811) by the latter authors. Surprisingly, *Kellicotia longispina*, which was the most abundant rotifer in the present study, has not been included in the species lists of neither of the previous studies.

Due to the particular characteristics of the gypsum karst lakes and also to the lack of studies concerning their zooplankton (Kuznetsova & Bayanov 2001; Stanković et al. 2010), comparisons between such ecosystems with other nearby lakes are inevitable. Considering its faunistic composition, Lake Amvrakia showed certain differences with nearby lakes, such as Trichonis Lake (Doulka & Kehayias 2008) and Stratos Reservoir (Kehayias et al. 2008). Indeed, the rotifers *Keratella tecta* (Gosse, 1851), *K. tropica* (Apstein, 1907), *Lecane luna* (Müller, 1776) and *Notholca squamula* (Müller, 1786) and the copepod *Th. dybowskii* were found only in Amvrakia Lake. On the other hand, the predator cladoceran *Leptodora kindtii* (Focke, 1884) was absent from this area although it is common to all the other lakes of western Greece (Kehayias et al. 2008; Doulka & Kehayias 2008, unpublished data).

Looking back in the geological history of western Greece, Lake Amvrakia was part of a greater lake that had been created by the Acheloos River outflow, at the end of the Pleiocene. Later on with the gradual diminishing of the water level, it was separated from the other karstic lakes of the area and continued as a completely independent aquatic ecosystem (Verginis & Leontaris 1978), while the others are still connected by natural or man-made canals with the Acheloos River. Thus, it is possible that this long-lasting geographical isolation could have been responsible for the existence of different species of zooplankton in this basin. This has been also suggested by Spartinou (1992), who reported a great number of endemic species of algae in the phytoplankton of this lake.

On the other hand, Stanković et al. (2010) claimed that gypsum karst lakes are expected to have significantly different community composition compared to other karstic lakes, due to their chemical characteristics of water. In particular, the specific habitat characteristics of these lakes, and especially their high conductivity, can influence the crustacean's community by reducing the number of species and leading to the dominance of one of them (Stanković et al. 2010). Bielańska-Grajner & Gładysz (2011) reported also that conductivity could greatly affect both species diversity and densities of rotifers. However, in both the above studies conductivity usually exceeded 2000 $\mu S\ cm^{-1}$. The most important difference in the chemical substance in the water of Lake Amvrakia in comparison to the nearby Trichonis Lake is the 3–4 times greater conductivity of the former. Nevertheless, apart from the previously mentioned dissimilarities in the species composition between the two lakes, there are not great differences in the number of species, while the common species seem to have similar seasonal variation in the two lakes. Thus, it is more probable that the geographical isolation of Lake Amvrakia from the other lakes of the area, and in less extent its particular chemistry, could have been responsible for the present species composition in this basin. Though, investigation of the genetic differences between the populations of some of the common species in all these lakes would help in affirming this hypothesis.

Considering the zooplankton diversity, there are remarkable similarities in the maximum and minimum values and the seasonal variation of the Shannon-Wiever diversity index (H') between the nearby lakes

Amvrakia and Trichonis (Doulka 2010). These results are also similar compared with other large Greek lakes, such as Lake Mikri Prespa (Michaloudi et al. 1997). In all these cases, there is a very clear trend over time with low diversity values in late autumn and in winter, with an increase in early spring to summer. Taking into account that the increased zooplankton diversity could be an indication of internal stability of an aquatic ecosystem (Michaloudi et al. 1997), communities structured in this manner are generally characteristic of stable physicochemical environments (Ferrara et al. 2002). In contrast, shallow productive lakes where the diversity index is too low and does not exhibit a seasonal pattern, are considered as very unstable ecosystems subjected to severe stress, such as the case of Lake Koroneia in northern Greece (Michaloudi & Kostecka 2004).

The crustacean community of Lake Amvrakia was dominated by the calanoid copepod *E. drieschi*, while the cyclopoid copepods *M. albidus* and *Th. dybowskii* were present most of the time but always having low contribution to the community. Their peak of abundance coincided with the lowest values of *E. drieschi* suggesting perhaps competitive interactions. *E. drieschi* was also the dominant crustacean in the nearby Trichonis Lake, while there were great similarities in its seasonal variation between the two lakes (Doulka & Kehayias 2008). Also, the year-round presence of nauplii and egg-bearing females of this species probably suggests that either it has multiple reproductive periods, or a continuous reproduction.

The results for the seasonal variation of the most important rotifer species are generally in accordance with previous studies from different areas: Doulka & Kehayias (2008) in Lake Trichonis, Michaloudi et al. (1997) in Lake Mikri Prespa, Ferrara et al. (2002) and Halvorsen et al. (2004) in European lakes. Specific temperature and food preferences result in a characteristic seasonal succession of the various rotifer species (Lair 1990), which might appeared in different order from year to year as it has been noticed in other areas (García et al. 2002).

Succession patterns in cladoceran species have been observed in several temperate lakes. The succession of *D. cucullata* and *D. orghidani* is similar to the pattern reported from other lakes (Michaloudi et al. 1997; Doulka & Kehayias 2008) and could be ought to competitive interactions between these species (Matveev 1987). On the other hand, the succession of *B. longirostris* and *D. orghidani* could be owed to their different food preferences. Thus, *D. orghidani* as a highly efficient bacteriofeeder was present in summer, while *B. longirostris* as a low efficient bacteriofeeder was present mainly in spring (Geller & Müller 1985). Additionally, the high abundance of Chlorophyceae and Cryptophyceae in spring (Danielidis et al. 1996) could have created favorable conditions for the growth and reproduction of *B. longirostris*, since they comprise the main food for this species (DeMott & Kerfoot 1982). Cyanobacterial blooms in the lake during the summer period (Vardaka et al. 2005) are probably responsible for the decrease of *D. cucullata* as they can greatly affect the growth and reproduction of this species (Michaloudi et al. 1997; Michaloudi & Kostecka 2004; Hansson et al. 2007).

Planktivorous fish selectively consume large zooplankton and shift zooplankton communities toward dominance by smaller species (Gliwicz & Pijanowska 1989). This shift in zooplankton size often leads to change in phytoplankton communities towards the increase of blue-green algae during summer (Vanni & Layne 1997), as it is probably the case of Amvrakia Lake (Danielidis et al. 1996; Vardaka et al. 2005). Yet, although there are eleven fish species in the lake (most of them cyprinids), which can have great predation impact on the crustacean zooplankton (Tátrai et al. 2003), it is not possible to assess this impact, as there is no such information from the area.

Influence of physicochemical parameters on zooplankton

There are numerous studies pointing out the importance of physical and chemical parameters on the community structure and the zooplankton dynamics in lakes. Temperature is considered to be a crucial factor influencing many aspects of the biology and ecology of the zooplanktonic organisms (Wetzel 2001). In the present study temperature played an important role for most of the rotifer and cladoceran species. It has been reported that temperature affects the metabolic rate of cladocerans and their occurrence and distribution (Moore et al. 1996; Huber et al. 2010 and references therein), although the quality and quantity of food are also determinants for the density and biomass of these organisms (Abrantes et al. 2006). Moreover, the strong influence of temperature on rotifer species has been demonstrated by others (Hoffmann 1977; Akbulut et al. 2008). Additionally, temperature seemed to be the most important abiotic factor controlling the seasonal variation of *Dreissena polymorpha* larvae, since its positive correlation with temperature has been found in other Mediterranean lakes (Michaloudi et al. 1997; Kehayias et al. 2008; Doulka & Kehayias 2008), as well as in lakes of the northern Europe (Stańczykowska & Lewandowski 1993).

The vertical distribution of the zooplankton in Lake Amvrakia presented a pattern according to which the maximum abundance was concentrated in the surface 0–20 m layer and in the strata where chl-*a* and DO were higher. This resembled the pattern described for Lake Trichonis by Doulka & Kehayias (2008, 2011) and, considering that most of the species were common between the two lakes, is pointing the influence of certain elements in the adaptation of this spatial distribution. In accordance with the present results, Doulka & Kehayias (2008) reported that the main factor affecting the group of copepods in Lake Trichonis was the concentration of dissolved oxygen, especially for the calanoid *E. drieschi* and nauplii. Oxygen concentration is considered among the most important abiotic parameters affecting the zooplankton along the vertical axis of the aquatic ecosystems, since most of these organisms tend to avoid living in hypoxic or anoxic conditions and remain restricted in the well oxygenated parts of the water column (see Żurek 2006; Vanderploeg et al. 2009 and references therein). However, in the present study a considerable number of specimens from all the crustacean species, larvae of *D. polymorpha* and the most abundant rotifers were recorded even in the deeper layer (35–40 m), which at the end of stratification period was anoxic. Generally, the persistence of freshwater planktonic animals to hypoxia is less well known and our knowledge about the possibilities of surviving in lakes which are anoxic and contaminated by H_2S is relatively limited (Żurek 2006). It has been documented that freshwater mussels, such as *D. polymorpha*, are able to survive short-term exposure (<5 days) to anoxic or hypoxic conditions in their habitat (Johnson & McMahon 1998). In addition, some crustacean species can survive in hypoxic and even anoxic conditions for a small period of time using hypoxic zones not accessible to fish as a potential refuge against fish predation during the daylight, while migrate towards shallower depths in the night (Vanderploeg et al. 2009). Doulka & Kehayias (2011) showed that most of the crustacean species found in the lake along with *D. polymorpha* larvae, present various types of diel vertical migration (DVM) with the general trend to be the ascent in shallower depth during the night. Although there is no information for the existence of DVM in Lake Amvrakia, as sampling was conducted only in morning hours, this ethological adaptation could explain the presence of zooplankton organisms in such unfavorable conditions during the day.

Chlorophyll-*a* seemed to be one of the major affecting parameters for all zooplankton groups in Lake Amvrakia. This could be explained considering that most of the rotifer species, as well as the cladocerans, the larvae of *D. polymorpha* and the calanoid *E. drieschi*, could be greatly depend on phytoplankton for their energy demands. The multiple regression analysis showed that the highest significant correlations were between chl-*a* concentration and rotifer abundance. Many authors have suggested that food availability has a major impact on rotifer's community (Devetter 1998; Wang et al. 2010) and, although many zooplanktonic species appear to respond to increased food availability, rotifers are expected to respond proportionally more than crustaceans because predation pressure limits large-bodied zooplankton (Beaver & Havens 1996). Also, *D. polymorpha* larvae as exclusively herbivores seem to have been influenced by the phytoplankton biomass as represented by chl-*a* concentration. However, several studies suggest that rather food quality than food quantity is an important factor for growth and reproduction of *D. polymorpha* (Stoeckmann & Garton 2001). Unfortunately, the present data on the chl-*a* concentration provided only indications of algal biomass and, consequently, the primary productivity, but no qualitative information on the phytoplankton of the lake.

Conductivity was among the major environmental variables influencing zooplankton in Lake Amvrakia, similarly to what have been reported by others (Stanković et al. 2010; Bielańska-Grajner & Gładysz 2011). The influence of conductivity to zooplankton in gypsum karst lakes is probably the result of the high concentration in sulfates in the water. As it was shown in the study of Soucek (2007), sulphate salts reduce filter-feeding rate in the cladoceran *Ceriodaphnia dubia* (Richard, 1894), and resulted to slower rates of growth in populations exposed to sulphate salts environment than unexposed populations. The above could explain the negative correlation of conductivity with the cladoceran *D. cucullata* and also the copepods *E. drieschi* and *M. albidus*, although more research on that issue would be required.

Water level is expected to exercise several indirect influences to the biotic elements affecting the total nutrient load within the lake, and consequently the chl-*a* and conductivity. Though, a direct effect caused by the reduction of the water level could have been the decrease of the abundance of *D. polymorpha* larvae in the second year. In this sense, the drop of water lever in the second year uncovered an extended area of the bottom of the lake, which was the habitat for the adult form of this mollusc, while this habitat reduction probably resulted to the diminishing of the reproduction capacity of the population.

The correlations of nutrients and silicates with various zooplankton species could be explained by taking into account some indirect effects. Usually, the negative correlation of nutrients to various species was associated with positive correlation to chl-a. This means that these species tend to present increased abundance in cases of nutrient's depletion, as the latter were utilized by the phytoplankton, which at the same time show elevated density. Consequently, this could indirectly indicate the importance of phytoplankton in the species variation. On the other hand, *K. longispina* and *Hexarthra* sp. presented positive correlations with silicates, therefore, they tend to increase in high concentrations of these ions. Considering that the abundance of diatoms is reversely related to the concentration of silicates, we could assume that these species do not increase when diatoms are abundant. Indeed, both *K. longispina* and *Hexarthra* sp. showed lower abundance in spring while increased in summer, in contrast to the diatoms (Spartinou 1992; Danielidis et al. 1996), which could indicate perhaps that diatoms are not preferable food for *K. longispina* and *Hexarthra* sp. However, more information on the phytoplankton variation, as well as on the diet and the trophic relations between the zooplanktonic species of the lake, would be essential in order to clarify and understand these interrelations.

In conclusion, the study of the zooplankton community in relation to environmental parameters in Lake Amvrakia revealed that the particular chemistry of this gypsum karst lake, as well as its geographical isolation from the other lakes of the area, could have been responsible for the present species composition of this basin.

In contrast, the species dynamics seems not to have been influenced in great extend by this particular environment in comparison to nearby lakes. The results on the abiotic elements of Lake Amvrakia along with the variation of the species diversity intimate a stable ecosystem. This stability is probably ought to the great depth and the moderate productivity of the lake, however, considering the various human impacts and especially the future climate effects, this unique ecosystem has to be under further inspection to achieve protection and efficient management.

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