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Spatial and temporal distribution of zooplankton in Lake Trichonis (Greece)

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The investigation of the zooplankton community in Lake Trichonis during a two-year survey (September 2003–August 2005) revealed 37 invertebrate species (26 rotifers, three copepods, seven cladocerans and one mollusc larva). The seasonal distribution followed a biacmic pattern in the first year and a monoacmic in the second. Copepoda prevailed, with the calanoid *Eudiaptomus driesci* being the dominant species. No differences in the horizontal distribution of the zooplankton community were found. The maximum abundance of the zooplankton community was recorded in the surface 0–10 m layer and abundance decreased with depth. The most important species of rotifers follow a vertical separation pattern, while the cladocerans revealed either a seasonal succession of dominance, or a vertical separation. Although Lake Trichonis holds the basic characteristics of an oligotrophic lake, the presence of certain species typical of eutrophic lakes, could reflect a possible alteration of its trophic state.

Keywords: zooplankton; abundance; spatial distribution; Lake Trichonis

Introduction

Lake Trichonis is situated in the western area of Greece at an altitude of 18 m a.s.l, with a surface area of 98.6 km^2, a maximum depth of 57 m and a catchment area of 421 km^2 (Zacharias et al. 2002). It is a warm monomictic lake, exhibiting a long period of thermal stratification and previous studies have classified it as oligotrophic to mesotrophic (Koussouris et al. 1993; Skoulikidis et al. 1998). Lake Trichonis is the largest natural lake in Greece and has great ecological and economical importance. It has been included in the protected areas of NATURA 2000 and is very rich in fish species, from which the economically most important is *Atherina boyeri* Risso, 1810, with an annual fish catch of 250 tn (Daoulas et al. 1993).

Several studies have been conducted in the past concerning the lake's physical and chemical characteristics (Overbeck et al. 1982; Tafas et al. 1997), water balance (Dimitriou et al. 2001), phytoplankton abundance and species composition (Tafas and Economou-Amilli 1997) and ichthyofauna (Daoulas et al. 1993). However, there is little information about the zooplankton community of Lake Trichonis, although zooplankton is a very important component of the lake's ecosystem and the prime source of energy for *A. boyeri* (Chrisafi et al. 2007).

All previous data come from the investigations of Koussouris (1978, 1979) and Koussouris et al. (1993). Kehayias et al. (2004) gave some recent information about the lake's zooplankton, based on four seasonal samplings in 2002–03, only at one station in the lake.

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The aim of the present study is to provide more comprehensive information about community structure and the spatial and temporal distribution of zooplankton, in order to contribute to the understanding of its ecological role in this significant ecosystem.

Materials and methods

Sampling was carried out at monthly intervals from September 2003 to August 2005 at three stations (A, B, C) with depths of 48, 35 and 25 m, respectively (Figure 1). Samples were taken with a conical plankton net (40 cm in diameter, 100 cm in length, 50 μm mesh size), which was manufactured to be a closing net with the addition of a second rope and a releasing trigger, analogous to those of the WP-2 closing net. Vertical hauls were conducted at 10 m depth intervals from near the bottom to the surface for all three stations. The net was towed at a speed of approximately 0.5 m sec^{-1}. All samples were taken in the morning and were preserved in 4% formalin. During the entire sampling period, water transparency was measured for each station with a Secchi disc (diameter 30 cm). During September 2004–August 2005 temperature, oxygen concentration, pH and conductivity measurements were taken at all three stations at 2 m intervals from the surface down to 40 m, using WTW portable instruments.

The species were identified using the keys of Rylov (1963), Ruttner–Kolisko (1974), Korovchinsky (1992), Alonso (1996) and Benzie (2005). For the abundance analysis, three counts of 1.5 ml subsamples from each sample were made on a Sedwick-Rafter cell having a total volume of 100 ml (Michaloudi 1997). In order to
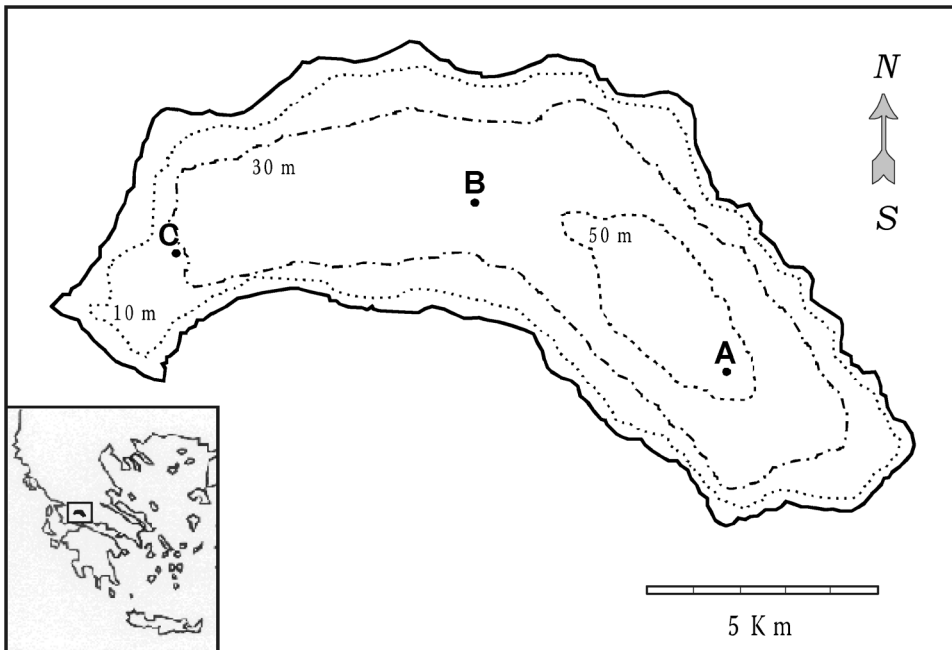

Figure 1. Lake Trichonis with the three sampling stations (A, B, C).

find out whether there were statistically significant differences in the abundance of total zooplankton and zooplankton groups between the two sampling periods and between the three stations, the parametric t-test and one–way ANOVA was applied, respectively. For the comparison of the vertical distributions of the zooplankton community, the median depth (e.g. the depth where 50% of the population exists) was calculated for each species and group according to Hofmann (1975) as follows:

$$S = \frac{\sum (N_{Ti} \times Ti)}{\sum N_{Ti}}$$

where S=median depth, N_{Ti}=the abundance in the depth i, and Ti=depth (m). Although the median depth cannot represent the actual vertical distribution of a species, it is a good numerical base for the application of statistics. Thus, annual or seasonal differences between the median depths of zooplankton species were tested using either a t-test or one-way ANOVA. Correlations between the abundance of the zooplankton species and the vertical profile of temperature and oxygen were made using Pearson's r correlation coefficient. All statistical tests were made on data transformed to log(x+1).

Results

Species composition

During the two years of investigation in Lake Trichonis, 35 zooplanktonic invertebrate species were found (24 rotifers, three copepods, seven cladocerans and one mollusc larva) as shown in Table 1. In comparison to previous studies, the list of species in the present study includes 10 new records. Among them there is a cladoceran *Diaphanosoma orghidani*, and nine rotifer species: the genus *Ascomorpha* sp., *Collotheca* sp. and *Monommata* sp., representatives of the family Bdelloida, and the species *Conochilus unicornis*, *Fillinia opoliensis*, *Hexarthra intermedia*, *Lecane quadridentata* and *Pompholyx sulcata*.

Seasonal variability

The mean integrated abundance of the total zooplankton in the whole sampling area ranged between 2.6 and 55.1 ind L^{-1} during 2003–04 and between 10.9 and 116.2 ind L^{-1} during 2004–05 (Figure 2). No statistically significant differences between the three sampling stations were found for any of them during the whole sampling period (one-way ANOVA, $p > 0.05$). The abundance of the total zooplankton showed a decrease after September, remained low during fall and winter and increased at the beginning of spring in both sampling periods (Figure 2). The seasonal fluctuation followed the biacmic pattern only in the first period (September 2003–August 2004) with a peak in April, which was the result of the increase of rotifers, and a second peak in July. However, during the second period (September 2004–August 2005) there was only one distinct peak of abundance in summer. There were statistically significant differences in the abundance of the total zooplankton between these two sampling periods (t-test, $p < 0.05$).

Copepods had the greatest average proportion within the zooplankton community of Lake Trichonis in both years accounting for 41.8% in 2003–04 and

Table 1. List of the zooplankton species found in Lake Trichonis during the present and previous studies. (1) Koussouris 1978, 1979, (2) Koussouris et al. 1993 (using sampling bottles and 50 μm mesh size plankton nets), (3) Kehayias et al. 2004 (using 100 μm mesh size plankton nets).

ROTIFERA	(1)	(2)	(3)	Present study	Indicators of oligotrophy	Indicators of eutrophy
Anuraeopsis fissa (Gosse, 1851)	+					
* *Ascomorpha* sp. (Perty, 1850)				+		
Asplanchna priodonta (Gosse, 1850)	+		+	+		
Asplanchnopus multiceps (Schrank, 1793)	+	+				
* Bdelloida				+		
Brachionus angularis (Gosse, 1851)	+	+				
B. calyciflorus (Pallas, 1766)	+	+	+	+		‡
B. c. f. *anuraeiformis* (Brehm, 1909)		+		+		
B. caudatus (Barrois and Daday, 1894)		+				
* *Collotheca* sp				+		
* *Conochilus unicornis* (Rousselet, 1892)				+		
Euchlanis dilatata (Ehrenberg, 1832)		+		+		
Fillinia longiseta (Ehrenberg, 1834)	+			+		‡
* *F. opoliensis* (Zacharias, 1898)				+		
F. terminalis (Plate, 1886)	+	+		+		
Gastropus stylifer (Imhof, 1891)		+		+		
Hexarthra sp. (Schmarda, 1854)		+				
H. mira (Hudson, 1871)	+	+		+		
* *H. intermedia* (Wiszniewski, 1929)				+		
Kellicottia longispina (Kellicott, 1879)	+		+	+		
Keratella cochlearis (Gosse, 1851)	+	+	+	+		
K. quadrata (Müller, 1786)	+	+	+	+		‡
* *Lecane quadridentata* (Ehrenberg, 1932)				+		
* *Monommata* sp.				+		
Ploesoma hudsoni (Imhof, 1891)	+	+		+	†	
P. truncatum (Levander, 1894)	+			+		
Polyarthra sp.				+		
P. vulgaris (Carlin, 1943)	+	+				
* *Pompholyx sulcata* (Hudson, 1885)				+		‡
Ptygura crystallina? (Ehrenberg, 1834)	+					
Synchaeta sp.		+		+		
Trichocerca birostris (Minkiewicz, 1900)	+	+				
T. capucina (Wierzejski, 1893)		+		+		
T. porcellus (Gosse, 1851)		+				
T. rattus (Müller, 1776)	+					
T. similis (Wierzejski, 1893)		+		+		

COPEPODA

	(1)	(2)	(3)			
Acanthocyclops viridis		+				
Arctodiaptomus dudichi (Kiefer, 1932)	+					
A. dudichi v. *Stephanidesi* (Pesta)		+				
A. steindachneri (Richard, 1897)	+	+				
Cyclops sp.		+				
Cyclops vicinus		+				

Table 1. (*Continued*)

ROTIFERA	(1)	(2)	(3)	Present study	Indicators of oligotrophy	Indicators of eutrophy
Eudiaptomus drieschi (Poppe & Mrazek, 1895)	+	+	+	+		
Macrocyclops albidus (Jurine, 1820)			+	+		
Megacyclops viridis (Jurine, 1820)	+					
Microcyclops varicans (G.O. Sars, 1863)			+	+		

CLADOCERA						
Alona sp.		+		+		
A. affinis (Leydig, 1860)	+					
Bosmina longirostris (O.F. Müller, 1785)	+	+	+	+		‡
Ceriodaphnia pulchella (Sars, 1862)			+	+		
Daphnia sp.		+				
D. cucullata (G.O. Sars, 1862)			+	+		‡
D. galeata (Sars, 1864)			+	+	†	
D. hyalina Leydig, 1860	+	+				
D. longispina (O.F. Müller, 1776)	+		+			
Diaphanosoma sp.			+			
* *Diaphanosoma orghidani* (Negrea, 1982)				+		
Leptodora kindtii (Focke, 1844)				+		

MOLLUSKA						
Dreissena polymorpha (Pallas, 1771)		+	+	+		

* New records in the zooplankton community of Lake Trichonis
‡ Species considered to be indicators of eutrophic conditions according to Gannon and Sternberger (1978), Geller and Müller (1981) and Pejler (1983).
† Species considered to be indicators of oligotrophic conditions according to Pejler (1983).
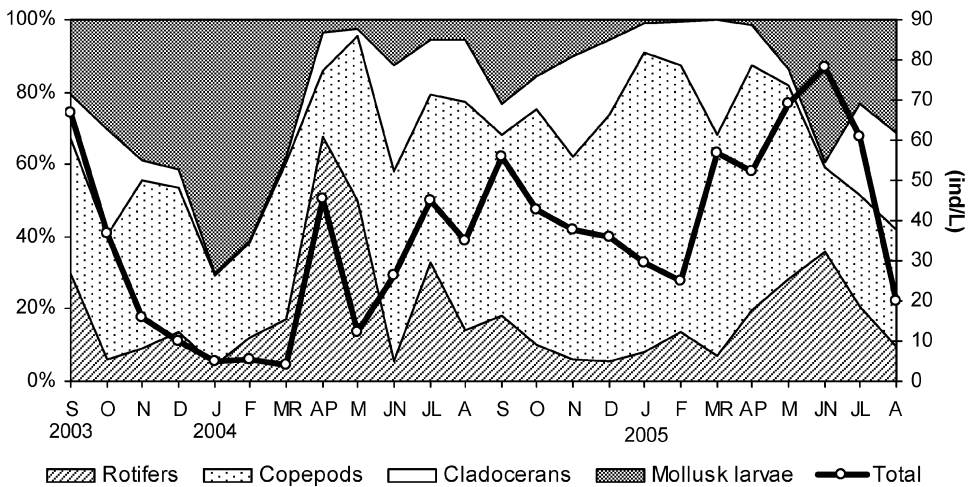

Figure 2. Seasonal variation of the total zooplankton abundance (ind L^{-1}) and percentage contribution of the main zooplanktonic groups to the total abundance.
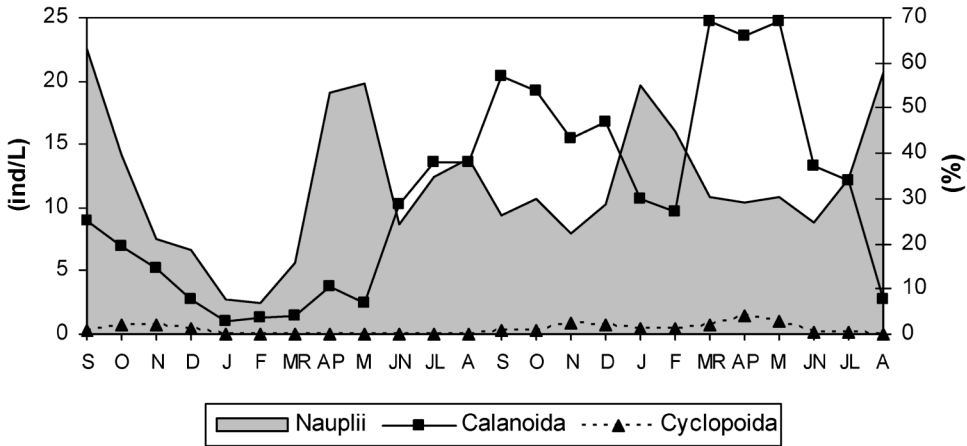
Figure 3. Seasonal variation of the abundance (ind L^{-1}) of calanoid and cyclopoid copepods and the percentage contribution of copepod nauplii.

51.2% in 2004–05, followed by rotifers (23.7 and 19.0% in 2003–04 and 2004–05, respectively), *Dreissena polymorpha* larvae (18.5 and 16.4%, respectively) and cladocerans (16.0 and 13.5%, respectively). Copepods also dominated the crustacean zooplankton (copepods + cladocerans) with a contribution to the total abundance of between 54 and 98%. The calanoid *Eudiaptomus drieschi* was the dominant species throughout the sampling period (Figure 3). The nauplii of all species were present in considerable numbers all year round, always having greater proportions just two months before the maximum of the total copepod abundance was recorded (Figure 3). Egg-bearing females were also present throughout the whole sampling period, with maximum percentage contribution in spring. Copepods showed a decrease of abundance from September 2003 to February 2004 and an increase from March to August 2004. However, the pattern of their seasonal variation altered in the second period, when copepods maintained the high abundance of September 2004 through February, while showing an increase in spring, and reaching the highest value in May 2005. In general, the mean abundance of the total copepods in the second period was 152.1% greater than of the first, and this difference was statistically significant (t-test, p=0.031).

The mean abundance of rotifers ranged from 0.23 to 30.71 ind L^{-1} in January and April 2004, respectively, while there were no statistically significant differences in the abundance between the two sampling periods (t-test, p>0.05). Rotifers showed a distinct pattern of seasonal variation according to which their abundance decreased from September to March and increased in spring in both sampling periods. However, in the first period there were two peaks of abundance, one in April and the other in July 2004, while in the second period there was only one maximum in June 2005 (Figure 2). The highest value of abundance in April 2004 was due to *Gastropus stylifer*, which comprised 82.5% of the rotifer community, while the peak in July 2004 was due to *Ploesoma truncatum* and *Synchaeta* sp. (Figure 4). *Kellicottia longispina* was the most important contributor to the maximum rotifer abundance in June 2005, followed by *G. stylifer* and *P. truncatum* (54.6, 16.0 and 15.4%, respectively).
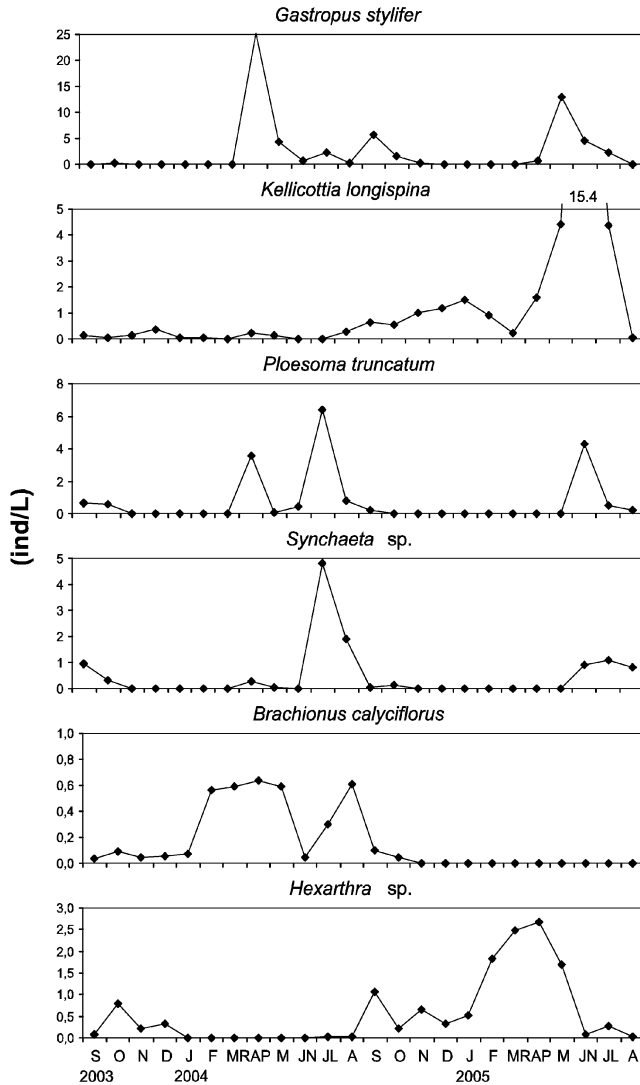
Figure 4. Seasonal variation of the abundance (ind L^{-1}) of the six most important rotifer species (*Gastropus stylifer*, *Kellicottia longispina*, *Ploesoma truncatum*, *Synchaeta* sp., *Brachionus calyciflorus* and *Hexarthra* sp.).

The mean abundance of cladocerans ranged between 0.03 ind L^{-1} in February 2004 to 17.9 ind L^{-1} in March 2005. *Bosmina longirostris* was the dominant species in the cladoceran community from December 2003 to May 2004, with an average proportion of 92.0%, while from June to October 2004 its contribution dropped to an average of 2.5%, rising again in November–December 2004 (Figure 5). In contrast, *Diaphanosoma orghidani* was dominant in the warmer periods, while an increase of its abundance was noticed in March 2005. *Daphnia cucullata* was the dominant species among the daphniids, reaching a peak of abundance in April 2005. However, *Daphnia* spp. was almost absent in the first sampling year, and only between April and July 2005 made significant contribution to the cladoceran
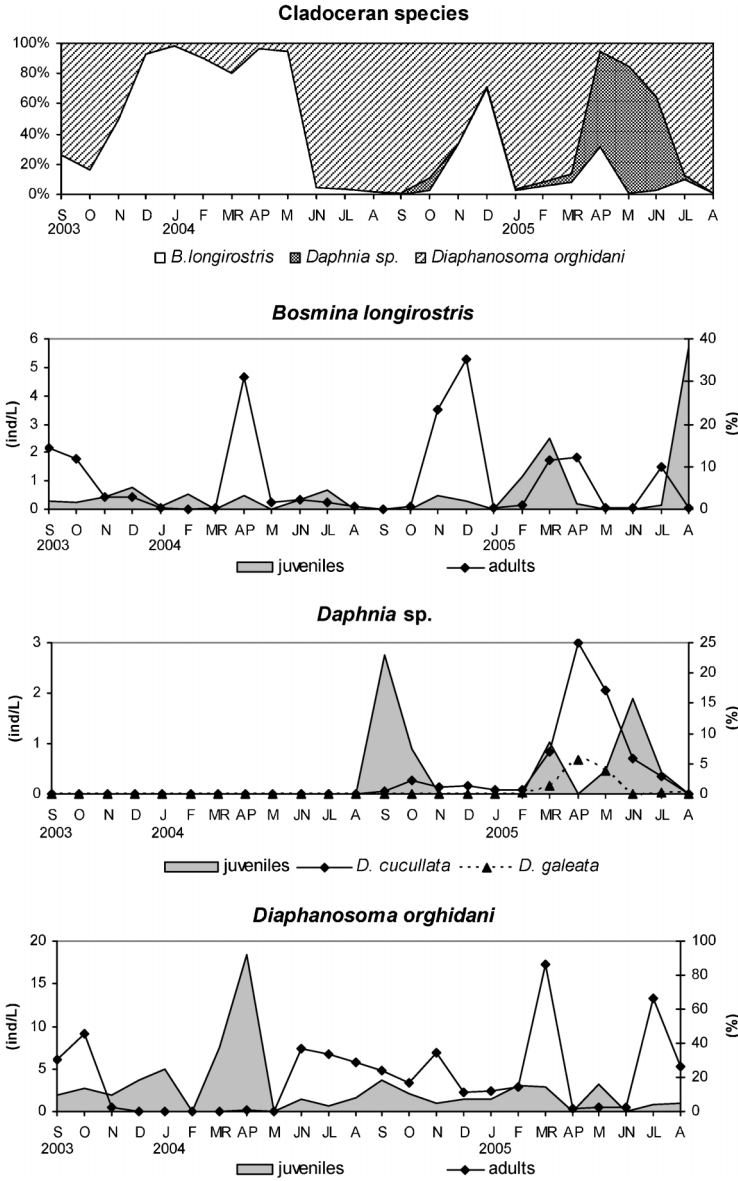
Figure 5. Seasonal percentage contribution of the cladoceran species to the abundance of the cladoceran community and seasonal variation of the abundance (ind L^{-1}) of the cladoceran species.

community. Juvenile stages for the three above species were present through almost the entire sampling period and in most cases high proportions of juveniles preceded the species peak of abundance (Figure 5).

Dreissena polymorpha larvae were present in the zooplankton throughout the sampling period (Figure 2), reaching peaks of abundance in September 2003 and 2004 and the maximum mean value in June 2005 (30.73 ind L^{-1}). The lower abundance values for this species were recorded in March–May 2004 and in January–April 2005.

Vertical distribution

The maximum abundance of the zooplankton community in Lake Trichonis was recorded in the surface 0–10 m depth layer in almost all sampling occasions. Although there was variation in the vertical distribution of the total zooplankton and of the individual species between the two sampling years (Figure 6), the comparison of their median depths revealed no statistically significant differences (t-test, $p > 0.05$). There were no statistically significant differences in the vertical distribution between the four seasons of each sampling year of the total zooplankton and rotifers (one-way ANOVA, $p > 0.05$). However, copepods, and especially the younger stages (copepodites of *Eudiaptomus drieschi* and nauplii), showed differences in their vertical distribution among the four seasons, only in the first sampling year (one-way ANOVA, $p = 0.019$ and $p = 0.0001$, respectively). Thus, during the winter, when the mixing of water resulted in the absence of thermal
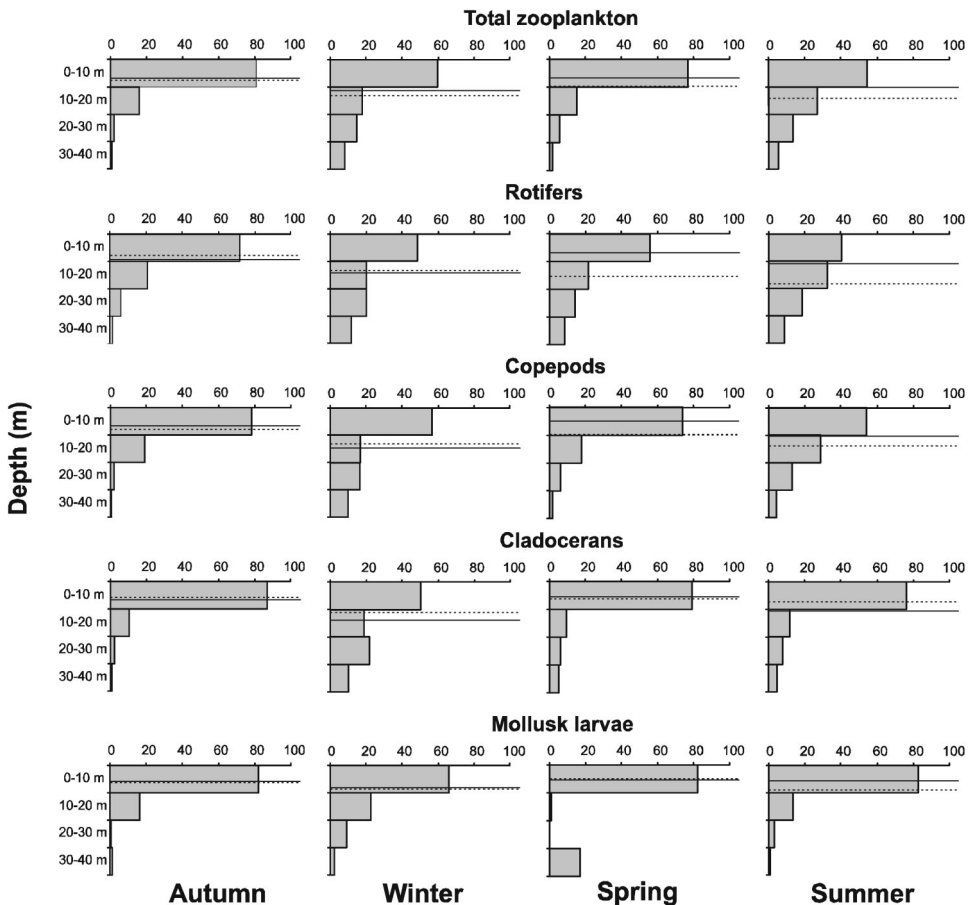

Figure 6. The vertical distribution of the total zooplankton and the main zooplanktonic groups as the mean percentage of total caught in the water column sampled in the four seasons during the whole sampling period. The average median depth (m) of each group in the first (2003–04) and the second sampling period (2004–05) are shown with the continuous and dotted line, respectively.

stratification (Figure 7), they were both distributed in deeper layers in comparison to other seasons. The cladoceran *Bosmina longirostris* also showed statistically significant differences ($p=0.005$) in its vertical abundance profile during the first
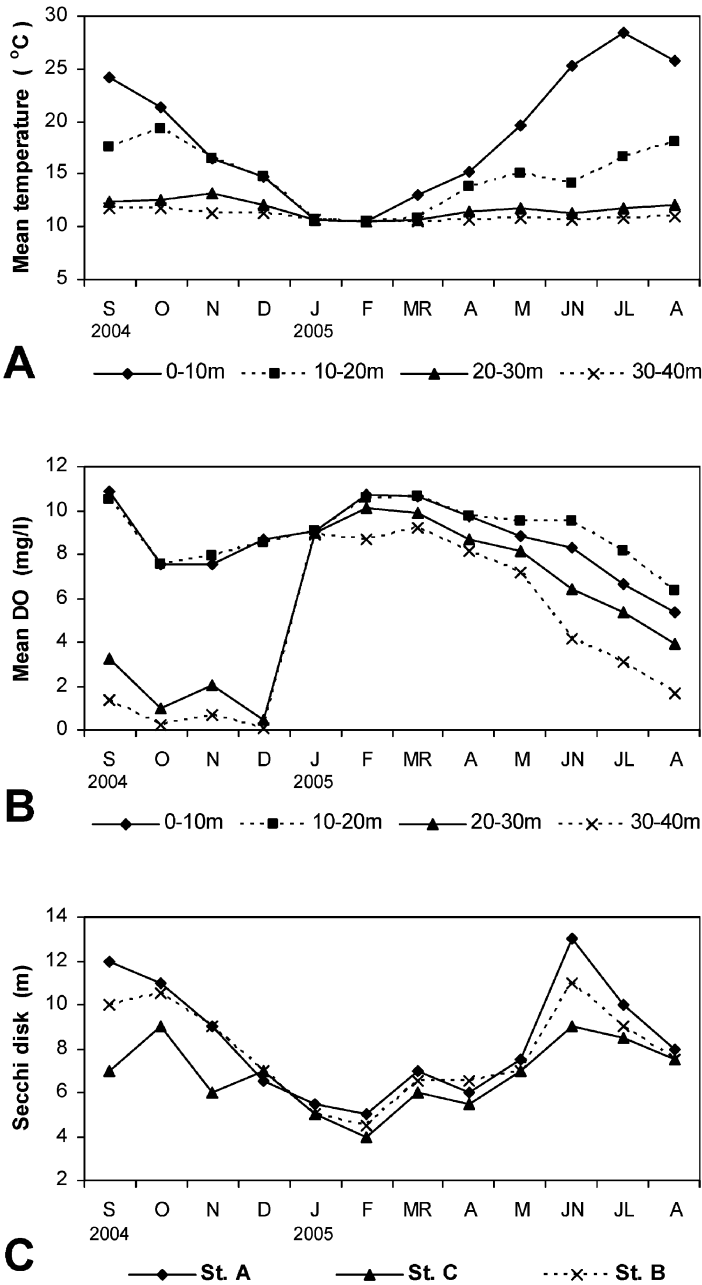

Figure 7. (A, B) The seasonal variation of the average temperature and oxygen content in each of the depth layers (0–10, 10–20, 20–30 and 30–40 m) during September 2004 to August 2005. (C) The seasonal variation of the water transparency in the three sampling stations during September 2004 to August 2005.

year, having uniform depth distribution in winter and occupying the deepest layers in summer 2004. In the second sampling year, the cladoceran *Diaphanosoma orghidani* and the rotifer *Kellicottia longisprina* showed significant differences between seasons having deeper distribution in the winter (p=0.019) and in summer (p=0.037), respectively.

Considering the median depths of rotifers in all sampling periods, a distinct vertical separation of species was recorded. For the numerically most important species such as *K. longispina*, *G. stylifer* and *Ploesoma* sp., there were statistically significant differences between their median depths for each sampling year and also for the whole sampling period (Figure 8A), with *K. longispina* having the deepest distribution and *Ploesoma* sp. the shallowest (one-way ANOVA, p<0.05). Statistically significant vertical separation was also found for the other three important rotifer species, *Brachionus calyciflorus*, *Hexarthra* sp. and *Synchaeta* sp. (one-way ANOVA, p<0.05), with the former being deeper than the others and the latter having the shallowest distribution (Figure 8B).

The adults and copepodites of the copepod *E. drieschi*, as well as the copepod nauplii (Figure 8C), had similar vertical distribution throughout the sampling period (one-way ANOVA, p=0.321). *Diaphanosoma orghidani* occupied shallower depths than *Bosmina longirostris* in most cases (Figure 8D), although no statistically significant differences in their vertical distribution were found. In September 2004, the newly-appeared daphniids (especially *D. cucullata*) were distributed deeper than the other two species until February 2005 and in June and July 2005. Considering the seasonal (Figure 5) and vertical distribution (Figure 8) of the above three cladoceran species it is noteworthy that when there was concurrence in the vertical distributions of species only one of them prevailed, as in April and December 2004 for *B. longirostris* and March 2005 for *D. orghidani*. When the species had equal abundances, there was a vertical separation, as in November 2004 for *B. longirostris* and *D. orghidani*, in March 2005 for all three species, in April 2005 for *B. longirostris* and *D. cucullata* and in July 2005 for *B. longirostris* and *D. orghidani*.

The total zooplankton as well as each group showed a positive correlation with both temperature and oxygen concentration along the vertical axis, (Pearson's *r*, p<0.001). The larvae of the mollusc *Dreissena polymorpha* and the rotifer genus *Synchaeta* sp. showed a strong relationship with temperature in the 0–10 m depth layers at all sampling stations (Table 2). On the other hand, there was negative correlation between the seasonal variation of the copepod nauplii and temperature at almost all stations and sampling depths, while the same was recorded for *Hexarthra mira* and the adults of *Macrocyclops albidus* in the 0–10 m depth layer and for the copepodites of *Eudiaptomus drieschi* in the deeper layers. In contrast to temperature, the oxygen content was positively correlated with the presence of crustaceans, especially in the deeper layers (Table 2). Among the rotifers, there were positive and negative correlations between the oxygen content and *H. mira* and *Synchaeta* sp., respectively, in the 0–10 m layer at stations A and C, and also a negative correlation with *Synchaeta* sp. at station A in the 10–20 m depth layer. The seasonal variation of water transparency showed a strong correlation with *D. polymorpha* mainly in the surface 0–10 m depth layer, while correlated also positively with *Synchaeta* sp. and negatively with *H. mira* only in the 0–10 m depth layer of station A. Negative correlations between transparency and the adults of *M. albidus* and nauplii were also found at various sampling depths (Table 2).
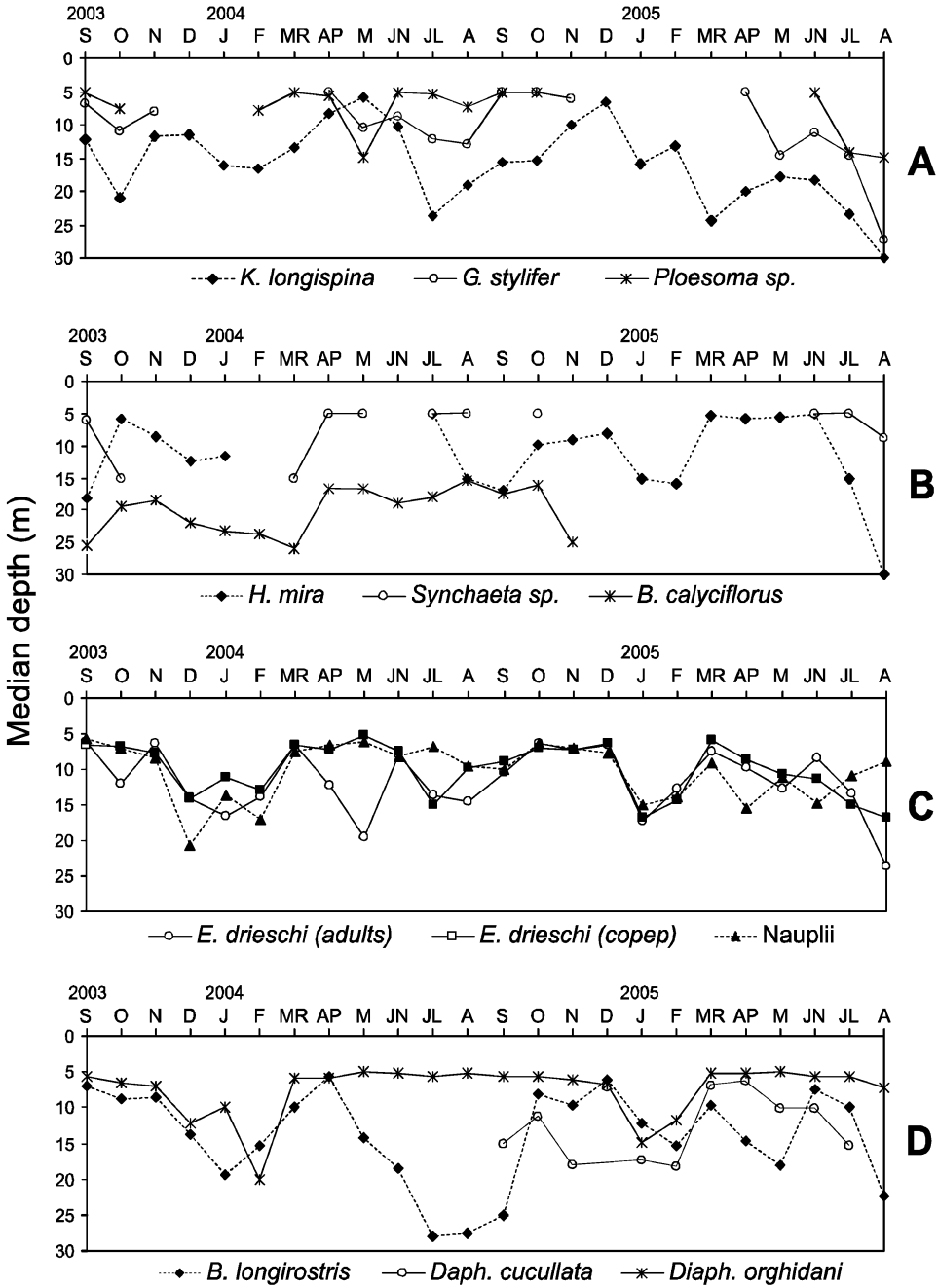
Figure 8. Seasonal variation of the median depths (m) of (A) the most important rotifer species *G. stylifer*, *K. longispina*, *P. truncatum*, (B) the rotifers *Synchaeta* sp., *B. calyciflorus* and *H. mira*, (C) the *Eudiaptomus drieschi* adults, copepodites and the copepod nauplii, and (D) the three most important cladocerans (*B. longirostris*, *D. cucullata* and *D. orghidani*).

Discussion

Species composition

The differences in the number of species recorded in the previous studies of Koussouris (1978), Koussouris et al. (1993) and Kehayias et al. (2004) and in the present study could be either attributed to different sampling methods, to taxonomical problems, or to a possible alteration in the composition of the zooplankton community of the lake during the last years.

Diaphanosoma orghidani is reported as a new record for Lake Trichonis in the present study, and was not found in the older studies of Koussouris (1978) and Koussouris et al. (1993), but was probably found by Kehayias et al. (2004) who did not identify it to species level. Considering the high abundance of this species in the present samples, and also in the samples of Kehayias et al. (2004), it must be assumed that during the past decades it must have been very rare or even absent from the zooplankton community of the lake.

The present study confirms the presence of *Daphnia cucullata*, which was also found by Kehayias et al. (2004). Instead of this species, Koussouris (1978) and Koussouris et al. (1993) reported the presence of *Daphnia hyalina* and *Daphnia longispina*. Considering that Kehayias et al. (2004) has also reported the presence of very few specimens of *D. longispina*, it seems that this species must be very rare in the lake, or its population must have been diminished during the last years. On the other hand, the presence of *D. hyalina* in Lake Trichonis could be erroneous since it is considered as a species of glacial lakes and is not found in Greece (Michaloudi et al. 1997), or perhaps it was misidentified, as it is often confused with *D. longispina*. Indeed, *Daphnia hyalina*, *D. cucullata* and *D. galeata* have been considered to hybridize and produce intermediate forms (Benzie 2005).

Seasonal variability

Lake Trichonis is characterized by a strong hydrological homogeneity along the horizontal axis, since the lake's water circulates during the unstratified period as a result of currents, surface seiche, temperature, water inflows and outflows (Zacharias and Ferentinos 1997; Zacharias et al. 2005). This probably has been the reason why no horizontal differences in any of the zooplankton groups and/or species, was found in the present study.

According to previous studies, Lake Trichonis is considered as oligo- to mesotrophic (Koussouris et al. 1993; Tafas et al. 1997; Skoulikidis et al. 1998). However, recent reports on the physicochemical characteristics of the lake speculated the possibility of an alteration in its trophic state towards a higher level (Doulka and Kehayias 2005). From the zooplankton point of view, there are several indications supporting the oligo- or eutrophic character of the lake. Thus, the seasonal variation of the zooplankton abundance during the first year of sampling (September 2003–August 2004) followed a biacmic pattern, which is characteristic of eutrophic lakes according to the PEG model (Sommer et al. 1986). However, during the second year (September 2004–August 2005) a monoacmic pattern (only one peak of abundance in summer) was observed, which is characteristic of oligotrophic lakes. The abundance values recorded in the present study are slightly higher compared to those of other large oligotrophic lakes of southern Europe, such as Lake Ohrid (Stankovic 1959), Lake Tavropou (Tsekos et al. 1992) and Lake Bracciano (Ferrara

Table 2. Correlation of species density with temperature, oxygen content and transparency during September 2004–August 2005 given as the Pearson's r correlation coefficient.

Temperature

Species	0–10 m St A	St B	St C	10–20 m St A	St B	St C	20–30 m St A	St B	30–40 m St A
H. mira	−0.701*	−0.589*	−0.478	0.046	−0.062	−0.060	−0.342	−0.314	−0.361
Synchaeta sp.	0.738**	0.662*	0.713**	0.320	0.476	0.295	0.150	0.035	−0.043
E. drieschi (c)	−0.284	−0.294	−0.482	0.210	0.051	0.079	−0.595*	−0.351	−0.598*
M. albidus (a)	−0.819**	−0.636*	−0.807**	0.044	−0.219	−0.394	−0.413	0.014	−0.512
Naupli	−0.550	−0.538	−0.655*	−0.573	−0.820**	−0.598*	−0.739**	−0.625*	−0.816**
Total copepods	−0.490	−0.447	−0.594*	0.120	−0.212	−0.198	−0.599*	−0.430	−0.837**
D. polymorpha	0.792**	0.954**	0.880**	0.708**	0.554	0.635*	0.163	0.367	−0.202

Oxygen

Species	0–10 m St A	St B	St C	10–20 m St A	St B	St C	20–30 m St A	St B	30–40 m St A
H. mira	0.585*	0.514	0.639*	0.426	0.461	0.555	0.282	0.287	0.246
Synchaeta sp.	−0.686*	−0.515	−0.647*	−0.674*	−0.179	−0.050	−0.054	−0.138	−0.156
E. drieschi (a)	0.658*	0.442	0.429	0.076	0.547	0.562	0.432	0.388	0.608*
E. drieschi (c)	0.621*	0.348	0.501	0.305	0.530	0.514	0.739**	0.505	0.515
M. albidus (c)	0.290	−0.059	0.335	0.045	0.011	−0.176	−0.677*	0.001	0.035
Naupli	0.369	0.695*	0.721	−0.039	0.338	0.046	0.733**	0.796**	0.827**
Total copepods	0.671*	0.508	0.626*	0.235	0.658*	0.479	0.717**	0.651*	0.833**

Table 2. (*Continued*)

Transparency

Species	0–10 m			10–20 m			20–30 m		30–40 m
	St A	St B	St C	St A	St B	St C	St A	St B	St A
H. mira	−0.610*	−0.502	−0.381	0.098	−0.168	−0.506	−0.331	−0.532	−0.470
Synchaeta sp.	0.625*	0.471	0.561	−0.006	0.324	0.393	−0.006	−0.009	−0.006
M. albidus (a)	−0.791**	−0.526	−0.738**	−0.127	−0.315	−0.265	−0.479	−0.450	−0.583*
Naupli	−0.541	−0.328	−0.378	−0.627*	−0.797**	−0.340	−0.728**	−0.713**	−0.509
D. polynorpha	0.820**	0.813**	0.809**	0.708*	0.568	0.398	0.008	−0.271	0.239

*p<0.05, **p<0.01.

et al. 2002), while they are significantly lower than those of other eutrophic lakes of Greece (Zarfdjian 1989; Michaloudi 1997). The dominance of calanoid copepods in the crustacean community during almost the whole two-year sampling period is considered as a characteristic of oligotrophic lake ecosystems (McNaught 1975). The presence of *B. longirostris* and especially the succession of this species and *Diaphanosoma orghidani* are similar to the situation described by Geller and Müller (1985) for eutrophic lakes. However, this was found only during the first year, while in the second year two other cladocerans were added to the community and the succession of species was altered. The rotifers *Fillinia longiseta*, *Keratella quadrata* and *Pompholyx sulcata* are typical representatives of eutrophic lakes (Gliwicz and Lampert 1990), while at the same time *Ploesoma hudsoni* and the cladocerans *Daphnia galeata* and *Leptodora kindtii* are characteristic of oligotrophic lakes (Gannon and Stemberger 1978). In conclusion, Lake Trichonis seems to retain the basic characteristics of an oligotrophic lake, while at the same time exhibited features of eutrophic lakes, indicating a tendency towards a shift in its trophic state.

Eudiaptomus drieschi was the dominant copepod in Lake Trichonis, being more abundant during the second sampling period. The differences in the abundance between the two sampling periods can not be easily explained, since there is little information about the seasonal distribution and reproduction of *E. drieschi* in other areas of its geographical distribution. According to the present results, 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. *Gastropus stylifer* showed maximum abundance in spring in both sampling years as it was reported also for Lake Mikri Prespa (Michaloudi et al. 1997). Elliott (1977) found this species from spring to autumn in lakes in England, while Berzins and Pejler (1989) considered it as a winter species. *Kellicottia longispina* was present in high abundance in late spring to summer of 2005, which is in accordance with the reports of Ferrara et al. (2002) and Halvorsen et al. (2004) in European lakes, and Michaloudi et al. (1997) in Lake Mikri Prespa. *Ploesoma truncatum* was also a species having higher abundance in the summer according to Berzins and Pejler (1989) and Ferrara et al. (2002), while the genus *Synchaeta* sp. has also been found in abundance in spring to early summer (Elliott 1977; Holst et al. 1998) in lakes of England and Germany, respectively. The preference of the latter species for the warmer seasons in the present study was reflected in its positive correlation with temperature in the surface 0–10 m layer. The only reports of *Hexarthra* sp. came from Burns and Mitchell (1980) in New Zealand who found high abundance in winter, while Zarfdjian (1989) only occasionally found the species *Hexarthra mira* in Lake Volvi. In Lake Trichonis this species was more abundant in the colder seasons and its seasonal variation correlated with lower temperatures. Finally, the results for the seasonal distribution of *Brachionus calyciflorus* coincide with the reports of Berzins and Pejler (1989) and Holst et al. (1998), while Zarfdjian (1989) reported the occasional presence of the species in Lake Volvi.

The preference of the genus *Diaphanosoma* sp. for the warm periods of the year is well known (Herzig 1984; Korovchinsky 1992). Zarfdjian (1989) reported that *Diaphanosoma orghidani* exhibited peak on abundance during summer in Lake Volvi (northern Greece), while in the winter the species disappeared and existed only in the

form of resting eggs. Present results showed that in Lake Trichonis, where the temperature regime is higher than in Lake Volvi, this species can be present all year-round.

Bosmina longirostris is a common cladoceran in European lakes where it seems to have a year-round presence (Hanazato and Yasuno 1987; Mason and Abdul-Hussein 1991). This species can utilize the low food availability in winter, and as a low efficiency bacteriofeeder, is expected to be more abundant in autumn and spring (Geller and Müller 1981; Michaloudi et al. 1997), which is in agreement with the present results. Considering the known preference of *B. longirostris* and *D. orghidani* for the colder and warmer periods, respectively, temperature must have played an important role in their seasonal distribution during the first period (September 2003–August 2004), when they showed a clear pattern of dominance in the colder and warmer seasons. However, no significant correlation between their density and temperature was recorded, since the correlation data came from the second sampling period (September 2004–August 2005), when there was a change in the succession of these species and also in the cladoceran community.

Daphnia cucullata is a thermophilous species having a maximum abundance in late spring and summer, although it can be present in the zooplankton throughout the year (Gliwicz et al. 1981; Zarfdjian 1989; Michaloudi et al. 1997). It is interesting to note here, that the emergence of *D. cucullata* in August 2004 coincided with that of *Leptodora kindtii*. The latter species is a typical predator on the zooplankton of inland waters, preying on other crustaceans and especially *Daphnia, Diaphanosoma, Conochilus* colonies and copepod nauplii (Lunte and Luecke 1990). Perhaps in this case a prey-predator relation could explain the almost simultaneous appearance of both species.

Dreissena polymorpha larvae were present throughout the sampling period in Lake Trichonis, which is in accordance with the reports of Stankovic (1959) for Lake Ohrid, but in contrast to the absence of this species during the colder periods from three lakes situated in northern Greece, Lake Megali Prespa, Lake Volvi and Lake Mikri Prespa (Zarfdjian 1989; Michaloudi 1997). Lewandowski (1982) stated that the duration of the planktonic larvae of this species in European lakes increases from northern to southern areas, as a result of the effect of temperature on its reproductive period. In contrast to the above three lakes, in both Trichonis and Ohrid lakes the water temperature does not drop below 9°C, which is possibly the lowest temperature limit that determines the prolonged planktonic phase of *D. polymorpha*. Temperature seemed to be the most decisive abiotic factor controlling the seasonal variation of this species, since it showed the most unambiguous correlation with temperature among all zooplankters in Lake Trichonis, as it was also reported by Michaloudi et al. (1997) in Lake Mikri Prespa.

Vertical distribution

The maximum zooplankton concentration in Lake Trichonis was recorded in the surface 0–10m and decreased with depth, and this pattern is common among the deep stratified lakes (Hanazato 1992; Wetzel 2001). It is remarkable that most of the zooplankton species and groups maintained the same pattern of vertical distribution in both sampling years, and no significant differences were recorded between them. This stability in the vertical distribution probably means that species

in the lake have adopted a vertical position which has proved beneficial for their survival.

Temperature and oxygen concentration are among the most important abiotic factors affecting the vertical distribution of zooplanktonic species, while others such as light penetration, food availability, competition and predation, form a multi-variate framework (Wetzel 2001). Temperature must have been the most important factor affecting the vertical distribution of *Diaphanosoma orghidani* which, as a thermophilous species (Korovchinsky 1992), was always found in the upper depth layers, with temperatures between 15 and 25°C. The oxygen content seems to be a crucial factor for the vertical distribution of several species, acting as a limiting factor only in the deepest layers and only during the stratification period.

In deep lakes with thermal stratification a pattern of vertical separation of species is common (Hanazato 1992; Armengol-Diaz et al. 1993) and is enhanced by interspecific competition, especially in cases of low food availability (Wetzel 2001). Considering the low phytoplankton densities in Lake Trichonis (Tafas and Economou-Amilli 1997), it could be suggested that the pattern of vertical separation of the most important rotifer species could be an adaptation in order to reduce competition among them and to gain a better exploitation of phytoplankton, on which they feed. However, there are no recent data on phytoplankton composition and abundance, as well as on the feeding of rotifers in Lake Trichonis, to support this hypothesis.

Theoretically, the coexistence of nauplii, copepodites and adults of *Eudiaptomus drieschi* in the same depth layer could lead to an intensive intra-specific competition, if all these parts of the population exploited the same resources (e.g. food) and since all stages had almost the same seasonal distribution. Although there are no references to the feeding and trophic preferences of this species, it could be assumed that there is a size selection for food particles, or that each ontogenetic stage shows preference for a specific type of food (Muck and Lampert 1984).

In the case of cladocerans, there were indications suggesting that they seem to have adopted different ecological strategies, such as space- or time-separation in order to reduce inter-specific competition, since competitive interactions have been reported for *Bosmina*, *Daphnia* and *Diaphanosoma* species (DeMott and Kerfoot 1982; Matveev 1987). However, competition can be seen also among copepods and cladocerans (McNaught 1975; Muck and Lampert 1984), but it is not possible to estimate the exact weight of it in the present study.

Predation is another factor which strongly influences the abundance and distribution of zooplankton (Wetzel 2001). There is a vast population of *Atherina broyeri*, which preys on zooplankton following the seasonal composition and abundance of the community in Lake Trichonis (Chrisafi et al. 2007). However, there is need of further research focusing on the diet preference and feeding of this fish species, in order to understand the dynamics exercised in the zooplankton community. Moreover, it is difficult to evaluate the affect of other predators, such as *Leptodora kindtii*, on zooplankton groups or species in the lake since no data exist on the feeding of this species in the area of study.

In conclusion, the present paper may be considered as an attempt to give more comprehensive information on zooplankton abundance and distribution in Lake Trichonis during the two years of investigation. The results on species composition, abundance and spatial distribution showed that the lake displays the basic

characteristics of an oligotrophic lake, while also exhibiting some eutrophic features. The existence of considerable qualitative and quantitative differences in the zooplankton community between the two years of study point to the need of an extensive monitoring of the biotic and abiotic elements of the ecosystem, since the lake is the largest in Greece and has great ecological and economical interest.

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