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Seasonal vertical distribution and diel migration of zooplankton in a temperate stratified lake

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Abstract: The investigation of the vertical distribution of the zooplankton community in the temperate Lake Trichonis during four seasons in 2005, showed the existence of vertical segregation among species, ontogenetic stages and sexes within and between the major groups. In each season, the two or three more abundant rotifer species distributed at separate depth layers, while this feature was maintained during the entire 24 h period, since no diel vertical migrations (DVM) were performed. In contrast, the crustacean community, comprised mainly by the calanoid copepod *Eudiaptomus drieschi* and the cladoceran *Diaphanosoma orghidani*, showed various patterns of DVM, being more pronounced in spring and summer. Females of *E. drieschi* distributed deeper than males, while the copepod nauplii were found mainly in the surface layer in all four seasons. Temperature was the most important abiotic factor affecting directly and indirectly the vertical distribution and migration of various species. During stratification, the metalimnion was the most productive layer in Lake Trichonis, having maximum values of dissolved oxygen and low transparency due to high concentration of organic matter and phytoplankton. The DVM patterns of the crustaceans indicate that the metalimnion acts probably as a daylight refuge against predation by *Atherina boyeri*, which is the dominant planktivorous fish in the lake.

Key words: zooplankton; vertical distribution; diel vertical migration (DVM); stratification; Lake Trichonis

Introduction

The vertical distribution of zooplankton has been thoroughly studied over the time, as one of the factors that determine the functioning of aquatic ecosystems. There are various biotic and abiotic parameters affecting the vertical distribution patterns of freshwater zooplankters, especially in stratified lakes which are characterized by pronounced vertical gradients of certain physical, chemical and biological elements (Ringelberg 1999; Wetzel 2001). The vertical stratification of such factors creates various microhabitats. Specifically, vertical gradients of light, temperature, oxygen, solar radiation and food availability as well as predation pressure by planktivorous fish have been identified as factors that affect the vertical distribution of zooplankton (Stich & Lampert 1981; Lampert 1989; Hanazato 1992; Dini et al. 1993; Kessler & Lampert 2004; Persaud & Williamson 2005; Thackeray et al. 2006; Helland et al. 2007; Gélinas & Pinel-Alloul 2008; Williamson & Rose 2009), driving these organisms to search for optimum habitats (Lampert et al. 2003). The patterns and duration of thermal stratification have been shown to influence the vertical distribution of several zooplankton groups in deep lakes (Burns & Mitchell 1980; Marcogliese & Esch 1992; Winder et al. 2003; Thackeray et al. 2006). Moreover, competition for limited resources can cause spatial-temporal niche separation among species (Ciros-Perez et al. 2001).

A particular case of depth-selection behavior is the diel vertical migration (DVM), exhibited by many zooplankton species in marine and freshwater systems (Hutchinson 1967; Lampert 1989; De Meester & Weider 1999; Ringelberg & Van Gool 2003). Three DVM patterns are recognized in freshwater ecosystems. The ascent of migrators in the water column in the evening and their descent in the morning is termed as "normal" DVM, while the ascent to shallow water at sunrise followed by a descent to deeper water at sunset is described as "reverse" DVM. The third pattern, "twilight" DVM, involves an ascent to the surface at sunset, a descent to deeper water around midnight, followed by a second ascent to the surface and then descent to deeper water at sunrise (Hutchinson 1967; Lampert 1989). Light changes at dusk and dawn are considered the triggering mechanism of this behaviour (Ringelberg & Van Gool 2003). Through migration, zooplankters can reduce predation risk by planktivorous fish (Lampert 1993; De Meester et al. 1999; Liu et al. 2006; Castro et al. 2007), avoid damaging by solar radiation (Williamson & Rose 2009), or derive a physiological and reproductive advantage from spending time in cooler waters during the day (Kessler & Lampert 2004). Different combinations of food, temperature and predation

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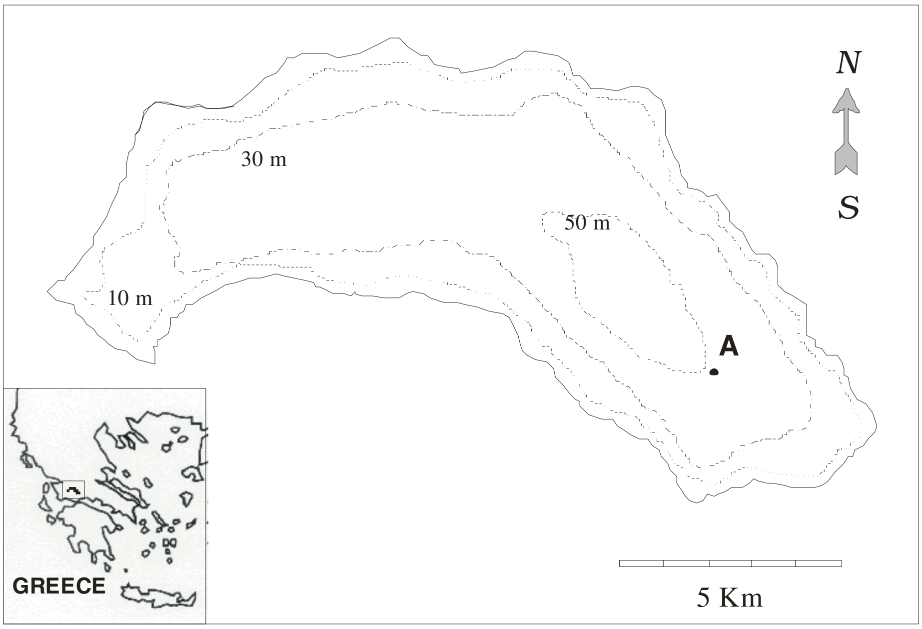

Fig. 1. Location of the sampling station A in Lake Trichonis.

pressure may cause the large variability in migration patterns observed (Lampert et al. 2003).

Lake Trichonis is the largest natural lake in Greece (surface area of 98.6 km^2, catchment area of 421 km^2), situated in the western part of the country (38°18′–38°51′ N, 21°01′–21°42′ E), at an altitude of 18 m a.s.l. It is a deep ($Z_{\max} = 57$ m, $Z_{\text{mean}} = 29$ m), warm monomictic lake, exhibiting a long period of thermal stratification, and has been classified as oligotrophic to mesotrophic (Skoulikidis et al. 1998). Lake Trichonis has great ecological importance and was included in the protected areas of NATURA 2000, it is also home to valuable commercial fishery of *Atherina boyeri* (Risso, 1810) (Leonardos 2001). Zooplankton is a very important component of the lake's ecosystem, as it constitutes the main prey of the zooplanktivorous *A. boyeri* (Chrisafi et al. 2007; Doulka et al. 2007), yet, there is little information about this element in Lake Trichonis. A two-year study conducted recently by Doulka & Kehayias (2008) provided some interesting data on the temporal and spatial distribution of zooplankton in the area. This study related the vertical segregation of zooplankton to low food availability (Doulka & Kehayias 2008). However, these results came from samples collected only in the morning hours without, consequently, providing information about the vertical distribution of zooplankton over the 24 h period.

Although there is a great number of studies on the vertical distribution and migration of zooplankton, this issue is still interesting because of the high complexity of the ecosystems and the alterations in the global climatic conditions which keep this ethological adaptation at the focus of attention in the aquatic ecology. And in deep temperate lakes, there is little information on the vertical distribution and DVM of the zooplankton community in relation to the main physical, chemical and biological parameters. Moreover, there is little information for Mediterranean lakes bearing specific features like the presence of *A. boyeri* as the main planktivore, thus trophic interactions in such ecosystems could be very interesting (Blanco et al. 2003; Castro et al. 2007). Considering the above, the present study aims to investigate the dynamics of the vertical distribution of zooplankton during the 24 h in the deep stratified Lake Trichonis, to recover possible alterations in the distributional patterns of zooplankton among seasons and to evaluate the influence of certain physicochemical and biological elements in this behavior.

Material and methods

Zooplankton samples were collected seasonally during four 24 h periods in winter, spring, summer and autumn 2005 in Lake Trichonis. Sampling was conducted at pelagic station A near to the deepest part of the lake with a depth of 48 m (Fig. 1). Vertical zooplankton samples were taken every 4 h, six times during a 24 h period, corresponding to the morning (09:00), midday (13:00), evening (17:00), night (21:00), midnight (01:00) and dawn (05:00). There was no moon-light on either occasion. Water column was sampled in 5 m intervals, spanning from 0 to 45 m, by integrating each 5 m depth stratum in a vertical haul with a closing plankton net, (50 μm mesh size, 40 cm in diameter and 100 cm in length). All samples were immediately fixed in 4% formalin; creating a solution with a final volume of 100 ml. Sampling with successive (and cumulative) hauls may induce mixture of the water column and consequently affect the vertical distribution of zooplankton (at least partially). In order to minimize this effect the following precautions were taken: A) The vertical hauls started from the surface 0–5 m and continued with 5–10 m, 10–15 m e.t.c. B) After the lowering of the net to the desired depth, the net was held still for at least 1 min before starting the haul. C) The towing of the net in the successive samples was performed from different sides of the boat (port – starboard). D) The time between the hauls was about 5 min, decreasing the influence of sampling procedures on the zooplankton organisms.

The zooplankton specimens were examined under a dissecting microscope and were identified to the lowest taxonomic level possible. 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 (Doulka & Kehayias 2008). In cases when less than 100 specimens were present in each of the subsamples, the whole sample was examined. For each copepod species, male and female specimens and copepodites were counted separately, while copepod nauplii were analyzed together, since it was not possible to distinguish between nauplii of different taxa. Numbers of specimens per sample were converted to percentages of the total specimens caught over the 0 to 45 m depth range.

Water transparency was measured with a Secchi disc, while temperature (T) and dissolved oxygen (DO) measurements were taken from the surface down to 40 m, using WTW portable instruments. For the estimation of chlorophyll-a (chl-a) concentration, water samples collected once per sampling date (at 09:00), at 10 m depth intervals, with a 2 L Ruttner water sampler, and analysis was performed spectrophotometrically (APHA, AWWA & WPCF 1998).

For the comparison of the vertical distributions of the zooplankton community, the weighted mean depth (WMD) was calculated for each species and group according to Hofmann (1975), as follows:

$$\frac{\mathrm{WMD} = \sum(N_{T_i} \times T_i)}{\sum N_{T_i}}$$

where WMD = weighted mean depth, N_{T_i} = the abundance in the depth i, and T_i = depth (m). Although the weighted mean depth cannot represent the actual vertical distribution of a species, it is a good numerical base for the application of statistics. Thus, differences between the WMDs of zooplankton species were tested using either a t-test or one way ANOVA on $\log(x)$ transformed data and were further expressed by the LSD (Least Significant Difference) test. In these tests the specie's WMDs calculated in each of the six different times, were treated as independent replicates, since there were no statistically significant correlation between sampling time and WMD (Pearson's r correlation coefficient, $P > 0.05$) for all zooplankton groups and species.

Correlations between the zooplankton abundance and the vertical profile of temperature, DO and chl-a for each season were made using Pearson's r correlation coefficient, on data transformed to $\log(x + 1)$. In particular, the abundance of zooplankton species in each 5 m depth stratum was correlated with the mean value of temperature and DO within the same stratum, while in the case of zooplankton and chl-a, average values corresponding to 10 m depth strata for both parameters were used.

Results

Physicochemical data

The temporal variations of temperature in Lake Trichonis lead to the development of a seasonal thermocline from April until November, causing highly stable water stratification within the lake. In winter, the temperature in the water column was almost homogenous and fluctuated between 13.2℃ at the surface and 10.5℃ at 40 m. In spring, the thermocline layer was developed between 8 and 24 m, having a temperature gradient of

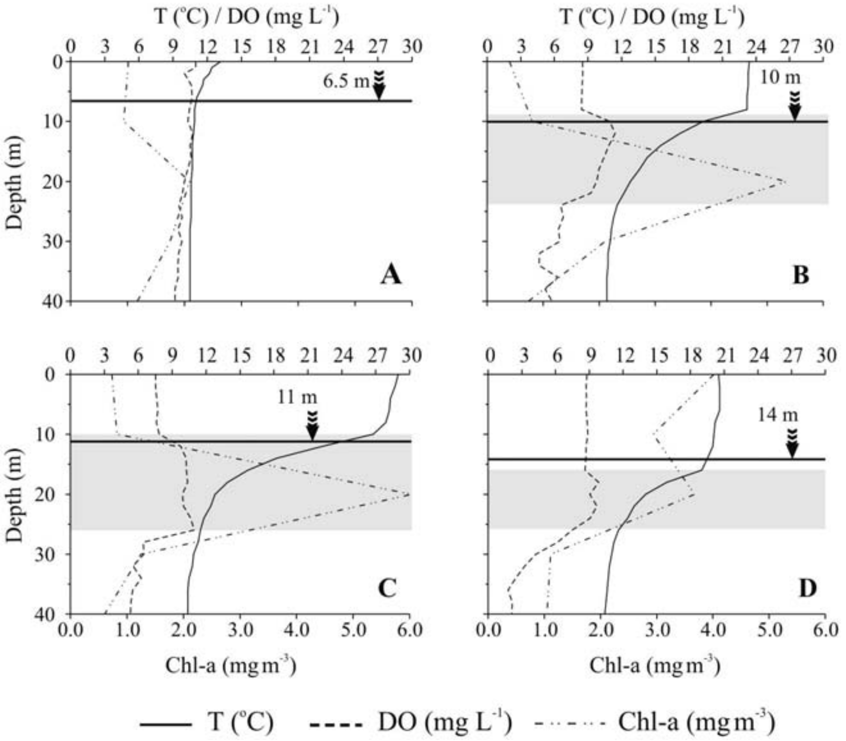

Fig. 2. Temperature, dissolved oxygen (DO) and chl-a vertical profiles in the sampling location, in winter (A), spring (B), summer (C) and autumn (D). The shadowed area indicates the range of the thermocline layer and the arrow indicates the Secchi disk depth.

11.6 ℃. In summer, it was formed slightly deeper (between 10 and 26 m) with a temperature gradient of 15.3 ℃ within its borders, while in autumn this layer was found between 16 and 26 m, with a weaker temperature gradient of 4.3 ℃ (Fig. 2).

The concentration of the dissolved oxygen (DO) was rather uniform along the water column in winter (11–9.2 mg L^{-1}). However, in all the other seasons when water stratification was apparent, the DO showed an increase in the range of the thermocline, with a maximum of 11.4 mg L^{-1} in spring, 10.9 mg L^{-1} in summer and 9.7 mg L^{-1} in autumn. The DO in the hypolimnion dropped under 6 mg L^{-1}, and the minimum value of approximately 2 mg L^{-1} was recorded below 35 m in autumn (Fig. 2). There were no differences in the vertical distribution of either temperature or DO among the sampling hours in all dates.

The concentration of chl-*a* in winter, spring and summer reached its maximum values at 20 m depth (2.1, 5.3 and 6.0 mg m^{-3}, respectively). In autumn, two chl-*a* peaks of 4.0 and 3.7 mg m^{-3} were recorded at the surface layer and at 20 m depth, respectively (Fig. 2). Finally, water transparency at the sampling site fluctuated between 6.5 m in winter, 10 m in spring, 11 m in summer and 14 m in autumn (Fig. 2).

Vertical distribution and diel migration of zooplankton
Four major taxonomic groups were recorded during this study. Copepoda were dominant during winter, spring and summer, while in autumn the larvae of the mollusk *Dreissena polymorpha* (Pallas, 1771) prevailed. Among copepods the calanoid *Eudiaptomus drieschi* (Poppe & Mrázek, 1895) was dominant, while the cyclopoid species *Macrocyclops albidus* (Jurine, 1820) and *Microcyclops varicans* (Sars, 1863) were scarce in the samples and were not considered in the study. *Kellicottia longispina* (Kellicott, 1879) was among the most abundant species in the rotifer's community throughout the sampling period. Along with *K. longispina*, *Hexarthra* sp. (Schmarda, 1854) in winter, *Gastropus stylifer* (Imhof, 1891) and *Ploesoma truncatum* (Levander, 1894) in spring, *Pompholyx sulcata* (Hudson, 1885) in summer and *Trichocerca similis* (Wierzejski, 1893) in autumn. Among the cladocerans, *Diaphanosoma orghidani* (Negrea, 1982) was the dominant species during the entire sampling period, while *Bosmina longirostris* (Müller, 1785) and *Daphnia* sp. (Müller, 1785) were found sporadically and in low abundance, thus they were excluded from further analysis.

There were differences in the vertical distribution of several rotifer species among seasons. Considering the WMD, statistically significant variations were recorded for *K. longispina* among the four sea-

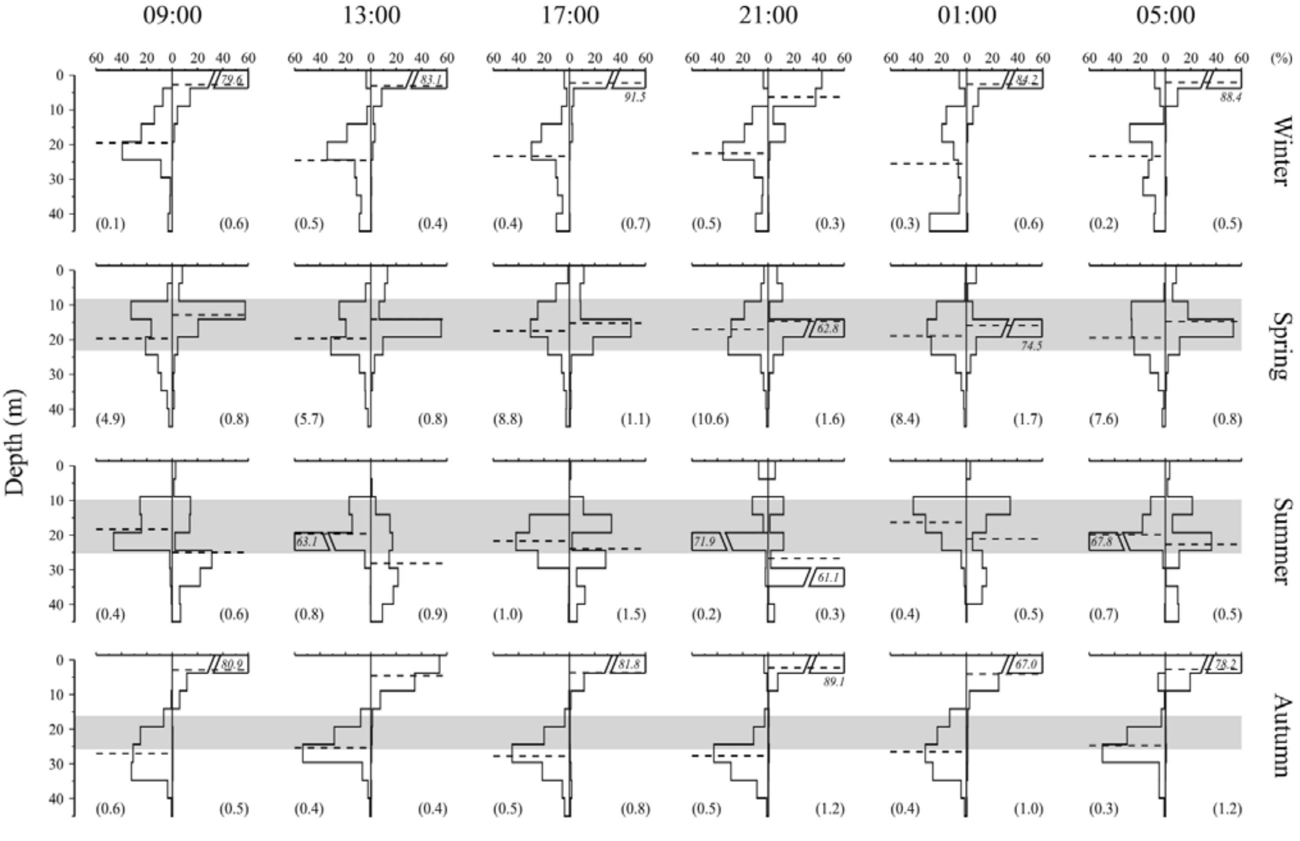

Fig. 3. Diel vertical distribution of *Kellicotia longispina* (left) and *Hexarthra* sp. (right) in winter, *K. longispina* (left) and *Gastropus stylifer* (right) in spring, *K. longispina* (left) and *Pompholyx sulcata* (right) in summer, *K. longispina* (left) and *Trichocerca similis* (right) in autumn, as percentages (%) of total caught in water column sampled. The shadowed area indicates the range of the thermocline layer and the dotted line indicates the weighted mean depth. Mean integrated abundance values (ind. L^{-1}) in the 0–45 m are shown in brackets.

Table 1. Correlation of species density with temperature, oxygen content and chlorophyll-a given as the Pearson's r correlation coefficient.

	09:00	13:00	17:00	21:00	01:00	05:00
Winter						
	Temperature					
Hexarthra sp.	0.972***	0.952***	0.934**	0.892**	0.958***	0.952***
E. drieschi	0.780*	0.914**	0.981***	0.918**	0.965***	0.989***
D. orghidani	0.954***	0.945***	0.931**	0.936**	0.925**	0.950***
Nauplii	0.977***	0.958***	0.895**	0.948***	0.956***	0.974***
	Chlorophyll-a					
K. longispina	0.745	0.975*	0.930	0.879	0.355	0.673
Spring	Temperature					
E. drieschi (ad)	0.854**	0.487	0.654	0.622	0.674	0.685
E. drieschi (cop)	0.658	0.132	0.654	0.584	0.768*	0.734*
D. polymorpha	0.817*	0.833*	0.739*	0.759*	0.786*	0.805*
D. orghidani	0.808*	0.914**	0.731*	0.870**	0.960***	0.831*
	Dissolved Oxygen					
K. longispina	0.548	0.509	0.792*	0.595	0.598	0.592
	Chlorophyll-a					
K. longispina	0.860	0.953*	0.620	0.876	0.869	0.883
Summer	Temperature					
E. drieschi (ad)	0.332	–0.022	0.157	0.825*	0.919**	0.891**
E. drieschi (cop)	0.830*	0.149	0.484	0.902**	0.551	0.300
D. polymorpha	0.849**	0.563	0.963**	0.788*	0.802*	0.871**
D. orghidani	0.737*	0.477	0.747*	0.826*	0.875**	0.856**
Nauplii	0.773*	0.622	0.686	0.858**	0.950**	0.813*
	Dissolved Oxygen					
K. longispina	0.812*	0.700	0.738*	0.561	0.747*	0.679
	Chlorophyll-a					
K. longispina	0.997**	0.913	0.913	0.736	0.763	0.894
Autumn	Temperature					
K. longispina	–0.755*	–0.520	–0.693	–0.721*	–0.740*	–0.504
E. drieschi (cop)	0.604	0.618	0.509	0.490	0.615	0.733*
	Chlorophyll-a					
E. drieschi (fem)	0.585	0.568	0.558	0.337	0.996**	0.980*

Explanations: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

sons (one way ANOVA, $P = 0.001$), for *Hexarthra* sp. between winter and summer (t-test, $P = 0.001$), and for *G. stylifer* between spring and autumn (t-test, $P = 0.002$). More specifically, *K. longispina* clearly avoided the surface in all four seasons and, during the stratified period, exhibited metalimnetic maxima following the deepening of the thermocline. *Hexarthra* sp. occupied the surface layer in winter, while in summer it was found within the thermocline layer. *G. stylifer* was found mainly within the metalimnion in spring, while in autumn it occupied the surface (0–5 m) layer (Fig. 3).

No plain diel vertical migration was apparent for the rotifer species. *Synchaeta* sp. (Ehrenberg, 1832) in summer was the only rotifer that occupied shallower depths during the daylight hours than during the night, changing its average day WMD over 3.5 m. This diel distribution resembled the "reverse" DVM pattern in which migrators move to deeper water strata during the night. Vertical segregation between the most abundant rotifer species in all seasons was noticed (Fig. 3). Thus, as indicated by their WMDs (t-test, $P = 0.000$), in winter the vertical distribution of *Hexarthra* sp., which was found in the surface 0–5 m layer, was statistically different than this of *K. longispina*, that was found deeper (between 15–25 m). In spring, statistically significant differences in the vertical distribution of the two more abundant species *K. longispina* and *G. stylifer* were recorded (t-test, $P = 0.000$). Both species were found mainly within the thermocline layer, however, *K. longispina* also inhabited the hypolimnion, while *G. stylifer* was also distributed in the epilimnion. In summer, the two most abundant rotifer species *P. sulcata* and *K. longispina* showed statistically significant difference in their vertical distributions (t-test, $P = 0.001$), with *P. sulcata* occupying deeper strata than *K. longispina*. On the other hand, the less abundant rotifer species *Synchaeta* sp. and *Filinia longiseta* (Ehrenberg, 1834) had similar diurnal vertical distributions (t-test, $P = 0.377$) and were found mainly in the surface layer (0–5 m), being vertically separated from the more abundant species. In autumn, *T. similis* and *K. longispina* were found mainly in the epilimnion and metalimnion, respectively (t-test, $P = 0.000$), occupying almost completely separate depth horizons (Fig. 3).

Positive correlation between the DO and the distribution of *K. longispina* in the vertical axis was recorded for most of the sampling hours in summer, while negative correlation with temperature was recorded for certain hours in autumn (Table 1). Moreover, *K. longispina* was the only rotifer species which showed positive correlation with chl-a in some cases in winter, spring and summer. Also, there was strong positive cor-

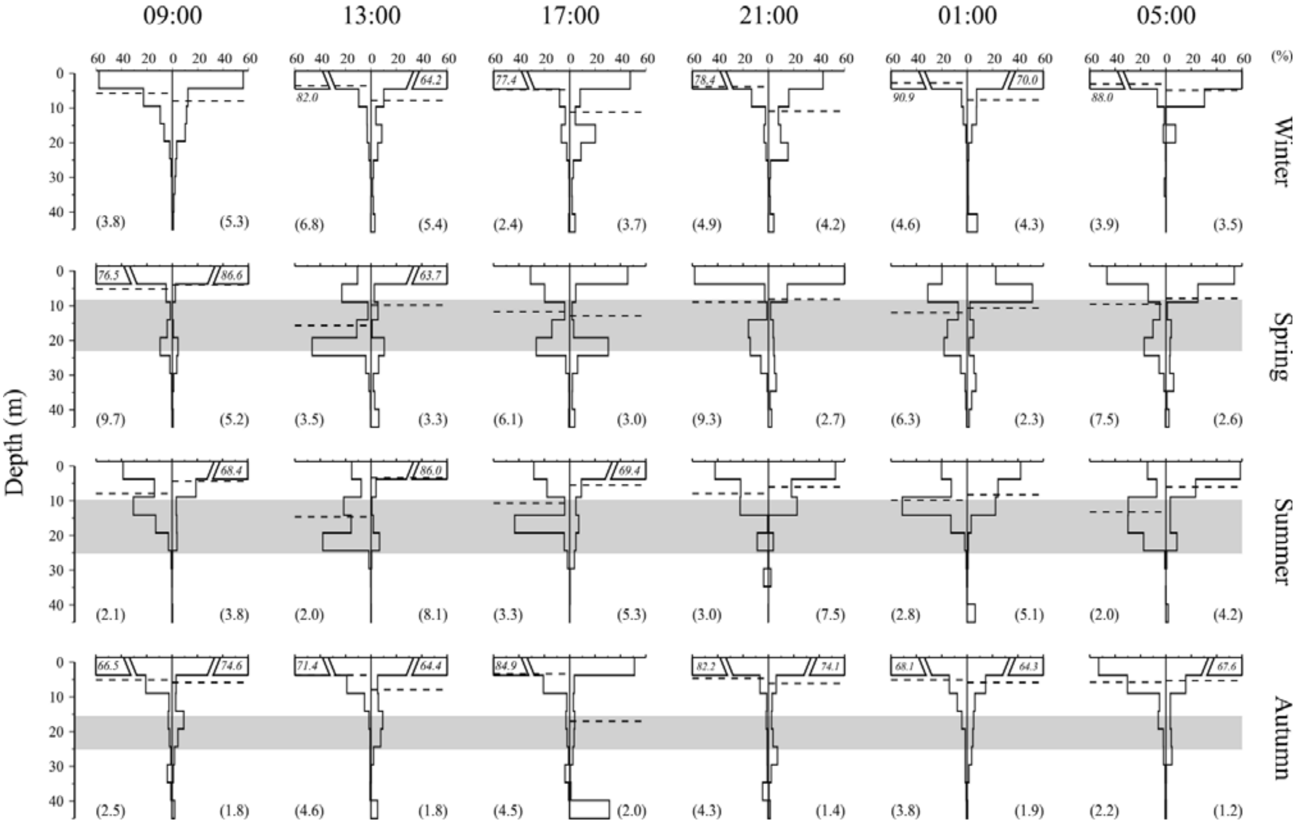

Fig. 4. Diel vertical distribution of the *Eudiaptomus drieschi* copepodites (left) and copepod nauplii (right) in the four sampling seasons, as percentages (%) of total caught in water column sampled. The shadowed area indicates the range of the thermocline layer and the dotted line indicates the weighted mean depth. Mean integrated abundance values (ind. L^{-1}) in the 0–45 m are shown in brackets.

relation between temperature and *Hexarthra* sp. for all the sampling hours in winter (Table 1).

Differences in the vertical distribution of the adults and copepodites of *E. drieschi* among seasons were noticed (one way ANOVA, $P = 0.022$ and $P = 0.000$, respectively), with both reaching deeper strata in spring and summer. Copepod nauplii were found mainly in the surface layer in all four seasons, reaching greater depths than the copepodites only in winter (*t*-test, $P = 0.001$). Contrary, in summer they had shallower distribution than the adults and copepodites (one way ANOVA, $P = 0.003$), especially during the daytime (Fig. 4). Statistically significant differences in between the WMDs of males and females of *E. drieschi* were recorded in winter, spring and autumn (*t*-test, $P = 0.031$, $P = 0.003$ and $P = 0.023$, respectively). In most cases, the WMD of females was greater than of males, which occupied mainly the surface (0–10 m) strata (Fig. 5).

There was positive correlation between temperature and the vertical distribution of the total population of *E. drieschi* for all the sampling hours in winter (Table 1). Positive correlation between the vertical distribution of the adult *E. drieschi* and temperature was recorded in spring and especially in summer but only for the night samplings between 21:00 and 05:00. *E. drieschi* copepodites were also positively correlated with temperature in several sampling hours in spring, summer and autumn, and nauplii in summer. Chl-*a* was positively correlated with the females of *E. drieschi* at midnight and dawn in autumn (Table 1).

Diel vertical migration patterns were recorded in spring and summer for adults and copepodites of *E. drieschi*, while during these vertical movements, most of the specimens entered the thermocline layer. In spring, males moved closer to the surface at night, shifting their average day depth over 4 m and resembling a “normal” DVM pattern. (Fig. 5). The diel alteration in the vertical distribution of the copepodites and females of *E. drieschi* in this season resembled the pattern of the “twilight” migration, in which the migrators approach the surface near dawn and dusk. In summer, both males and females seemed to perform “normal” DVM, avoiding the surface during the day and ascending in the night, shifting their average day depth over 5.9 and 3.8 m respectively. In autumn, the increased presence of the females within the thermocline layer during the night, 5.9 m below their average day depth, reflects the pattern of “reverse” DVM. The same pattern could be reflected in the diel vertical displacement of nauplii in summer. However, in most cases the vertical displacement of nauplii was within the range of the epilimnion, except in spring, when a great proportion of this stage was found in the lower part of the metalimnion in a bimodal distribution pattern (Fig. 4).

The cladoceran *D. orghidani* inhabited mainly the surface 0–10 m layer during the four seasons, while in spring and summer its distribution reached the metalimnion (Fig. 6). This species distributed shallower than

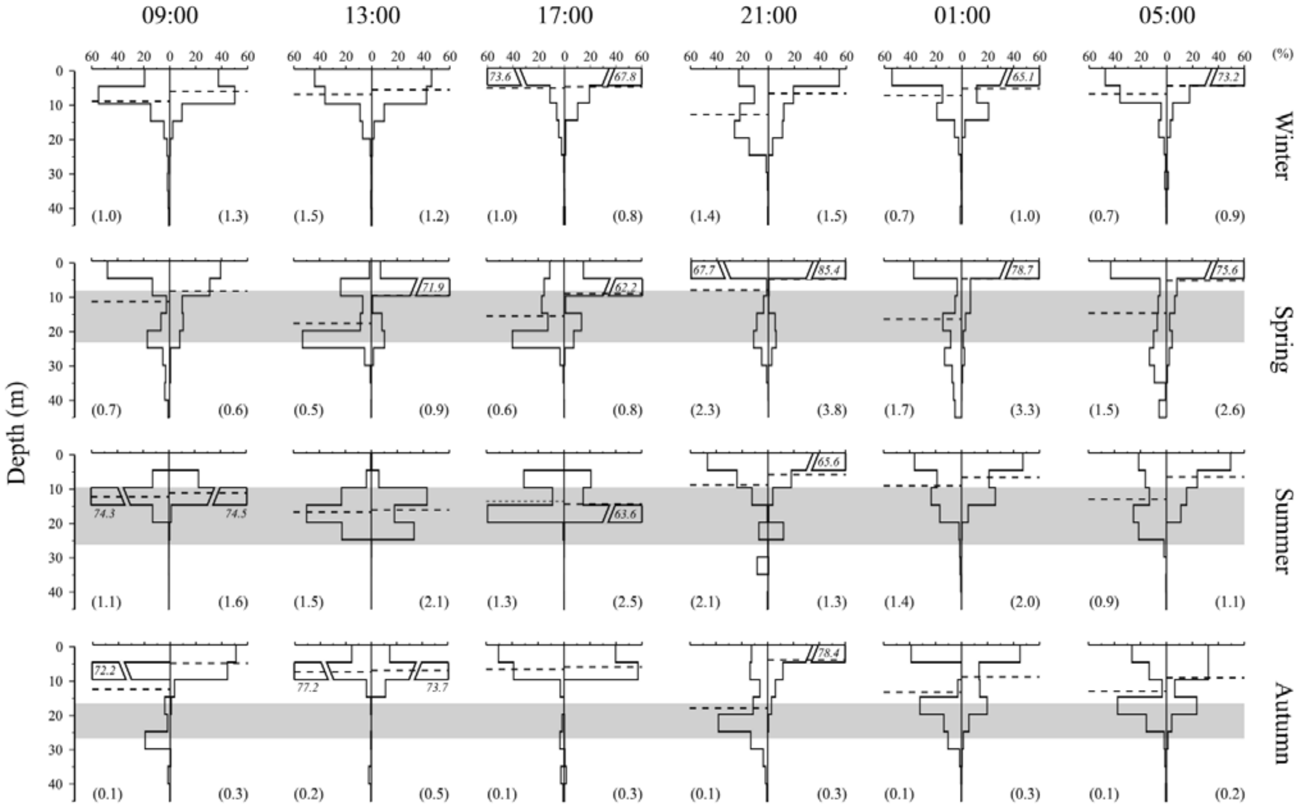

Fig. 5. Diel vertical distribution of female (left) and male (right) specimens of *Eudiaptomus drieschi* in the four sampling seasons, as percentages (%) of total caught in water column sampled. The shadowed area indicates the range of the thermocline layer and the dotted line indicates the weighted mean depth. Mean integrated abundance values (ind. L^{-1}) in the 0–45 m are shown in brackets.

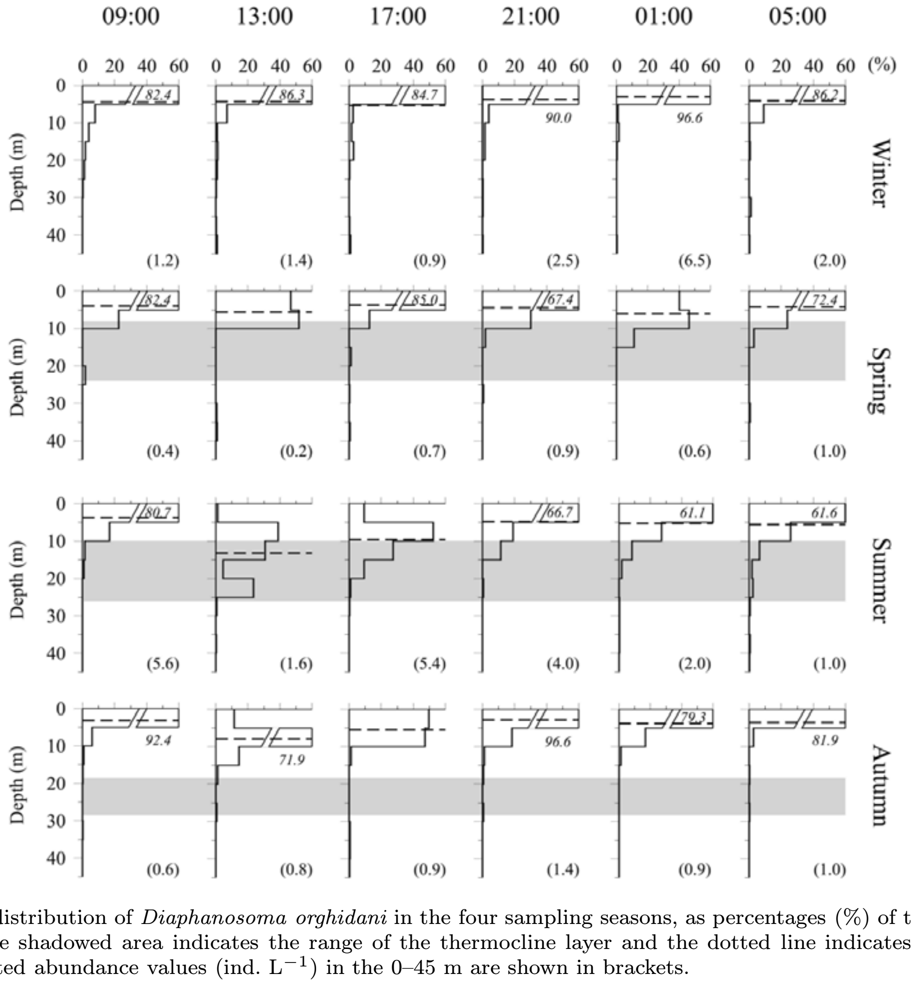

Fig. 6. Diel vertical distribution of *Diaphanosoma orghidani* in the four sampling seasons, as percentages (%) of total caught in water column sampled. The shadowed area indicates the range of the thermocline layer and the dotted line indicates the weighted mean depth. Mean integrated abundance values (ind. L^{-1}) in the 0–45 m are shown in brackets.

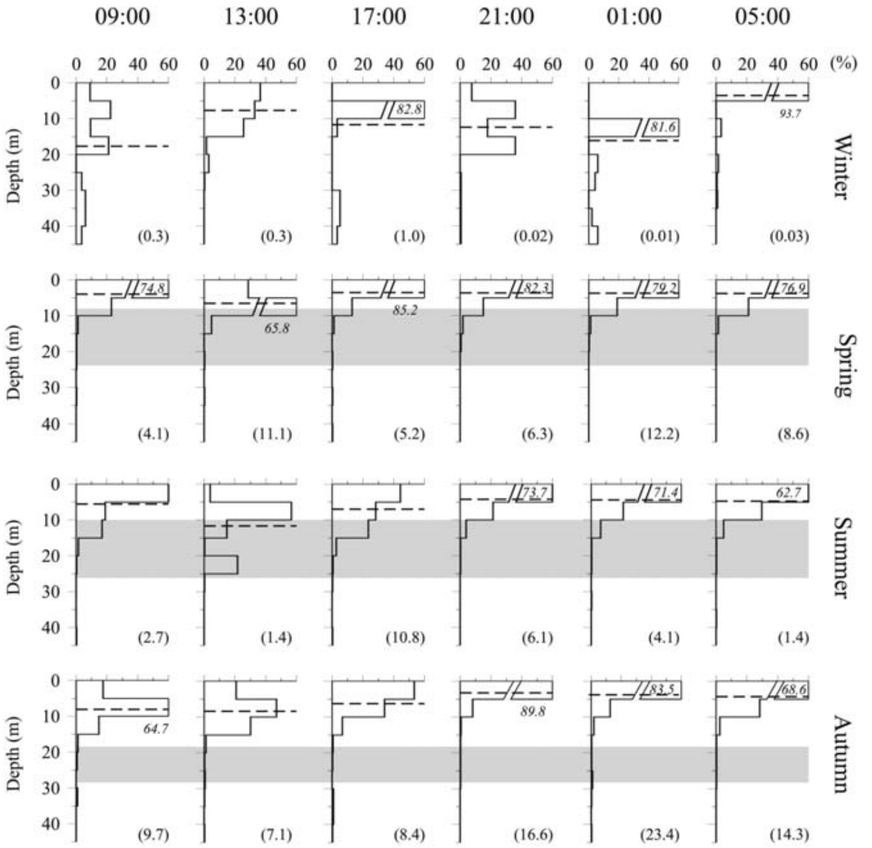

Fig. 7. Diel vertical distribution of *Dreissena polymorpha* in the four sampling seasons, as percentages (%) of total caught in water column sampled. The shadowed area indicates the range of the thermocline layer and the dotted line indicates the weighted mean depth. Mean integrated abundance values (ind. L^{-1}) in the 0–45 m are shown in brackets.

the adults (t-test, $P < 0.05$) of *E. drieschi* during the entire sampling period and also shallower than copepod nauplii (t-test, $P < 0.01$) in all seasons except summer, when *D. orghidani* reached its maximum abundance in the lake. Vertical separation between *D. orghidani* and the copepodites of *E. drieschi* was recorded in spring and summer (t-test, $P = 0.000$ and $P = 0.020$, respectively), with the former having shallower distribution than the latter.

An apparent “normal” DVM pattern was recorded for *D. orghidani* only in summer, when this species descended vertically in the midday entering the thermocline layer, while ascended over 3.6 m to the surface during the night hours. In autumn, *D. orghidani* performed an analogous vertical displacement as in summer, but did not enter the thermocline layer. Positive correlation between temperature and *D. orghidani* for most of the sampling hours in summer was noticed (Table 1).

The larvae of the mollusk *D. polymorpha* occupied mainly the epilimnion and were found in depths greater than 30 m only in winter (Fig. 7). During this season, the larvae were found in very low abundance and the diurnal variation of their vertical distribution was more intense, nevertheless no pattern of DVM was evident. In spring and summer, the population descended from the surface at midday and reached the lower layers of the metalimnion in the latter season. In autumn the gathering of the mollusk larvae in the surface layer during the night time, possibly reflects a small amplitude “normal” DVM, with a difference between the average day and night depth of 3.7 m. The vertical distribution of the mollusk larvae was positively correlated with temperature in almost every sampling hour in summer (Table 1).

Discussion

The seasonal water stratification in a lake ecosystem and the consequent formation of the thermocline (metalimnion) causes spatial variations in the zooplankton community structure (Bronmark & Hansson 1998; Thackeray et al. 2005). The metalimnion in Lake Trichonis is a layer of low transparency due to high concentration of organic matter and phytoplankton. On the other hand, the light intensity within this layer allows photosynthesis, which is benefited by the high nutrient concentrations released by decomposition processes. During the stratification period, the chlorophyll-*a* maximum found within the range of the metalimnion is known as deepwater chlorophyll maximum (DCM) and is a common feature for large oligotrophic lakes (Padisak et al. 1997; Williamson et al. 1996; Barbiero & Touchman 2001; Winder & Hunter 2008). As phytoplankton growth is enhanced within the metalimnion, oxygen production increases and the concentration of dissolved oxygen is favored by the decreasing temperature, resulting in the metalimnetic oxygen maximum occurring during stratification. Due to the prolonged stratification period, Lake Trichonis showed a minimum saturation value of dissolved oxygen in the lower hypolimnion in autumn, a common phenomenon in stratified lakes (Wetzel 2001). However, anoxic conditions were not recorded in the lake thus oxygen content should not be a restricting factor for the vertical dispersion of zooplankton. Consequently, the metalimnion in Lake Trichonis is the most productive depth stratum, due to the intense variation of abiotic and biotic variables within its boundaries creating a unique habitat for zooplankters.

The composition of the zooplankton community and the abundance of species during the seasonal study in Lake Trichonis were in agreement with the reports of Doulka & Kehayias (2008) for the same area. Considering the vertical distribution of the community throughout the sampling period, the general trend was the existence of vertical segregation among species, ontogenetic stages and sexes within and between the major zooplankton groups. Selection of different depth layers by the most abundant rotifer species has also been previously reported by Doulka & Kehayias (2008). Different tolerance of abiotic conditions by the rotifer species could cause vertical segregation of species (Mikschi 1989), however, the vertical fluctuation of those conditions in Lake Trichonis do not support this hypothesis. On the other hand, food limitation and resource competition are known to be capable of regulating the community structure of herbivorous zooplankton in natural environments, whereas spatial niche separation can minimize exploitative competition (Ciros-Perez et al. 2001 and references therein). Lake Trichonis has been characterized as an oligotrophic aquatic ecosystem considering the low phytoplankton densities (Tafas & Economou-Amilli 1997). Thus, it could be suggested that the most abundant species of rotifers could follow this vertical segregation in order to reduce the intra-specific competition for the exploitation of phytoplankton, which comprises their food (Doulka & Kehayias 2008). However, there are no qualitative or quantitative data on the phytoplankton community spanning the entire water column, nor information on the feeding of rotifers in Lake Trichonis to support this hypothesis.

In contrast to the reports of Doulka & Kehayias (2008), the present study revealed the existence of vertical separation between the ontogenetic stages of *Eudiaptomus drieschi* within the 24 h period in summer. In this period of intense stratification, nauplii were distributed within the epilimnion, being clearly separated during the daytime from adult copepods, which were found mainly in the metalimnion. It could be suggested that the divergence of these age groups reduces food competition in the warm epilimnion, while the higher temperature in this stratum enhances the faster development of the younger stages (Zadereev & Tolomeyev 2007; Rhyne et al. 2009). Nauplii have been reported to reduce competition with older ontogenetic stages by staying at different depth strata (Rejas et al. 2007). Zadereev & Tolomeyev (2007) reported that nauplii and early copepodites of the calanoid *Arctodiaptomus salinus* in Shira Lake (Russia) resided in the epilimnion even though the maximum of chlorophyll-*a* was located below the thermocline, suggesting that these ontogenetic stages prefer this location in order to maximize their fitness by ensuring the highest growth rate. Depth segregation was also observed between male and female *E. drieschi* and it was prominent almost in all times, with females residing in deeper strata. Female calanoid copepods have been found to prefer deeper strata than males in other cases as well (Svensson 1997a, b; Schabetsberger & Jersabek 2004; Jamieson 2005).

Atherina boyeri is the dominant planktivorous fish in Lake Trichonis with great ecological and also commercial importance, as it represents the main source of fishing revenues (Leonardos 2001). *A. boyeri* has been found to prey upon copepodites and especially adults of *E. drieschi*, but not upon nauplii (Chrisafi et al. 2007; Doulka et al. 2007). Predation pressure on zooplankton in Lake Trichonis has not been determined, however, predation by most pelagic fish is generally restricted to the upper illuminated part of the water column (Zaret 1980; Gliwicz & Pijanowska 1988). Taking into account that crustaceans are capable of seeking refuge in habitats less convenient to predators (Neil 1990; Pasternak et al. 2006), the daytime residence of adult copepods to the metalimnion, where light conditions and water clarity do not facilitate visual predation, probably acts as a predator avoidance mechanism against *A. boyeri.* This behaviour is more essential during summer, when the abundance of this predator species in the lake reaches maximum values (unpublished data). Thus, the vertical segregation of the ontogenetic stages of *E. drieschi* could be attributed to the potential different predation pressure exercised by planktivorous fish. In this sense, the deeper distribution of the females, which had larger "visual signal" than the males due to the presence of eggs, may constitute an anti-predator strategy.

Rotifers did not show clear diel vertical migration in any of the four seasons in Lake Trichonis. Although there are references on DVM of some of the species/genera found in the present study [e.g. *T. similis* and *G. stylifer* in Piaseczno Lake by Grzegorz et al. (2006); *K. longispina* in Lake Crescent by Rainey et al. (2007); *Synchaeta pectinata* in Kruczy Staw Lake by Karabin & Ejsmont-Karabin (2005)], rotifers are not expected to perform pronounced migrations due to their small size and poor swimming abilities (Armengol & Miracle 2000; Zhou et al. 2007). *Synchaeta* sp. seemed to be the only rotifer performing DVM following the "reverse" pattern in summer. Reverse migration has often been reported for rotifers, while its adaptive significance may reside in either avoiding predation by invertebrate predators, or competition with cladocerans and copepods (Rejas et al. 2007).

Diel vertical migration of the dominant calanoid copepod *E. drieschi* was recorded, with differences in the amplitude of the vertical displacement, as well as in the DVM patterns followed by the ontogenetic stages and sexes. The thermocline layer seems to drastically affect this behavior, since migrating phenomena were more intense during the stratified period. The most accepted explanatory mechanism for DVM in zooplankton is the avoidance of visual predation in the illuminated epilimnetic waters (Dodson 1990; Lampert 1993; Han & Straškraba 2001). The predation avoidance theory can explain the "normal" and "twilight" migration patterns of copepodites and adult *E. drieschi* in Lake Trichonis. Since both comprise prey for a visual predator as *A. boyeri*, they gain higher protection by remaining in the deeper layers of the thermocline during the daylight and ascending to the epilimnion during the hours of lower visibility (Zaret & Suffern 1976). Thus, the thermocline layer, which is a layer of low transparency due to high concentration of organic matter and phytoplankton, acts as a refuge for crustaceans more susceptible to fish predation. However, the alteration in the migratory movement of females in autumn to "reverse" DVM, as well as the same pattern exhibited by nauplii in winter and summer, could be indicative of avoiding predation by invertebrate predators e.g. *Leptodora kindtii* being more abundant in the summer as reported by Doulka & Kehayias (2008), or of avoiding competition with cladocerans and larger copepods (Rejas et al. 2007). It must be pointed that, copepod nauplii were not distinguished between calanoid and cyclopoid species in Lake Trichonis. This fact could complicate the observations, while it could explain the bimodal vertical distributions that were observed in some cases.

Diaphanosoma orghidani distributed shallower than *E. drieschi* in most of the sampling periods except in summer, when the stratification in the lake was more intense and its abundance was maximum. There is evidence that most of the dominant crustacean species became more aggregated in the vertical plane with increase in thermal stratification (Thackeray et al. 2006; Helland et al. 2007). Moreover, since *D. orghidani* is also a common prey for *A. boyeri* (Doulka et al. 2007), its vertical migration to deeper strata (reaching the lower metalimnion), could be a predation avoidance mechanism, as in the case of copepods.

The wide vertical dispersion of *Dreissena polymorpha* larvae along the water column in winter is in agreement with Lewandowski & Eijsmont-Karabin (1983) who reported a uniform vertical distribution for the mollusk during the unstratified period. Contrary, during the stratified period, the larvae of the mollusk *D. polymorpha* have been found to be restricted within the epilimnion (Lewandowski & Eijsmont-Karabin 1983), as it was found in the present study. The larvae of *D. polymorpha* have been reported to undergo vertical migrations (Sprung 1993). The normal DVM pattern performed by *D. polymorpha* larvae in autumn seems to be in accordance with Einsle & Walz (1972), who reported a descent of the larvae to the lower epilimnion at noon and dusk.

Temperature and DO are considered among the main abiotic factors governing habitat utilization by zooplankton in the vertical axis (Kessler & Lampert 2004; Thackeray et al. 2006; Helland et al. 2007). Certain species prefer to distribute within the warm epilimnetic waters, while others in the colder metalimnion. *D. orghidani*, which showed positive correlation with temperature and was found in the upper depth layers, is considered as a thermophilus species (Korovchinsky 1992). In contrast, *K. longispina* has been reported to avoid the surface layers and restricted in deeper strata (Grzegorz et al. 2006; Rainey et al. 2007). Grzegorz et al. (2006) claimed this species as oxyphilous and pointed that *K. longispina* in Piaseczno Lake (Poland) remained in the metalimnion throughout the whole diurnal cycle and seemed to be affected by the oxygen and trophic conditions. The positive correlation of *K. longispina* with the DO and with chl-*a* in the present study is in accordance with the above reports.

The results of the present study indicated seasonal changes in the vertical distribution of certain rotifer species. It has been reported that rotifers show a tendency of concentrating their populations within gradient zones and migrating downwards during stratification, following the thermocline (Armengol-Diaz et al. 1993). The seasonal vertical distribution of *K. longispina* and *Hexarthra* sp. was characteristic of this tendency, while the vertical distribution of *G. stylifer* in spring was constricted within the temperature gradient layer.

The vertical variation of temperature seems to have affected also the distribution of *E. drieschi* in winter. The absence of vertical movements throughout the 24 h period and the strong correlation of the total population with temperature, could be explained based on the theory of the greater metabolic gains (e.g., faster growth and egg development) provided by the higher surface temperature (Kessler & Lampert 2004), especially in the colder season of the year. In spring and summer however, the positive correlation of *E. drieschi* with temperature was restricted to the night hours, as other factors probably made the surface waters unfavorable during the daylight.

In conclusion, the vertical distribution and diel migration of the major zooplanktonic crustaceans in Lake Trichonis seemed to follow the fundamental ecological adaptations of predation avoidance and reduction of inter- and intra-specific competition. On the other hand, given the low food availability in this oligo-mesotrophic ecosystem and the limited swimming capability of rotifers, it could be suggested that the most abundant species of this zooplankton group would rather segregate vertically in order to reduce intraspecific competition, than expend energy in a large scale diel vertical displacement. Temperature is among the most important abiotic factors for the distribution of rotifers, while the dominant planktivorous fish *A. boyeri* seems to exercise major influence and maybe regulate the behavior of the larger zooplankton organisms, such as crustaceans. Further research on this issue is already in progress, to provide more comprehensive information on the adaptive significance of zooplankton vertical migration in this stratified lake of low productivity.

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