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AQUATIC WEEDS

Influence of hydrophyte abundance on the spatial distribution of zooplankton in selected lakes in Greece

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Abstract Submerged hydrophyte vegetation consists of a highly important biotic component of maintaining lake ecosystems towards a "clear water" ecological status. Aquatic macrophytes are well known to play a significant multidimensional role in lakes by competing with phytoplankton growth, stabilising sediment and offering refuge to fishes, macro-invertebrates and littoral zooplankton, amongst others. Zooplanktons that are associated with macrophyte beds, in particular, may act as a positive feedback mechanism that contributes to maintaining a clear-water state. Although there are several studies investigating the relationships between macrophytes and zooplankton in European lakes, few have yet been carried out in Greek lakes. Seasonal field sampling was conducted from spring 2006 to autumn 2008 in four lakes of northwestern Greece. Zooplankton samples were collected from within hydrophyte beds in each lake to estimate their relative abundance and species density. Hydrophyte abundance and composition was recorded on a five-point scale. Moreover, water samples were analysed to determine nutrient and chlorophyll-*a* concentration. Pearson correlations between zooplankton density and key physicochemical variables were conducted to distinguish significant abiotic variables related with major zooplankton groups. Kruskal–Wallis non-parametric analysis was used to test for significant differences in zooplankton composition and environmental variables amongst the five hydrophyte abundance classes. In addition, Canonical correspondence analysis was used to distinguish possible correlations amongst the macrophyte and zooplankton species. Zooplankton density was significantly higher in dense macrophyte vegetation. Small-sized species (e.g. Rotifera) dominated the zooplankton community, indicating the eutrophic nature of the lakes. Large Cladocera were present in low abundance and were mostly littoral. The current research contributes to a better understanding of relationships between biotic groups in selected Greek lakes.

Keywords Aquatic macrophytes · Zooplankton · Rotifers · Spatial distribution · Greek lakes

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Introduction

It is well known that aquatic macrophytes play a multidimensional role in the functioning of lake ecosystems. Numerous studies have shown the importance of aquatic macrophytes in reducing sediment resuspension, altering nutrient status, affecting the occurrence of associated organisms and providing refuges to small invertebrates (Scheffer, 1998). Thus, the presence of aquatic macrophytes have the capacity to maintain a clear-water state or even change water quality from a turbid to clear water state (Blindow et al., 1993; Jeppesen et al., 1999).

There are several studies that acknowledge the relationship between macrophyte beds and zooplankton communities, and which highlight their role in providing a positive feedback mechanism that helps maintain a clear-water state (Blindow et al., 2000). Macrophyte beds offer refuge to large-bodied grazer species such as *Daphnia*, which migrate horizontally from open water to littoral macrophyte beds (Burks et al., 2002). Moreover, mesocosm experiments demonstrated that large-bodied Cladocera dominated densely vegetated enclosures, whereas smaller rotifers and cyclopoid copepods proliferated in vegetation-free enclosures (Jeppesen et al., 2002). There are disadvantages, however, to inhabiting the macrophyte beds. These include competition with other zooplankton, food scarcity, chemical inhibition, adverse abiotic conditions and increased predation pressure from macrophyte-associated invertebrates (Burks et al., 2001, 2002). A further disadvantage for zooplankton is associated with the higher density of small fishes and other predators that congregate in macrophyte beds, especially under conditions of increased turbidity (Tolonen et al., 2001; Nurminen & Horppila, 2002; Burks et al., 2006).

Studies on the zooplankton composition of lakes in Greece have revealed that rotifers are the most abundant functional group (Michaloudi et al., 1997; Michaloudi & Kostecka, 2004; Moustaka-Gouni et al., 2006). However, there are only a few studies that investigate the structural relationships between macrophyte assemblages and zooplankton community. One such study revealed that Greek lakes with greater macrophyte coverage support a higher proportion of large-sized zooplankton species (Kagalou & Leonardos, 2009).

The objectives of this study are (a) to investigate the possible influence of aquatic macrophyte abundance on the spatial distribution of zooplankton in selected Greek lakes; (b) to provide additional data regarding the composition of zooplankton communities in certain lakes in Greece; and (c) to evaluate the ecological status of the lakes investigated using relevant data collected during this study. An additional aim is to determine the ecological role played by aquatic macrophytes and their interactions with other resident biotic groups in these Greek freshwater ecosystems. This information will contribute to the development of a detailed management strategy, as required under the Water Framework Directive.

Materials and methods

Study area

Our research was carried out in four lakes (Table 1) that are located in the region of Macedonia in northwestern Greece (Fig. 1). The basic morphological characteristics of the four lakes are presented in Table 1. Some relevant details regarding each lake are presented below.

Lake Mikri Prespa is located in northwestern Greece, with a small section extending in Albania. The surface area of the watercourse is ca. 47 km^2. It has an average depth of ca. 4.1 m and the maximum depth of 8.4 m. The lake is protected by European

Table 1 Key morphological characteristics of the four Greek lakes studied during this research

Lakes	Level (m a.s.l.)	Lake area (km^2)	Volume (10^6 m^3)	Average depth (m)	Maximum depth (m)	Retention time (years)
Mikri Prespa	853	47	221	4.1	8.4	3.4
Kastoria	629	27.9	144	4.4	9.1	2.3
Vegoritis	524	53	1530	28.9	48	9.5
Petron	527	14.4	37	2.6	5	–

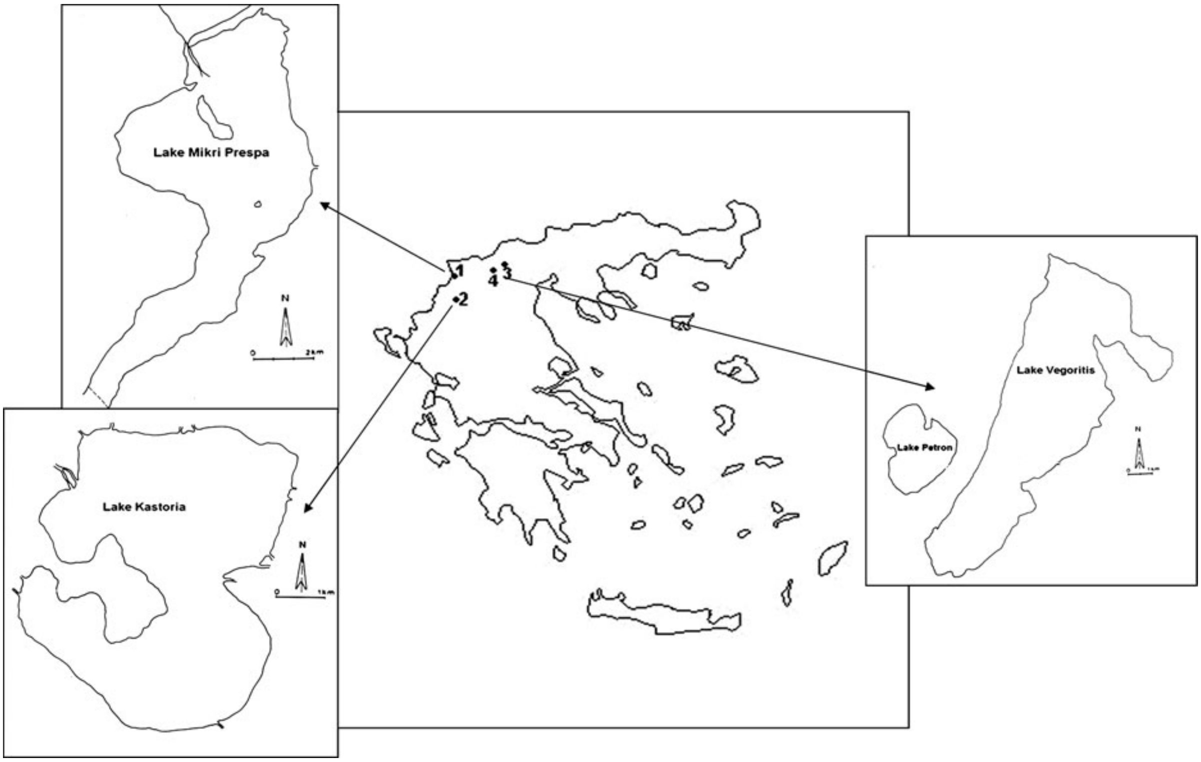


Fig. 1 The location of the studied lakes. *1* Mikri Prespa, *2* Kastoria, *3* Vegoritis, *4* Lake Petron

legislation and international conventions (Ramsar) as it represents an extremely important site in respect of fish and bird biodiversity (Catsadorakis, 1997).

The mean surface area of Lake Kastoria is ca. 27.9 km^2. It has an average depth of 4.4 m and maximum depth of 9.1 m. The city of Kastoria is located on the western sector of the lake and discharges from here have resulted in increased eutrophication, as reflected by increased cyanobacterial blooms, sediment pollution and increased toxin concentrations (Moustaka-Gouni et al., 2007).

Lake Vegoritis is one of the largest water impoundments in Greece. It is a deep lake with surface area of 53 km^2, a mean depth 28.9 m and maximum depth 48 m. For more than the last five decades, the lake has been suffering from a variety of environmental problems, principally resulting from agricultural and industrial pollution. This disruption is compounded by the huge decrease of water volume (water level decreased by 32 m between the 1950s and 2002) that resulted from the need to meet increasing hydro-electrical demand in the period from 1956 to 1985 (Gianniou & Antonopoulos, 2007). Field sampling was conducted in the southern part of the lake, an area with extended reedbeds and abundant submerged vegetation.

Lake Petron is a shallow lake with a surface area of 14.4 km^2, a mean depth of 2.6 m and a maximum depth of 5 m. The lake discharges into Lake Vegoritis, which is impacted by agriculture pollution and a significantly reduced water volume.

The above mentioned four lakes represent a typical Greek lake ecosystem sharing common characteristics such as, high nutrient concentration, introduction of several fish species and the presence of adjacent agricultural or urban environments (Zacharias et al., 2002; Kagalou & Leonardos, 2009). Thus, these lakes were deemed suitable for investigating the role played by submerged vegetation in influencing the spatial distribution of associated zooplankton communities, as the findings will likely be representative for the majority of Greek lakes.

Field work

Field sampling was carried out at 27 sites along the littoral zone during vegetation periods (spring to autumn) of 2006–2008. A total of 70 zooplankton samples were collected from the littoral zone, within the macrophyte beds, at sites of approximately 1–1.5 m deep. Some 35 and 20 samples were, respectively, collected during the spring summer and autumn periods of 2006 and 2007, while 15 samples were collected during spring and summer periods in 2008. Almost equal numbers of samples were taken from each of the four lakes (18 and 17 samples from lakes Kastoria and Mikri Prespa from lakes Vegoritis and Petron, respectively). The sampling was performed using a tube (1-m length and 10-cm diameter), and subsamples were pooled into a vessel to provide an integrated sample of approximately 10 l. A volume of 6–7 l was finally concentrated through a 50-μm net and immediately fixed with Lugol's solution.

At each site, aquatic macrophyte abundance was recorded according to a five-point scale (1: scarce or no vegetation, 2: several individuals, 3: small patches of vegetation, 4: continuous vegetation, and 5: macrophyte bed covering 100% of water column) by visual estimation. A rake was used to determine abundance when water transparency was limited (Fig. 2).

The following environmental variables were measured in the field using a portable multimeter instrument YSI and a Secchi disk: pH, dissolved oxygen, conductivity, temperature, and Secchi depth. Water samples from these sites were also collected and returned to the laboratory for further analysis. Concentration values for nitrate, nitrite, ammonium, carbonate, bicarbonate and chlorophyll-*a* were determined according to the analytical procedure of APHA (1992).

Rotifer and Cladocera were identified to genus or species level. Proportional abundances and densities for each taxon and major taxonomic group were calculated using a counting cell. Shannon–Wiener and evenness indices were calculated at each site for the zooplankton and aquatic macrophytes.

Data analysis

Kruskal–Wallis non-parametric test was used to examine the differences of variables' median amongst the abundance classes of submerged vegetation.

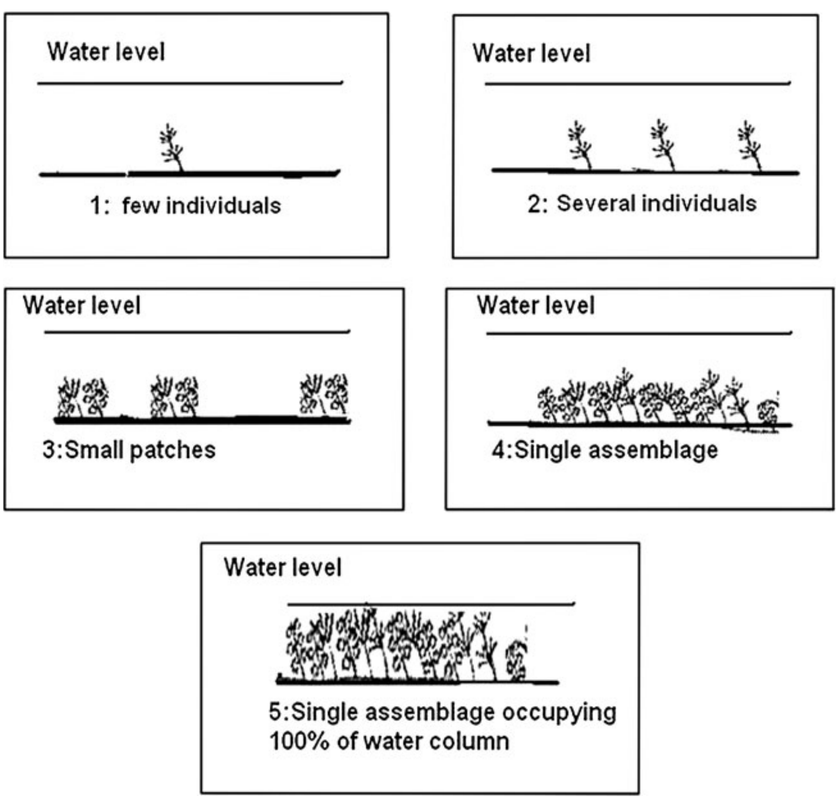


Fig. 2 A schematic illustration of the five-point scale of macrophyte assemblage abundance

The median method tests the null hypothesis that two or more independent samples have the same median. The Kruskal–Wallis test is a one-way analysis of variance by ranks and does not make any assumptions about the distribution of the data. Pearson correlations were run between physicochemical and zooplankton parameters to distinguish key abiotic variables that may affect zooplankton distribution. In addition, ordination analysis CCA (Canonical Correspondence Analysis) was performed (PC-ORD 4) between data sets comprising macrophyte abundances and zooplankton densities to assess possible relationships between aquatic macrophyte species and zooplankton species.

Two data matrices, therefore, were used, one containing the proportional abundances of key zooplankton species and one including submerged macrophyte abundance data. All the data were log transformed except the macrophyte abundances that were modified according to Beals-Smoothing transformation (De Cáceres & Legendre, 2008).

Results

Hydrophyte vegetation

A total of 15 hydrophytes were recorded (Appendix 1) within the macrophyte beds in the four lakes that were surveyed in northwestern Greece. *Ceratophyllum demersum* was the most abundant species present in the four lakes, followed by *Potamogeton pectinatus* and *Myriophyllum spicatum*. Other submerged and floating leaved species were also recorded and these species contributed in lower abundances (Appendix 1). *C. demersum* is a common hydrophyte and can be found in high abundance in most Greek waters, where it seems to dominate and suppress other hydrophytes (Papastergiadou et al., 2002).

Zooplankton composition

A total of 14 Cladocera species and 39 rotifers were identified in the four lakes studied (Appendix 2). The most abundant Cladocera species were *Chydoridae* spp. and *Bosmina longirostris*. Chydoridae species are considered to be common (Walseng et al., 2006) and, therefore, it was expected that it would be present in high abundance amongst the samples. *Alona* spp. and *Chydorus sphaericus* prefer grazing over periphyton (Mastrantuono & Mancinelli, 2005) and, therefore, are present mainly in the littoral zone within macrophyte beds. While relatively small Cladocera species (*Bosmina* spp.) were abundant, large Cladocera species, such as *Daphnia* spp., only contributed low abundance values.

Several species of Rotifera that were recorded during the current research are commonly found in eutrophic lakes (e.g. *Keratella quadrata*, *Anuraeopsis fissa*, *Trichocerca* spp., *Filinia longiseta*, *Brachionus* spp.). The results of this study indicate that there is a dominance of rotifers in the studied lakes, with the possible exception of lake Vegoritis where Copepoda and rotifers contribute equally to the total zooplankton abundance (Fig. 3).

The proportional abundance of Cladocera, regardless of the season or the sample site, varied from 12% in lake Kastoria to 23% in lake Mikri Prespa (Fig. 3), while the proportional abundance of Rotifera was 83% in lake Kastoria and 53% in Mikri Prespa.

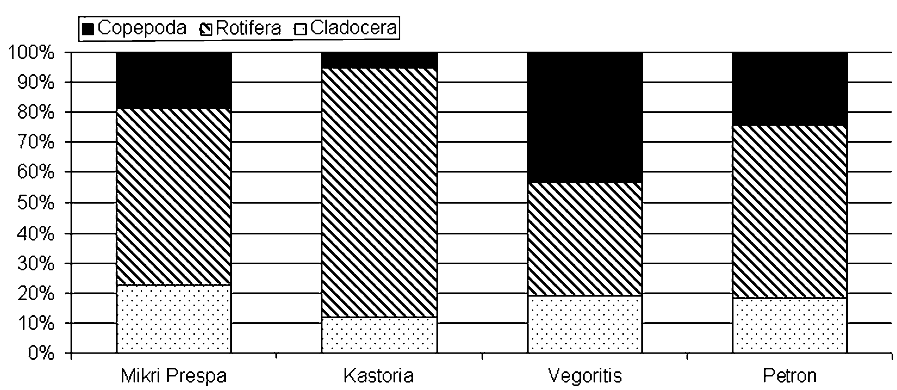


Fig. 3 Proportional abundances of three major taxonomic groups of zooplankton for the four studied lakes

Table 2 Mean values for physicochemical parameters amongst the four lakes studied

	Mikri Prespa	Kastoria	Vegoritis	Petron
Total phosphorus (mg/l)	125.5 (22.7)	133 (18.7)	178.3 (60.7)	142.5 (19.9)
Dissolved inorganic nitrogen (mg/l)	644.4 (165.8)	390.5 (76.5)	425.7 (98.5)	415.9 (69.9)
Chlorophyll-*a* (mg/m^3)	17.4 (2.9)	21.3 (2.2)	6 (0.83)	30.8 (6.73)
pH	7.8 (0.12)	8.1 (0.12)	7.95 (0.16)	7.3 (0.17)
DO (mg/l)	9.8 (0.6)	8.89 (0.46)	5.47 (0.57)	4.67 (0.32)
Conductivity (μS/cm)	292.1 (3.93)	334.3 (3)	718.9 (39.6)	852.5 (15.7)
Secchi depth (m)	1.21 (0.24)	0.53 (0.03)	0.88 (0.28)	0.36 (0.04)

Standard error in brackets

Relations between trophic state and zooplankton abundance

All of the studied lakes are characterised by high concentrations of total phosphorus, as expected (Table 2). Elevated total phosphorus concentration are a common characteristic of Greek lakes (Zacharias et al., 2002; Kagalou & Leonardos, 2009), even in lakes with relatively low chlorophyll-*a* concentrations (e.g. Lake Vegoritis).

Pearson correlations were run between zooplankton and physicochemical variables to distinguish abiotic parameters that may influence zooplankton distribution. The results revealed several significant correlations, the most notable of which was the correlation amongst Rotifer density, chlorophyll-*a* and soluble reactive phosphorus concentration (Table 3). This result is not surprising as, in eutrophic ecosystems, small-sized zooplankton tend to dominate. Specifically, of the four lakes investigated, three presented high chlorophyll-*a* concentrations and high Rotifera densities, whereas lake Vegoritis was characterised by lower concentration of chlorophyll-*a* and lower abundances of Rotifera (Fig. 3).

Zooplankton and aquatic vegetation associations

The results of the Kruskal–Wallis test showed that the median values for chlorophyll-*a*, conductivity, pH, total zooplankton density, Rotifera density, Copepoda density and evenness index were statistically different. The mean values and standard errors of key variables for each abundance class of submerged vegetation are given on Table 4. Diversity and evenness indices' values were low for the zooplankton and aquatic macrophytes amongst the five abundance classes (Table 4). The differences recorded for chlorophyll-*a* concentration (Fig. 4) can be attributed to possible competition between the macrophytes and phytoplankton. Total zooplankton density, as well as Rotifera and Copepoda density was significantly higher at sites with the highest submerged macrophyte abundance (class 5) (Figs. 4, 5). The results indicate that total zooplankton density corresponds to a gradient of increased abundance of submerged vegetation (Fig. 4; Table 4). However, there was no significant difference in Cladocera density amongst the abundance classes of submerged vegetation, although the highest Cladocera densities were

Table 3 Correlations of major functional zooplankton groups and physiochemical parameters

	Chlorophyll-*a*	DIN	SRP	Total phosphorus	Conductivity	Dissolved oxygen	pH
Cladocera	NS	NS	NS	NS	0.424**	−0.250*	−0.363**
Rotifera	0.306*	NS	0.271*	NS	NS	NS	NS
Copepoda	NS	NS	NS	NS	0.470**	−0.458**	−0.443**

NS non significant

* $P \leq 0.05$, ** $P \leq 0.001$

Table 4 Mean values and standard error (in brackets) of zooplankton densities and key variables amongst five classes of submerged macrophyte vegetation

	1	2	3	4	5
Chlorophyll-*a* (mg/m^3)	23.9 (4.4)	24.5 (8.7)	13.7 (1.9)	12.6 (3.7)	27.3 (6.0)
pH	7.9 (0.2)	8.1 (0.2)	7.9 (0.1)	7.4 (0.1)	7.9 (0.2)
DO (mg/l)	7.6 (1.1)	8.2 (0.8)	8.2 (0.6)	6.0 (0.9)	5.2 (0.7)
Total zooplankton density (ind/l)	45 (3.5)	95.1 (25)	178.1 (47.4)	228.2 (52.3)	597.3 (167.9)
Cladocera density (ind/l)	8.5 (3.8)	13.3 (5.1)	15.5 (3.7)	54.3 (17.6)	53.2 (17.3)
Rotifera density (ind/l)	29.2 (2.1)	68.9 (23.6)	142.5 (46.4)	80 (27.5)	435.8 (174.4)
Copepoda density (ind/l)	7.3 (2.2)	13.3 (4.4)	20.1 (3.4)	96.2 (23.7)	108.2 (26.1)
Macrophyte Shannon–Wienner index	0.5 (0.2)	0.54 (0.1)	0.59 (0.1)	0.65 (0.1)	0.42 (0.14)
Zooplankton Shannon–Wienner index	1.6 (0.1)	1.5 (0.1)	1.6 (0.1)	1.6 (0.1)	1.4 (0.2)
Zooplankton Evenness index	0.87 (0.02)	0.78 (0.07)	0.76 (0.03)	0.75 (0.04)	0.62 (0.07)
Macrophyte Evenness index	0.54 (0.15)	0.62 (0.1)	0.6 (0.07)	0.57 (0.08)	0.38 (0.12)

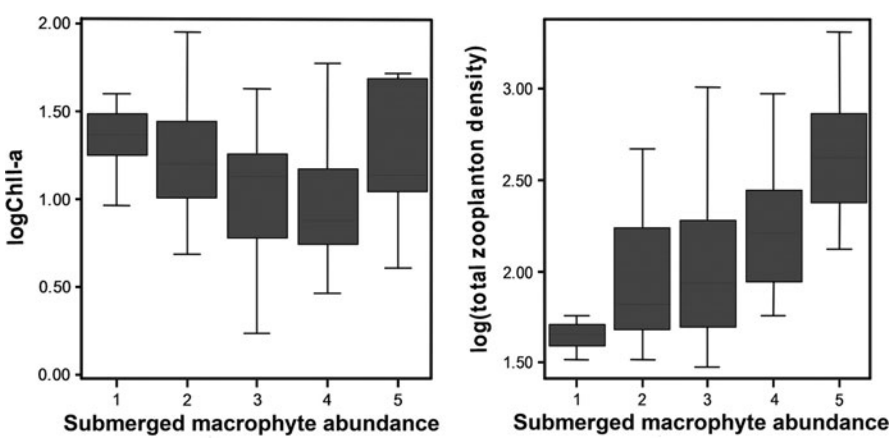


Fig. 4 Boxplots for Log Chlorophyll-*a* and Log Zooplankton density amongst the four lakes and submerged macrophyte vegetation abundance scale

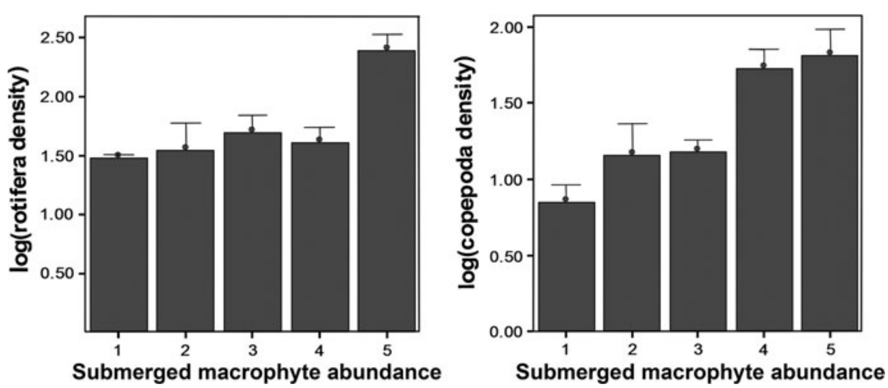


Fig. 5 *Bars* represent mean values and whiskers standard error of log (Copepoda density) and log (Rotifera density) for each submerged macrophyte vegetation abundance class

recorded for the Class 4 and Class 5 of hydrophytes vegetation (Table 4).

The results of CCA assigned Axis 1 as a significant gradient (Table 5). Most Rotifera species and *C. sphaericus* are positioned to the left part of the plot, along the *C. demersum* vector. A lesser representation of these species is aligned to *M. spicatum* (Fig. 6). The fact that *C. demersum* is a common and

Table 5 Interset correlations for ten macrophyte species and the eigen values of the three axes

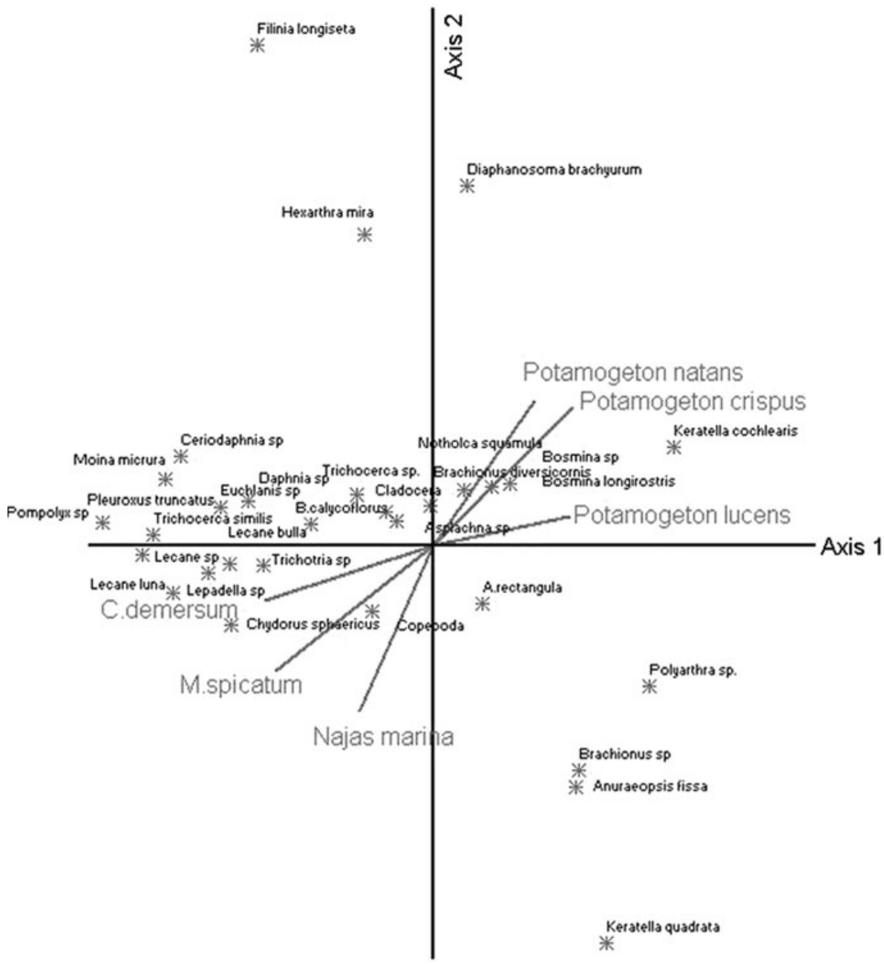
	Axis 1	Axis 2	Axis 3
Eigen value	0.273	0.16	0.118
Pearson correlation	0.807	0.643	0.691
Correlations			
Potamogeton pectinatus	−0.058	0.749	0.065
Potamogeton perfoliatus	−0.433	−0.117	0.137
Myriophyllum spicatum	−0.676	0.147	−0.365
Najas marina	−0.101	−0.357	−0.481
Valisneria spiralis	−0.517	0.109	−0.189
Ceratophyllum demersum	−0.336	−0.479	−0.172
Potamogeton lucens	0.267	0.343	0.092
Trapa natans	0.740	−0.502	0.058
Potamogeton crispus	0.574	−0.093	0.401
Potamogeton natans	0.540	−0.228	0.415

abundant hydrophyte in many Greek lakes could possibly explain this finding. On the right part of the plot, fewer species are associated with hydrophytes of simpler structure such as *Potamogeton natans*, *Potamogeton lucens*, and *Potamogeton crispus*, whose physical structure is less complex than either *C. demersum* or *M. spicatum* (Fig. 6).

Discussion

In the last few decades, aquatic vegetation in lakes throughout Greece has been heavily impacted by eutrophication and other anthropogenic disturbances. Recent publications refer to the decline of aquatic vegetation in Greek lakes and a shift from submerged macrophyte dominance to a phytoplankton dominated state (Papastergiadou et al., 2002; Kagalou et al.,

Fig. 6 Canonical Correspondence Analysis biplot illustrating the relationships between macrophyte and zooplankton abundances



2008; Kagalou & Leonardos, 2009). In some cases, a huge loss of submerged vegetation has been recorded (Stefanidis & Papastergiadou, 2007; Papastergiadou et al., 2010). This study revealed a relatively small number of hydrophytes and low diversity values in the four lakes investigated, a common feature of eutrophic lakes in Greece (Papastergiadou et al., 2002).

With the exception of lake Mikri Prespa (Michaloudi et al., 1997), there are few previous studies of zooplankton species in the studied lakes to permit a comparison with current data. The contribution of this study is, therefore, considered to be significant. According to Kagalou & Leonardos (2009), zooplankton communities in Greek lakes comprise mainly small-sized species (rotifers). This finding was confirmed by results from this study. Moreover, the differences that were found between the proportional abundances of major taxonomic groups of zooplankton underline important aspects of the trophic and ecological conditions of these lakes. Lake Kastoria is heavily impacted by nutrient pollution and anthropogenic disturbance, and, as a consequence, the lake has suffered increased filamentous and toxic cyanobacteria blooms in the last few years (Moustaka-Gouni et al., 2007). The low abundance of Cladocera in lake Kastoria probably explains the absence of grazing over phytoplankton, according to Moustaka-Gouni et al. (2006). Under these conditions, smaller sized zooplanktons (rotifers) are able to feed on bacteria and smaller algae and, thus, become dominant. On the other hand, lake Mikri Prespa contains a more balanced zooplankton community composition, possibly reflecting, a less-disturbed ecosystem hosting a diverse biotic environment (Catsadorakis, 1997; Crivelli et al., 1997).

According to the results of this study, chlorophyll-*a* and total phosphorus concentrations were elevated, underlining the anthropogenic impacted environments under study (Gianniou & Antonopoulos, 2007; Moustaka-Gouni et al., 2007). Significant correlations between chlorophyll-*a* concentration and Rotifera abundance indicate the effects of eutrophication on zooplankton composition. Small-sized zooplankton, like the Rotifera, tends to be dominant in eutrophic conditions. In this study, three of the studied lakes presented high values of chlorophyll-*a* concentration and higher Rotifera densities, whereas lake Vegoritis was characterised by lower concentration of chlorophyll-*a* and lower abundances of Rotifera.

This research has also linked high total zooplankton density with dense hydrophyte beds. This finding is supported by other studies (Basu et al., 2000; Kuczyńska-Kippen & Nagengast, 2003). In respect of rotifers, there are many species (e.g. *Lecane* genus) that inhabit aquatic macrophyte beds. This reflects their primary morphological (small size, flattened body) and behavioural (feed on epiphytes) characteristics (Green, 2003; Ali et al., 2007). Moreover, there are studies that indicate that planktonic species like *Keratella* and *Brachionus* can occasionally be attached on macrophytes (Arora & Mehra, 2003; Green, 2003). On the other hand, the fact that Cladocera abundances were not statistically different amongst the vegetated areas could be explained by the fact that several of the most abundant Cladocera species (e.g. *Bosmina* spp.) recorded in this study can be characterised as pelagic (Lauridsen et al., 2001) and, therefore, would be unlikely to be present in high densities within macrophyte beds. Increased density values for Cladocera recorded within denser vegetated beds could be attributed to a significant number of littoral Cladoceran (e.g. *Chydorus*) species present in these samples.

The small numbers of large Cladocera species in the zooplankton samples is an important feature of the studied lakes as large-sized zooplankton appears to be absent or in low abundances in Greek lakes. The absence or low abundances of large Cladocera, such as *Daphnia* species, could be an indication of fish predation pressure (Jeppesen et al., 1999; Jack & Thorp, 2002). It should be considered that the majority of the Greek lakes are characterised by fisheries that are dominated mainly by carp and other small fishes (Kagalou & Leonardos, 2009). These, undoubtedly, can affect the spatial distribution of large Cladocera. Although there are no data regarding the composition and abundance of fish species in the lakes presented in this article, it is accepted that, in lakes where littoral zone is dominated by small fishes, the densities of crustacean zooplankton within the macrophytes beds are the same or lower than the density found in scarce vegetated areas or open water (Burks et al., 2002; Iglesias et al., 2007). This supports the results of the current research. In addition, Vardaka et al. (2005) have highlighted the increasing occurrence of cyanobacteria blooms in

Greek lakes and have noted that cyanobacteria are resistant to grazing. This could explain the dominance of small-sized zooplankton over the larger grazers.

The results also highlighted a possible positive relationship between *C. demersum* and several Rotifera and *C. sphaericus*. It is well known that plants with a complex structure are more closely associated with higher zooplankton density (Ali et al., 2007). For example, plants with complex or dissected leaves provide a greater substrate area for foraging and more cover from predators than undissected plants. On the other hand, species like *Bosmina* spp., whose distribution has been demonstrated not to vary amongst the vegetated and open water or scarce vegetated areas, seemed to associate more with macrophytes with a less complex morphology.

In conclusion, the results of this study showed that aquatic vegetation does influence the composition and abundance of major functional taxonomic groups of zooplankton. It was also demonstrated that there were differences regarding the proportional abundances of major functional groups amongst the studied lakes, possibly due to the degree of anthropogenic impacts. Despite the heavily impacted environment of the studied lakes, several littoral species contributed to the total zooplankton diversity and abundance, emphasising the role of aquatic vegetation in providing habitat for many zooplankton species.

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