



# What drives benthic macroinvertebrate dispersal in different lake substrata? The case of three Mediterranean lakes

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**Abstract** Benthic macroinvertebrate communities from different lake zones are known to respond differently to environmental parameters and human pressures. The objectives of this study were to explore the spatial and temporal variability of benthic communities, investigate the effect of environmental factors on their assemblages and assess their response to eutrophication in the profundal and sublittoral zones of three Greek eutrophic lakes (Volvi, Kastoria and Mikri Prespa). These lakes are subjected to different land uses in their catchment areas. Samplings were conducted bi-annually (spring and autumn). Sixteen taxa were collected in the sublittoral and eleven in the profundal zone of the studied lakes. Among them,

some species were recorded for the first time in the studied lakes. The dominant species were *Potamothrix hammoniensis* (Michaelson, 1901) (Oligochaeta), *Chaoborus (Chaoborus) flavicans* (Meigen, 1830) and *Chironomus (Chironomus) gr. plumosus* Linnaeus, 1758 (Diptera), reflecting the eutrophic status of these waterbodies. Benthic communities, their functional traits (microhabitat preferences and feeding types), diversity and rarity species differed among lakes. Especially Lake Prespa, as a potentially ancient lake, hosts an endemic oligochaete community. Altitude and eutrophication (expressed as P-PO<sub>4</sub> and BOD<sub>5</sub> concentrations) were the main environmental factors explaining spatial and temporal variability in the assemblages. Based on the Greek Lake Benthic invertebrate Index, the ecological quality of the studied lakes was estimated as good to moderate. Benthic macroinvertebrates from both lake zones are associated with eutrophication, which is related to anthropogenic activities. Therefore, these lake zones should be included in assessment methods linking benthic invertebrate assemblages to eutrophication.

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## Introduction

Freshwater ecosystems are one of the most diverse habitats on the Earth and reflect the effects of activities occurring in their basins (Magnuson et al. 2006). Multiple and varied threats, such as changing climate, invasions, harmful algal blooms, microplastic pollution, impact freshwater ecosystems (Reid et al. 2019). Their biodiversity decreases even faster than in terrestrial or marine systems, despite the efforts to prevent this loss (Collen et al. 2014). Therefore, long-term conservation and efficient management often request a multidisciplinary concept to determine how aquatic biodiversity, water and habitat quality dynamics relate across different water bodies (Hill et al. 2016).

Benthic macroinvertebrate communities are usually used in biomonitoring due to their high sensitivity and response to pressures (Bonada et al. 2006; Birk et al. 2012). They are present on organically rich substances in the upper layer of the sediment (Matisoff and Wang 1998). Benthic assemblages act as “ecosystem engineers” and make a crucial contribution to aquatic ecosystem services as sediment oxygenation via bioturbation, internal nutrient loading and other biogeochemical processes (Covich et al. 1999). Moreover, they play a fundamental role as key species in food chains and food webs (Covich et al. 1999). Potential food sources are phytoplankton, bacteria and organic debris (Biswas et al. 2009). In turn, they serve as prey for higher-class organisms such as fish (Zimmer et al. 2001) and they can act as biological indicators to track water quality conditions (e.g., Rossaro et al. 2007; Miler et al. 2013; Lazaridou et al. 2018).

In lakes, macroinvertebrate assemblages differ among the littoral, sublittoral and profundal lake zones, which are considered as subsystems, responding differently to natural variability and human-induced pressures (Pilotto et al. 2012, 2015). Within the profundal zone, shifts in species composition are related mostly to eutrophication (Bazzanti et al. 2012; Jyväsjärvi et al. 2012; Pilotto et al. 2012), whereas in sublittoral and littoral zones to morphological alterations of lakeshores (Miler et al. 2013; McGoff et al. 2013), acidification (Schartau et al. 2008) and wave action (Johnson et al. 2004; Stendera and Johnson 2008). Littoral zone microhabitats tend to exhibit high macroinvertebrate species richness, due to their

heterogeneity and productivity, compared to other lake strata (Pilotto et al. 2015). In small lakes, sublittoral macroinvertebrate assemblages demonstrate lower variation in density and species number among years than those occupying the profundal lake area because of alternating oxygen conditions (Hämäläinen et al. 2003). In contrast to littoral and sublittoral benthic communities, profundal assemblages are often low in species richness and are primarily dominated by oligochaetes (Burlakova et al. 2018). However, community composition varies according to the studied region and relevant stressors (e.g., Sterling et al. 2016; Tolkkinen et al. 2016; Jonsson et al. 2017).

Until now, several international legislations, directives and guidelines have been established with the aim of promoting the assessment and conservation of biodiversity (i.e., the European Biodiversity Strategy to 2020; EC 2011) and the good ecological quality of water bodies (i.e., Water Framework Directive, WFD; EC 2000). The latter necessitates all European Member States to protect and improve the quality of their aquatic ecosystems concerning pressure-specific stressors. An essential step in the ecological quality assessment of water bodies is the quantification of single and combined effects of multiple stressors on biota (Solimini et al. 2009), recognizing that biogeographic, morphometric and geological factors, as well as water chemistry, may influence species composition (Heling et al. 2018). Additionally, the utility of different biological elements should be reliably proved before they can be applied in the assessments of the ecosystems (Tolonen et al. 2020).

However, a plethora of studies have yet been published on the use of benthic macroinvertebrates for river ecological quality assessments (e.g., Hering et al. 2010; Birk et al. 2012). On the contrary, substantially fewer surveys have addressed the efficiency of benthic macroinvertebrate assemblages for monitoring water quality in lakes (e.g., Johnson et al. 2004; Brauns et al. 2007) and even less have relied on distinct taxa assemblages in the sublittoral/profundal zones (e.g., Jyväsjärvi et al. 2014; Lau et al. 2017; Ntislidou et al. 2018). This is mainly due to sampling and identification difficulties as well as to the biogeographical and spatial variation of environmental lakes' characteristics (Poikane et al. 2016). However, it is crucial to assess the impact of pressures because profundal benthic assemblages respond to eutrophication, whereas the littoral ones, which have the highest

richness and diversity, mainly to morphological alterations of lakeshore (Miler et al. 2013). Among Mediterranean countries, studies focusing on benthic assemblages in Greek lakes are also scarce (Petridis 1993; Petridis and Sinis 1993, 1995, 1997; Kagalou et al. 2006; Bobori et al. 2018).

The aim of the present study contribute to fulfill these knowledge gaps and to: (a) investigate the diversity and structure of benthic macroinvertebrate communities in the profundal and sublittoral zones of three Greek lakes (Volvi, Kastoria and Mikri Prespa), (b) examine the environmental effects on benthic macroinvertebrate assemblages, and (c) explore benthic macroinvertebrate response to eutrophication. We also provide a dataset that contains benthic macroinvertebrate records of these lakes concerning their rarity and endemism. Understanding the drivers that structure benthic macroinvertebrate distribution in lakes is of key interest to manage the effects of environmental changes. The present study will contribute to fill this gap, especially for the Mediterranean lakes.

## Material and methods

### Study area

Three lakes, located in Northern Greece, were selected as case studies due to different land uses in their catchment areas (Fig. 1, Table 1). Lake Volvi (40° 37' N and 23° 21' E) is a relatively deep, warm monomictic lake (Vardaka et al. 2005) and constitutes part of the National Wetland Park of Lakes Koronia, Volvi and Macedonian Temp (Table 1, Fig. 1). Despite the minor industrial and domestic development in the catchment, agricultural activities are intensive, dominated by maize, alfalfa and cereal crops (Vogiatzis et al. 2008). Lake Kastoria (40° 30' N, 21° 18' E) is an urban, shallow, polymictic lake (Table 1, Fig. 1). Until 1995, it was the acceptor of sewage effluents, affecting thus its water quality and causing algal blooms (Moustaka et al. 2006). Lake Mikri Prespa (40° 44' N, 21° 04' E) is a shallow, polymictic lake (Vardaka et al. 2005) (Table 1, Fig. 1). Its catchment area is affected by minor anthropogenic pressures (cultivated plots and livestock; Tziritis 2014). The three lakes are under a strict protection status since they have been designated as areas of

community interest (Birds and Habitats Directives; EC 2009/147, EEC 1992/43), while the two of them (Lakes Volvi and Mikri Prespa) are RAMSAR sites (RAMSAR 1974). Some of their limnological characteristics and land uses in their catchment areas, according to Corine Land Cover 2012 (EU 2018), are provided in Table 1.

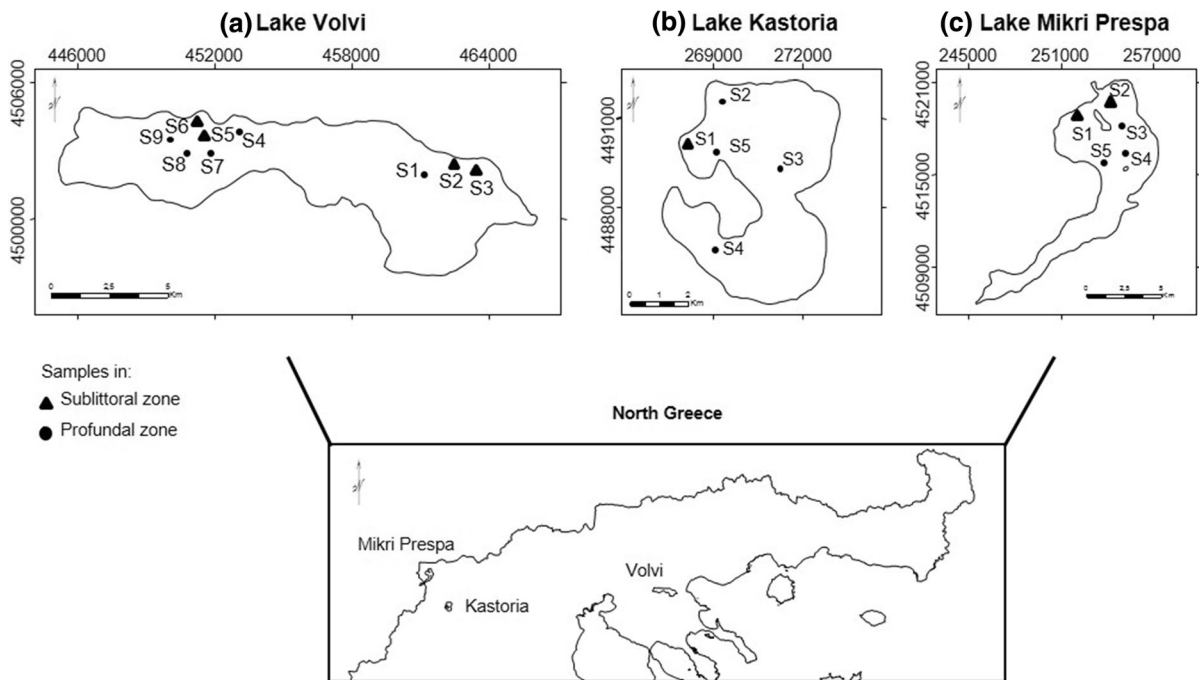
### Sampling and laboratory procedures

A total of 19 stations in the profundal and sublittoral zones of the studied lakes were sampled in autumn 2011 and early spring 2012, using an Ekman–Birge grab (three replicates, 225 cm<sup>2</sup> sampling area) (Fig. 1). Sediment samples were sieved with a 200-μm mesh (Rosenberg and Resh 1993) and fixed in 4% neutralized formaldehyde. Macroinvertebrates were sorted and identified to species or genus level. Their abundance was converted to density as individual per m<sup>2</sup> (ind. m<sup>-2</sup>). Chironomids and oligochaetes were slide-mounted prior to identification using the proper keys (Wiederholm 1983, 1986; Timm 2009). Immature stages of oligochaetes were identified based on the particular characters of the setae.

Water samples were collected at each station, 1 m above the sediment, using a Niskin-type sampler. Water temperature (°C), conductivity (mS cm<sup>-1</sup>), pH and dissolved oxygen (DO, mg L<sup>-1</sup>) were measured in situ using portable probes. Concentrations of nitrite (NO<sub>2</sub>-N, mg L<sup>-1</sup>), nitrate (NO<sub>3</sub>-N, mg L<sup>-1</sup>) and ammonium (NH<sub>4</sub>-N, mg L<sup>-1</sup>) nitrogen, phosphorus orthophosphate (PO<sub>4</sub>-P, mg L<sup>-1</sup>), total suspended solids (TSS, mg L<sup>-1</sup>) and biological oxygen demand (BOD<sub>5</sub>, mg L<sup>-1</sup>) were determined according to APHA (2005). Sampling depth (m) and Secchi disk depth (cm) were also recorded in situ, with the latter been used as a proxy of water transparency.

### Diversity indices and functional traits

Benthic macroinvertebrate assemblages at each lake were described using the following diversity indices: Shannon–Wiener ( $H'$ , Shannon and Weaver 1949), Weighted Diversity Index ( $Hw'$ , Rossaro et al. 2011), Margalef ( $d'$ , Margalef 1958) and Pielou's evenness index ( $J'$ , Magurran 1988). The functional approach associates subgroups constituted of individuals of the same type as to microhabitat preferences and feeding types. We selected these traits due to their ability to



**Fig. 1** Sampling stations in lakes **a** Volvi, **b** Kastoria and **c** Mikri Prespa

**Table 1** Limnological characteristics and land uses according to Corine Land Cover 2012 in the catchment areas of the studied lakes

Characteristics	Lake Volvi	Lake Kastoria	Lake Mikri Prespa
Surface area (km <sup>2</sup> )	72.0	28.9	47.4
Maximum depth (m)	27.3	9.2	8.4
Mean depth (m)	13.8	4.4	4.1
Catchment area (km <sup>2</sup> )	1,290	283	261.2
Altitude (masl)	37	630	853
Trophic status <sup>a</sup>	Eutrophic	Hypertrophic	Eutrophic
Artificial areas (%)	1.1	1.6	0.3
Agricultural areas (%)	43.5	35.9	12.6
Forest and semi-natural areas (%)	49.8	51.6	63.1
Wetlands (%)	0.3	0.7	4.1
Water bodies (%)	5.3	10.2	19.9

<sup>a</sup>Vardaka et al. (2005)

indicate physical and ecological changes and their use in developing a trait-based bioassessment approach (Menezes et al. 2010). The Asterics software was used to estimate the functional traits for microhabitat preferences and feeding types (Table 2) (version 4.0.4; Wageningen Software Labs 2005).

#### Ecological quality assessment

To evaluate the ecological quality of the studied lakes, the Greek Lake Benthic invertebrate Index (GLBiI;

Ntislidou et al. 2018) was applied. The index is based on three metrics, the number of taxa (Taxa\_Tot) and the Simpson's diversity index (Simpson\_Tot) in the profundal and sublittoral zones and the relative contribution of Chironomidae in the profundal zone (%Chironomidae\_Prof). The GLBiI is a multimetric index with a clear response to eutrophication, while the three metrics constituting the index are related to factors corresponding to lake hydromorphology and chemistry (Ntislidou et al. 2018).

**Table 2** Description of the studied functional traits

Preference for a certain microhabitat <sup>a</sup>
<i>Pel</i> → Pelal: mud; grain size < 0.063 mm
<i>Arg</i> → Argyllal: silt, loam, clay; grain size < 0.063 mm
<i>Psa</i> → Psammal: sand; grain size 0.063–2 mm
<i>Aka</i> → Akal: fine to medium-sized gravel; grain size 0.2–2 cm
<i>Lit</i> → Lithal: coarse gravel, stones, boulders; grain size > 2 cm
<i>Phy</i> → Phytal: algae, mosses and macrophytes including living parts of terrestrial plants
<i>Pom</i> → particulate organic matter, such as woody debris, CPOM, FPOM
<i>Oth</i> → other habitats
Feeding types <sup>b</sup> (Schweder 1992)
<i>Fgr</i> → Grazers/scrapers
<i>Fga</i> → Collectors/Gatherers
<i>Fxy</i> → Xylophagous taxa
<i>Fpr</i> → Predators
<i>Fmi</i> → Miners
<i>Fsh</i> → Shredders
<i>Faf</i> → Active filter feeders
<i>Fpf</i> → Passive filter feeders
<i>Fpa</i> → Parasites
<i>Fot</i> → Other Feeding Types

<sup>a</sup>Schmedtje and Colling (1996)

<sup>b</sup>Schweder (1992)

## Data analyses

The nonparametric Kruskal–Wallis and Mann–Whitney U tests were applied to extract significant spatial and temporal differences in environmental parameters and taxa distribution among stations and between sampling periods (autumn and spring), respectively. Pearson's correlation analysis extracted relationships between environmental variables and benthic macroinvertebrate abundances. The above statistical analyses were performed using the statistical package SPSS (version 21.0).

The relative importance of environmental parameters in explaining the composition of benthic communities in the profundal and sublittoral zones was explored by redundancy analysis (RDA). Prior to this analysis, a detrended correspondence analysis (DCA) was applied, revealing that the total gradient length was less than three times the standard deviation, thus indicating a linear relationship between the environmental parameters and the benthic macroinvertebrate density data. To retain the significant environmental parameters in RDA, the Monte Carlo permutation test (499 permutations,  $p < 0.05$ ) and the inflation factor ( $< 20$ ) were used. Densities and environmental parameters were  $\log(x + 1)$  transformed, except

temperature and pH, which were standardized. All ordinations were performed with the statistical program CANOCO version 4.5.1 (ter Braak and Šmilauer 1998).

The similarity analysis routines ANalysis Of SIMilarity (ANOSIM) was applied to identify differences between profundal and sublittoral zones for benthic macroinvertebrate communities and functional trait categories. Additionally, the SIMilarity PERcentage Analysis (SIMPER) was performed to determine the taxa and functional trait categories that contributed the most to the observed similarities and differences between groups (profundal and sublittoral zones) with a cut-off of 90% (Clarke et al. 2014). Both analyses were based on the Bray–Curtis similarity index (Clarke et al. 2014) and were conducted using Primer v6 software (Clarke and Gorley 2006).

## Results

### Environmental parameters

The environmental parameters measured in the studied lakes are given in Table 3. The highest concentrations of PO<sub>4</sub>-P (0.034 mg L<sup>-1</sup>), NO<sub>3</sub>-N (0.770 mg

**Table 3** Means and ranges [in brackets] of environmental parameters in the three studied lakes

Parameters	Lake Volvi	Lake Kastoria	Lake Mikri Prespa
<i>S</i> _Depth (m)	17.2 [9.0–23.0]	5.9 [4.0–9.2]	5.7 [3.0–8.5]
<i>Trans</i> (m)	1.6 [0.9–2.5]	2.0 [1.1–3.3]	2.6 [1.2–4.0]
TSS (mg L <sup>-1</sup> )	8.0 [1.4–25.4]	3.8 [1.2–8.6]	3.5 [1.2–10.8]
WT (°C)	12.8 [7.9–18.1]	11.2 [9.7–12.4]	9.4 [7.6–10.2]
Cond (mS cm <sup>-1</sup> )	0.90 [0.82–0.95]	0.32 [0.28–0.38]	0.27 [0.24–0.31]
pH	8.32 [7.17–8.64]	8.06 [7.41–8.43]	8.29 [8.01–8.40]
DO (mg L <sup>-1</sup> )	9.44 [7.50–11.99]	7.39 [4.58–9.98]	10.24 [8.13–12.20]
<i>BOD</i> <sub>5</sub> (mg L <sup>-1</sup> )	2.34 [0.21–5.56]	1.39 [0.18–2.91]	2.60 [0.24–4.08]
NO <sub>3</sub> -N (mg L <sup>-1</sup> )	0.203 [0.041–0.771]	0.105 [0.022–0.179]	0.159 [0.024–0.316]
NO <sub>2</sub> -N (mg L <sup>-1</sup> )	0.029 [0.001–0.145]	0.005 [0.001–0.011]	0.004 [0.001–0.007]
NH <sub>4</sub> -N (mg L <sup>-1</sup> )	0.066 [0.004–0.369]	0.086 [0.001–0.353]	0.119 [0.001–0.514]
PO <sub>4</sub> -P (mg L <sup>-1</sup> )	0.015 [0.001–0.034]	0.003 [0.001–0.004]	0.003 [0.001–0.010]

*S*\_Depth sampling depth, *Trans* transparency, *TSS* total suspended solids, *WT* water temperature, *Cond* conductivity, *DO* dissolved oxygen, *BOD*<sub>5</sub> biological oxygen demand

L<sup>-1</sup>) and NO<sub>2</sub>-N (0.150 mg L<sup>-1</sup>) were recorded in Lake Volvi, whereas the highest NH<sub>4</sub>-N concentrations (0.514 mg L<sup>-1</sup>) in Lake Mikri Prespa. Within each lake, none of the environmental parameters exhibited significant differences among stations (Kruskal–Wallis test,  $p > 0.05$ ), whereas a significant seasonal pattern was evident in all lakes (Mann–Whitney test  $p < 0.05$ ). Higher eutrophication was noticed in Lake Volvi than in the other two lakes. Temporal significant ( $p < 0.05$ ) differences among the majority of the environmental parameters were observed in Lake Volvi, apart from nitrogen nutrients (NO<sub>3</sub>-N, NO<sub>2</sub>-N, NH<sub>4</sub>-N). In lakes Kastoria and Mikri Prespa, five (DO, pH, conductivity, BOD<sub>5</sub>, transparency) and three (DO, pH, transparency) out of the 11 environmental parameters studied differed significantly ( $p < 0.05$ ) between the sampling periods, respectively.

#### Benthic community composition and structure

A total of 53,466 specimens, belonging to 16 macroinvertebrate taxa, were identified with the most abundant belonging to *Potamothenis hammoniensis* (Oligochaeta) and *Chaoborus* (*Chaoborus*) *flavicans* (Diptera) (Table 4). Empty shells of *Valvata* sp. Müller, 1773 (in lakes Volvi and Kastoria), *Unio* sp. Retzius, 1788 (in Lake Kastoria) and *Dreissena presbensis* Kobelt, 1915 (in lakes Volvi and Mikri Prespa) were detected. The profundal zone was characterized by the highest densities and the lowest diversity (11 taxa,

Table 4), with *P. hammoniensis* (67.5%) and *C. (Chaoborus) flavicans* (23.5%) dominated benthic assemblages (Fig. 2). The same taxa were also the most abundant in the sublittoral zone (69.3% and 18.6%, respectively) of the lakes, where 16 taxa were identified (Table 4).

In lakes Volvi and Kastoria, most benthic macroinvertebrates belonged to oligochaetes (> 50%) and Diptera (> 20%), followed by Nematoda and Hirudinea. Oligochaeta comprised more than 45% of the whole community (> 65% and 46%, respectively), with *P. hammoniensis* being the dominant species. However, in Lake Kastoria (stations S3, S5 in autumn and S1 in spring), the most abundant species was *C. (Chaoborus) flavicans* (> 39%). Diptera dominated (> 53%) the benthic macroinvertebrate assemblages of Lake Mikri Prespa, with *C. (Chaoborus) flavicans* being the dominant species, except stations S1 (autumn) and S2 (autumn and spring), where *P. hammoniensis* was more abundant (> 52%).

No spatial differentiation in benthic densities was observed among stations (Kruskal–Wallis test,  $p > 0.05$ ) and between sampling periods (Mann–Whitney test  $p > 0.05$ ) within each lake. The structure of benthic assemblages was also similar in both lake zones studied (ANOSIM: Lake Volvi  $R = 0.312$ ,  $p = 0.07$ ; Lake Kastoria  $R = 0.362$ ,  $p = 0.178$ ; Lake Mikri Prespa  $R = 0.131$ ,  $p = 0.210$ ). This similarity was owned mainly to the presence of *P. hammoniensis* and *C. (Chaoborus) flavicans* in both lake strata (Table 5).

**Table 4** Presence of benthic macroinvertebrate taxa in lakes Volvi (V), Kastoria (K) and Mikri Prespa (MP) in autumn 2011 and spring 2012

Taxonomic group	V	K	MP
Insecta-Diptera			
Chironomidae			
Chironominae			
<i>Chironomus (Chironomus) gr. plumosus</i> Linnaeus, 1758	P/S	P/S	P/S
<i>Cryptochironomus (Cryptochironomus) gr. defectus</i> (Kieffer, 1913)	P/S		
<i>Cladopelma viridulum</i> (Linnaeus, 1767)	S		
<i>Endochironomus tendens</i> (Fabricius, 1775)	S		
<i>Microchironomus tener</i> (Kieffer, 1918)	P/S		
<i>Psectrocladius (Psectrocladius) psilopterus</i> (Kieffer, 1906)		S	
<i>Tanytarsus</i> sp. van der Wulp, 1874			S
Tanypodinae			
<i>Procladius (Holotanypus) choreus</i> (Meigen, 1804)	P/S	P/S	
Chaoboridae			
<i>Chaoborus (Chaoborus) flavicans</i> (Meigen, 1830)	P/S	P/S	P/S
Ceratopogonidae	P/S	P/S	P/S
Annelida-Oligochaeta			
Tubificidae			
Tubificinae			
<i>Potamothrix hammoniensis</i> (Michaelsen, 1901)	P/S	P/S	P/S
<i>Peipsidrilus pusillus</i> Timm, 1977			P/S
<i>Tubifex tubifex</i> (Muller, 1774)			P/S
<i>Psammoryctides</i> sp. Hrabe, 1964			P/S
Anellida-Hirudinea			
Erpobdellidae		S	
Nematoda	P/S		P/S

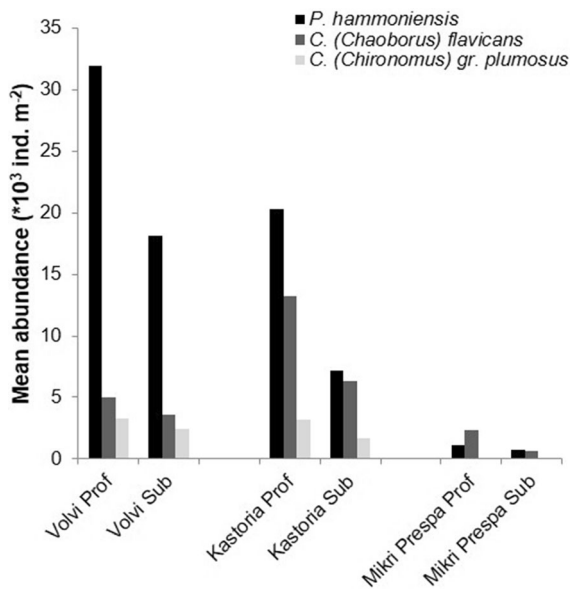
P profundal, S sublittoral zone

### Diversity indices and functional traits

All diversity indices exhibited their highest values in Lake Mikri Prespa (Fig. 3). Shannon–Wiener ( $H'$ ), Weighted Diversity ( $Hw'$ ) and Pielou's evenness ( $J'$ ) indices were highly correlated with depth ( $r = 0.647$ ,  $r = 0.629$  and  $r = 0.477$ ,  $p < 0.05$ , respectively) and conductivity ( $r = 0.531$ ,  $r = 0.639$  and  $r = 0.559$ ,  $p < 0.05$ , respectively) and Margalef index ( $d'$ ) with depth and  $\text{NO}_2\text{-N}$  ( $r = 0.354$  and  $r = 0.354$ ,  $p < 0.05$ , respectively) (Table 6).

Benthic macroinvertebrate communities showed a preference for particulate organic matter (Pom; 28–78%) and mud (Pel; 16–37%) in all lakes in both zones (Fig. 4a). Considering the different feeding types, collectors/gatherers (fga) were dominant in both zones of lakes Volvi (80–83%) and Kastoria (49–65%), followed by predators (fpr) (32–46%) (Fig. 4b). In Lake Mikri Prespa, predators mostly

contributed to the benthic macroinvertebrate composition of the profundal and sublittoral zone (Fig. 4b). However, no clear spatial pattern was evident between the two lake zones when feeding and habitat traits were compared (ANOSIM, Microhabitat preferences:  $R = 0.006$ ,  $p = 0.341$ ; Feeding type:  $R = -0.026$ ,  $p = 0.630$ ). The SIMPER analysis, though, extracted the preference for particulate organic matter as the main trait differentiating the two lake zones (Table 7). The same analysis revealed that collectors/gatherers (fga; Profundal zone: 59.0% and sublittoral zone: 60.4%) contributed more than the other feeding groups to benthic assemblage structure in both profundal and sublittoral zones (Table 7). Generally, the low dissimilarity of benthic assemblages between the two zones, ranging from 19.6 to 21.2% (Table 7), indicates homogenous lake systems.



**Fig. 2** Mean density of the most abundant benthic species from the profundal (Prof) and sublittoral (Sub) zones of lakes Volvi, Kastoria and Mikri Prespa in autumn 2011 and spring 2012

### Ecological quality

The ecological quality of the studied lakes was assessed using the GLBiI. The lakes Volvi and Mikri Prespa were classified as water bodies of good quality (0.68 and 0.63, respectively), whereas the ecological quality of Lake Kastoria was classified as moderate (0.53). Apparently, not all the metrics included in the GLBiI assessed the quality of each lake with the same class. Only in the case of Lake Kastoria, the three metrics had the same quality class (“Taxa\_Tot” = 0.53, “Simpson\_Tot” = 0.50, “%Chironomidae\_Prof” = 0.55). In the case of Lake Volvi, the metric “%Chironomidae\_Prof” equaled 1.02, assessing thus the lake with high quality, whereas the rest metrics with moderate (“Taxa\_Tot” = 0.44, “Simpson\_Tot” = 0.60). Lake Mikri Prespa was classified as having good quality by two metrics (“Simpson\_Tot” = 0.68, “%Chironomidae\_Prof” = 0.62) and moderate by “Taxa\_Tot” (0.59).

### Relationships between environmental parameters and benthic macroinvertebrate communities

The RDA analysis applied on the profundal samples showed that two (altitude and depth) out of the 13 environmental parameters were the best predictors

(Monte Carlo test,  $p < 0.05$ ) in explaining benthic macroinvertebrate community composition. The first two ordination axes explained 49.6% of the total species variance and 85.4% of the species—environmental parameter relation. Axis I (eigenvalue 0.411) was related to altitude (intra-set correlation 0.618) and Axis II (eigenvalue 0.085) to P-PO<sub>4</sub> and transparency (intra-set correlations 0.739 and - 0.663, respectively). Both axes separated stations of Lake Mikri Prespa from stations of the other lakes. Specifically, stations of Mikri Prespa were positively correlated with altitude ( $r = 0.618$ ) and negatively with P-PO<sub>4</sub> ( $r = - 0.246$ ) (Fig. 5a). *P. hammoniensis* and *C. (Chaoborus) flavicans* were correlated with P-PO<sub>4</sub> (Fig. 5b). Moreover, *Peipsidrilus pusillus* found in Mikri Prespa were negatively correlated with sampling depth (Fig. 5b).

Regarding the sublittoral zone, RDA revealed altitude and BOD<sub>5</sub> as the most statistically significant (Monte Carlo test,  $p < 0.05$ ) parameters affecting benthic macroinvertebrate assemblages. Axis I (eigenvalue 0.580) explained 72% of benthic taxa and environmental parameters variability and was positively correlated to altitude (intra-set correlation 0.833, Fig. 6a). Axis II (eigenvalue 0.098) was positively correlated with BOD<sub>5</sub> (intra-set correlation 0.548, Fig. 6a). The cumulative percentage variance between benthic macroinvertebrates and environmental parameters explained by Axis II was 84.2%. Stations of Lake Mikri Prespa were related to altitude and characterized by *M. tener* and *E. tendens* (Fig. 6b). Stations from Lake Kastoria were associated with BOD<sub>5</sub> and were defined by *Psectrocladius (Psectrocladius) psilopterus* and Ceratopogonidae.

### Discussion

Understanding the structure of benthic macroinvertebrate communities in the different lake zones is essential in biomonitoring programs, as they are constrained by multiple drivers of changes and respond unevenly to distinct human disturbances (Pilotto et al. 2012). This study enhances our knowledge about the composition of benthic macroinvertebrates of the studied lakes. In sublittoral and profundal zones we found similar benthic assemblages composed of species known to be sensitive to eutrophication (Wiederholm 1980; Jónasson 2004). Our



**Table 5** SIMPER analysis (both similarity and dissimilarity) for benthic macroinvertebrate densities in the profundal and sublittoral zones in lakes Volvi, Kastoria and Mikri Prespa

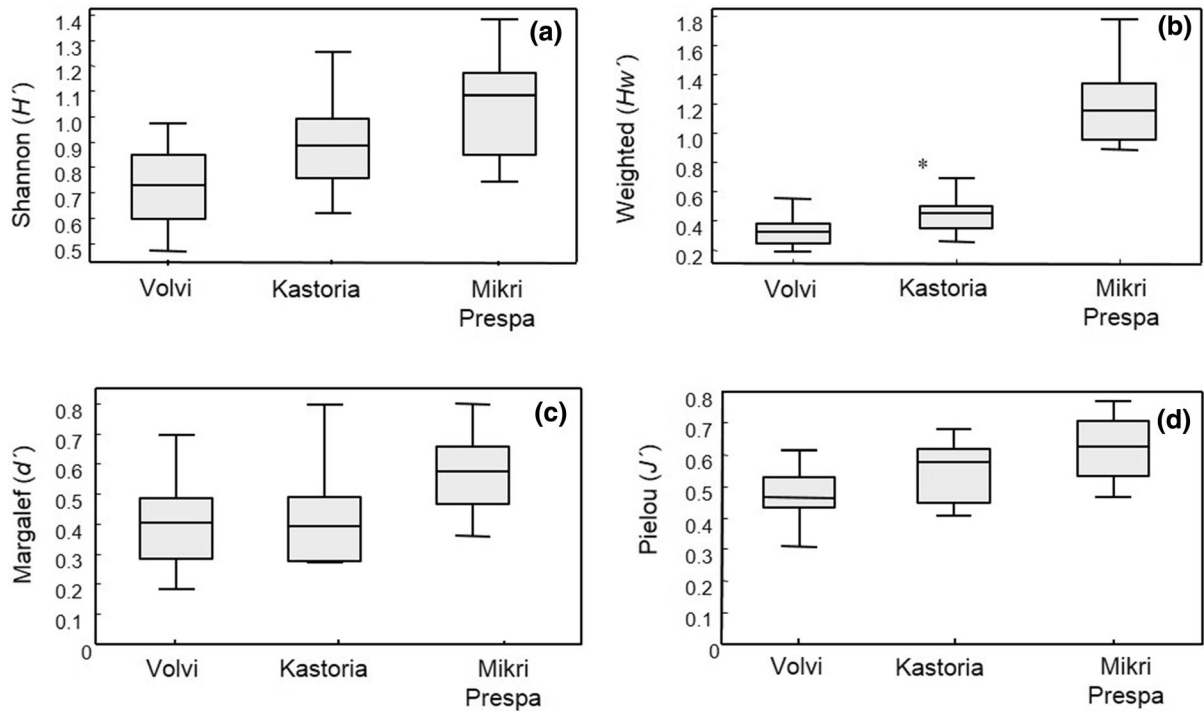
Profundal	Lakes		
	Volvi	Kastoria	Mikri Prespa
Average similarity:	87.9%	86.4%	81.7%
Taxa	Contribution (%)	Contribution (%)	Contribution (%)
<i>P. hammoniensis</i>	36.6	33.8	27.3
<i>C. (Chaoborus) flavicans</i>	29.9	29.3	31.5
<i>C. (Chironomus) gr. plumosus</i>	26.5	26.8	10.7
Sublittoral			
Average similarity:	84.1%	82.5%	80.4%
Taxa	Contribution (%)	Contribution (%)	Contribution (%)
<i>C. (Chaoborus) flavicans</i>	30.3	23.9	25.8
<i>P. hammoniensis</i>	24.9	23.0	24.4
<i>C. (Chironomus) gr. plumosus</i>	22.4	19.5	13.5
Profundal/Sublittoral			
Average dissimilarity:	17.5%	19.5%	20.6%
Taxa	Contribution (%)	Contribution (%)	Contribution (%)
<i>P. (Holotanypus) choreus</i>	31.7	13.6	–
Nematoda	18.7	16.91	–
<i>M. tener</i>	14.6	–	–
Ceratopogonidae	–	24.75	23.11
<i>Psammoryctides</i> sp.	–	–	17.73
<i>T. tubifex</i>	–	–	17.48

observations supported that benthic macroinvertebrates of these lake zones were also functionally homogenous. Moreover, our data revealed that the driving factor affecting benthic macroinvertebrate assemblages is eutrophication in the profundal and sublittoral zones of the studied lakes. Thus, our results suggest that communities belonging to these lake strata could be treated together regarding benthic macroinvertebrate responses to disturbance.

Our knowledge on benthic macroinvertebrate communities for the studied three lakes is dated before 25 years (Economidis 1991; Koussouris et al. 1987, 1989, 1991; Petridis and Sinis 1995, 1997) with a more recent exception (Ntislidou 2019). The total number of taxa referred in the previous studies was higher than in the present study [i.e., Volvi: 12 (Economidis 1991) and Mikri Prespa: 15 (Petridis and Sinis 1995)]. Among the macroinvertebrate taxa documented by Economidis (1991) and Petridis and Sinis (1995) are the littoral species *Dicrotendipes nervosus* (Staeger 1839) and *Einfeldia* sp., that were not found in the current study, due probably to the restriction of our sampling campaigns only in the

profundal and sublittoral zones of the lakes, excluding the littoral zone, which is generally more diverse in Mediterranean lakes (Pilotto et al. 2015).

However, our surveys revealed the occurrence of some species, which have not been previously reported in the studied lakes. The chironomid species *E. tendens*, *Cladopelma viridulum* and *P. (Psectrocladius) psilopterus* are recorded for the first time in the Greek freshwaters (Ntislidou et al. 2019). *Cryptochironomus (Cryptochironomus) gr. defectus* was known in Greece, but it was recorded for the first time in Lake Volvi (Ntislidou et al. 2019). Among Oligochaeta, the rare species *P. pusillus* was until now only known from Northern Europe [i.e., Germany (Haybach and Timm 2013), Slovakia, Serbia and Austria (Šporka et al. 2008; Atanacković et al. 2011)]. Here, this species is recorded for the first from Lake Mikri Prespa. This potentially ancient lake hosts an endemic oligochaete community, isolated within narrow zoogeographical boundaries defined by the lakes Megali Prespa, Ohrid, Skadar and Dojran (Albrecht et al. 2012).



**Fig. 3** Box-and-Whisker plots of benthic macroinvertebrate diversity indices **a** Shannon–Wiener ( $H'$ ), **b** Weighted ( $Hw'$ ), **c** Margalef ( $d'$ ) and **d** Pielou's evenness ( $J'$ ) estimated in lakes Volvi, Kastoria and Mikri Prespa. Solid lines at the center of

boxes indicate median values, boxes represent inter-quartile ranges (25–75%), outer lines the highest and lowest values, and symbol \* the outlier values

**Table 6** Pearson correlation coefficient ( $r$ ) between the environmental parameters and diversity indices Shannon–Wiener ( $H'$ ), Weighted ( $Hw'$ ), Margalef ( $d'$ ) and Pielou's evenness ( $J'$ ) of benthic communities in lakes Volvi, Kastoria and Mikri Prespa

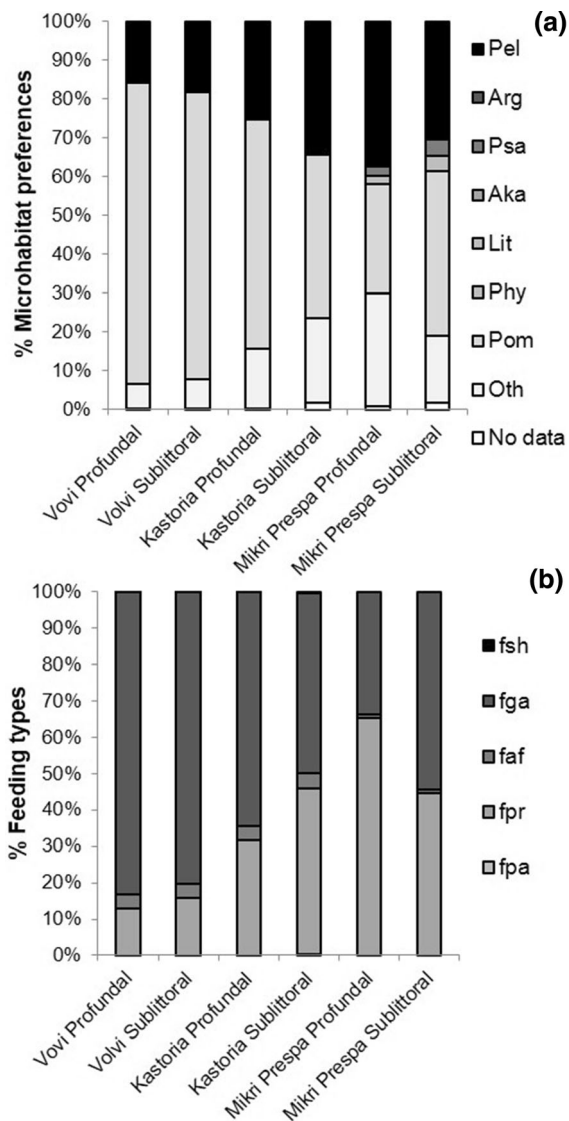
Parameters	$H'$	$Hw'$	$d'$	$J'$
S_Depth	$r = 0.647^*$	$r = 0.629^*$	$r = 0.354^*$	$r = 0.477^*$
TSS	$r = 0.236$	$r = 0.277$	$r = 0.258$	$r = 0.146$
WT	$r = 0.344^*$	$r = 0.412^*$	$r = 0.321^*$	$r = 0.255$
Cond	$r = 0.531^*$	$r = 0.639^*$	$r = 0.311$	$r = 0.559^*$
pH	$r = 0.122$	$r = 0.092$	$r = 0.205$	$r = 0.024$
DO	$r = 0.202$	$r = 0.320$	$r = 0.296$	$r = 0.127$
BOD <sub>5</sub>	$r = 0.058$	$r = 0.039$	$r = 0.066$	$r = 0.200$
NO <sub>3</sub> -N	$r = 0.160$	$r = 0.081$	$r = 0.016$	$r = 0.186$
NO <sub>2</sub> -N	$r = 0.411^*$	$r = 0.301$	$r = 0.354^*$	$r = 0.290$
NH <sub>4</sub> -N	$r = 0.054$	$r = 0.100$	$r = 0.168$	$r = 0.033$
PO <sub>4</sub> -P	$r = 0.499^*$	$r = 0.399^*$	$r = 0.348^*$	$r = 0.390^*$

*S\_Depth* sampling depth, *TSS* total suspended solids, *WT* water temperature, *Cond* conductivity, *DO* dissolved oxygen, *BOD<sub>5</sub>* biological oxygen demand

\* $p < 0.05$ : significant values

In the mud substrate of lakes, oligochaete is generally one of the prevailing components of the benthos, as is chironomid larvae (Wiederholm 1980).

Accordingly, Tubificidae and Chironomidae were the dominant taxa in the three lakes studied. *P. hammoniensis* was dominant among the tubificids and *C.*



**Fig. 4** Percentage composition of benthic macroinvertebrate communities' structure in relation to **a** microhabitat preferences and **b** feeding types for the sublittoral and profundal zones of lakes Volvi, Kastoria and Mikri Prespa

(*Chironomus*) gr. *plumosus* mainly prevailed from chironomid species. *P. hammoniensis* is distributed worldwide, generally inhabiting silt and clay bottoms (Risnoveanu and Vadineanu 2002) and it is tolerant to pollution (van Haaren and Soors 2013). *Chironomus* (*Chironomus*) gr. *plumosus* can tolerate the hypoxic conditions that often prevail in organic-rich fine sediments (Heling et al. 2018). *C. (Chaoborus) flavicans* was also a dominant species in Lake Mikri

Prespa, as in previous studies (Petridis and Sinis 1995, 1997), indicating the eutrophic state of the lake.

In the studied lakes, a typical benthic fauna of the Mediterranean profundal and sublittoral lake zones was recorded belonging to oligochaetes and chironomids (Bazzanti et al. 2012), which are well known to be sensitive to eutrophication (Wiederholm 1980; Lang 1990). The profundal zone was colonized by few taxa, very resistant to low water oxygenation. The structure of benthic assemblages in this zone is less complex than in other lake zones, as it is mostly affected by changes in lake productivity due to oxygen depletion and organic food material concentration (Bazzanti et al. 2017). In addition, our data indicated that sublittoral and profundal zones were dominated by the same species [*P. hammoniensis* and *C. (Chaoborus) flavicans*]. Generally, eutrophication reduces benthic macroinvertebrate diversity and abundance, as well as increases faunal similarity among depth zones (Bazzanti and Seminara 1987; Bazzanti et al. 2012).

Knowledge of community functional trait composition is crucial in studying community–environment relationships and human-induced ecosystems degradation (Heino 2008). The benthic macroinvertebrate functional traits have been extensively studied for river ecosystems (e.g., Bady et al. 2005; Bonada et al. 2007; Feld et al. 2014), dam-removal (e.g., Renöfält et al. 2013; Tullós et al. 2014; Sullivan and Manning 2017) and reservoirs (e.g., Fanny et al. 2013; Beghelli et al. 2020). Moreover, during the last years, Chironomidae, as one of the most diverse and widely distributed dominant group within aquatic macroinvertebrates, is claimed to be suitable for functional diversity across various environmental gradients (e.g., Serra et al. 2016; 2017; Milošević et al. 2018; Jiang et al. 2019; Antczak-Orlewska et al. 2020). However, few studies have been conducted for lake benthic communities (e.g., Bazzanti et al. 2017; Tolonen et al. 2018). The functional structure of macroinvertebrate assemblages in both zones of the studied lakes did not differ. The profundal and sublittoral habitats were characterized by the high presence of collectors/gatherers, alongside with predators. Especially in Lake Mikri Prespa, predators dominated, although the lake is populated by invertivorous fish (Petriki 2015). Collectors/gatherers are considered common benthic feeding traits in the profundal lake zone, favored by the sinking of organic matter, which constitutes the

**Table 7** SIMPER analysis (both similarity and dissimilarity) of benthic macroinvertebrate functional trait categories of the profundal and sublittoral zones in the lakes (Volvi, Kastoria and Mikri Prespa)

Average similarity: Types	Profundal 78.3% Contribution (%)	Sublittoral 79.5% Contribution (%)	Average dissimilarity: 21.2% Types	Contribution (%)
<i>Microhabitat preference</i>				
Pom	49.8	48.5	Pom	31.2
Pel	28.2	26.7	Oth	19.0
Oth	19.0	17.1	Pel	17.0
<i>Feeding types</i>				
Fga	59.0	60.4	Fga	42.0
Fpr	32.0	30.0	Fpr	39.5
			Faf	12.2

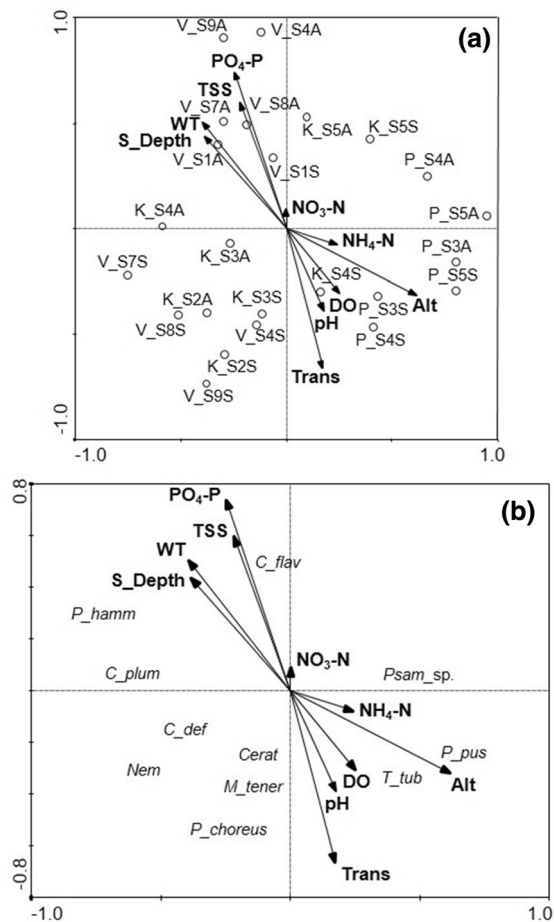
main source of nutrients in this lake stratum (Hamerlík and Brodersen 2010; Oliveira and Nessimian 2010; Frainer et al. 2016). Undoubtedly, shredders, grazers and miners lack from profundal and sublittoral zones due to the absence of light (Bazzanti et al. 2017). Regarding the functional trait microhabitat preference, macroinvertebrates showed a preference for particulate organic matter and mud. Both lake zones are characterized by homogenous habitats, fine sediments and no vegetation (Jónasson 2004). Still, much work has to be conducted to figure out the efficacy of using functional traits of lake macroinvertebrate communities (Heino 2008; Frainer et al. 2016; Tolonen et al. 2018).

The ecological quality of lakes assessed by the application of the GLBiI was characterized as “good” for lakes Volvi and Mikri Prespa and “moderate” for Lake Kastoria. Regarding each metric from GLBiI, the lowest values were estimated for the species richness (“Taxa\_Tol”). Eutrophication decreases diversity and enhances homogeneity in the sublittoral and profundal zones (Bazzanti et al. 2017). The latest estimation of their ecological quality based on benthic macroinvertebrates was moderate (Ntislidou et al. 2018), due to human activities leading to their degradation (Latinoopoulos et al. 2016; Petriki et al. 2017). Recovering these lakes necessitates more severe mitigation measures, which are included in the national River Basin Management Plans (RBMP, <http://wfdver.ypeka.gr/en/home-en/>) to fulfill the goals set by WFD.

The geographical factor (altitude) and eutrophication ( $P-PO_4$ ,  $BOD_5$ ) were the main environmental

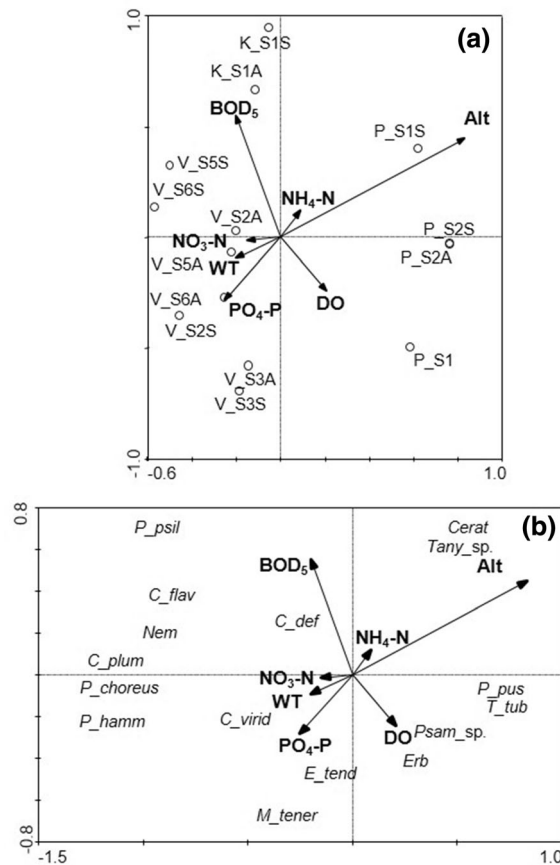
factors structuring benthic macroinvertebrate communities in the studied lakes. The inclusion of altitude in the RDA is likely a surrogate for climate effect and accounts for differences among lakes (Donohue et al. 2009). Shifts in climatic and geographic factors are reflected by other environmental properties, such as water and air temperature, precipitation, catchment area and vegetation cover characteristics (Hamerlík et al. 2010). Studies covering a wide range of altitude found a decrease of species richness with increasing altitude (e.g., Rahbek 1995). Our findings showed that benthic communities from Lake Prespa and especially *P. pusillus*, *Tanytarsus* sp. and Ceratopogonidae are related to altitude. Moreover, the positive relationships found between nutrients and sublittoral and profundal macroinvertebrate densities pose evidence that these benthic assemblages could provide useful information for the classification of lakes’ eutrophication status. Several studies have previously identified the importance of phosphorus as an essential factor in shaping macroinvertebrate communities (e.g., Fried-Petersen et al. 2020; Heino and Tolonen 2017; Bazzanti et al. 2012). According to Heino and Tolonen (2017), total phosphorus sets limits to the distribution of certain species preferring high-primary-productivity lake habitats. In our study, *P. hammoniensis*, *C. (Chaoborus) flavicans* and *M. tener* are affected mainly by phosphorus concentration.

Lakes are unique systems, and they are especially vulnerable to nutrient enrichment caused by human activities. Thus, it is crucial to identify these impacts for lake ecosystems. Regarding lakes Volvi, Kastoria



**Fig. 5** Ordination of **a** sampling stations and **b** benthic macroinvertebrate densities in relation to environmental parameters with respect to the first and second axes of the redundancy analysis. Data referred to the sublittoral zone of lakes Volvi (V), Kastoria (K) and Mikri Prespa (P) in autumn (A) 2011 and spring (S) 2012. Alt: Altitude, DO: Dissolved Oxygen, S\_Depth: Sampling Depth, Trans: transparency, TSS: total suspended solids, WT: water temperature. *C\_def*: *C. (Cryptochironomus) gr. defectus*, *C\_flav*: *C. (Chaoborus) flavicans*, *C\_plum*: *C. (Chironomus) gr. plumosus*, *Cerat*: Ceratopogonidae, *M\_tener*: *M. tener*, *Nem*: Nematoda, *P\_choreus*: *P. choreus*, *P\_hamm*: *P. hammoniensis*, *P\_pus*: *P. pusillus*, *Psam\_sp.*: *Psammoryctides* sp., *T\_tub*: *T. tubifex*

and Mikri Prespa, we showed that environmental parameters related to eutrophication influence the structure of sublittoral and profundal benthic communities of these lakes. The effects of these shifts are a reduction in the diversity of benthic macroinvertebrates and an increase in the number of taxa with a high tolerance for pollution. Since these lake ecosystems are located in protected areas, the present results



**Fig. 6** Ordination of **a** sampling stations and **b** benthic macroinvertebrate densities in relation to environmental parameters with respect to the first and second axes of the redundancy analysis. Data referred to the sublittoral zone of lakes Volvi (V), Kastoria (K) and Mikri Prespa (P) in autumn (A) 2011 and spring (S) 2012. Alt: altitude, DO: dissolved oxygen, WT: water temperature. *C\_def*: *C. (Cryptochironomus) gr. defectus*, *C\_flav*: *C. (Chaoborus) flavicans*, *C\_plum*: *C. (Chironomus) gr. plumosus*, *C\_virid*: *C. viridulum*, *Cerat*: Ceratopogonidae, *E\_tend*: *E. tendens*, *Erb*: Erpobdellidae, *M\_tener*: *M. tener*, *Nem*: Nematoda, *P\_choreus*: *P. choreus*, *P\_hamm*: *P. hammoniensis*, *P\_pus*: *P. pusillus*, *Psam\_sp.*: *Psammoryctides* sp., *P\_psil*: *P. (Psectrocladius) psilopterus*, *Tany\_sp.*: *Tanytarsus* sp., *T\_tub*: *T. tubifex*

could contribute to decision makers develop and implement management plans for maintaining ecosystems' biodiversity and improving ecosystem services. Such programs of measures could include actions for reducing diffuse pollution, improving the coverage of the sanitation network, increasing the efficiency of the existing Waste Water Treatment Plants and restoring the riparian zones to improve their ecological status. Although the studied lakes are under the surveillance

of the institutional protection management (e.g., Management Bodies), the existing protection should be enhanced more to ensure their integrity. Restoration programs that integrate hydromorphological, physicochemical and biological elements of the studied lake catchment areas are of high priority for future management strategies. Consequently, the understanding of the biological and ecological requirements of benthic assemblages, according to our outcomes, will contribute to this field.

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**Availability of data and material** Data are available on request from the authors.

#### Declarations

**Conflict of interest** All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

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