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ZOOPLANKTON IN ANCIENT AND OLIGOTROPHIC LAKE OHRID (EUROPE) IN ASSOCIATION WITH ENVIRONMENTAL VARIABLES

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ABSTRACT

Zooplankton is studied in the ancient, tectonic, oligomictic and oligotrophic Lake Ohrid (Macedonia, South Eastern Europe). The main aim of this study was to assess the seasonal and spatial patterns of the zooplankton functional feeding guilds in relation to the environmental conditions. Metalimnion of the lake was detected as the most productive environment, where biomass of the phytoplankton and abundance of the zooplankton reached their maxima. Pelagial zooplankton of low abundance (25 ± 22 ind. L^{-1}) consisted of 16 species including two endemic copepods, *Arctodiaptomus steindachneri* (Richard, 1897) and *Cyclops ochridanus* (Kiefer, 1932). Copepods obtained remarkable share (60%) in the zooplankton assemblage. Microphagous zooplankton was mainly comprised of the most abundant rotifer *Kellicottia longispina* (Kellicott, 1879) in summer, and copepod nauplii during the spring *Eudiaptomus gracilis* (Sars, 1862) and *C.ochridanus,* and autumn *C.ochridanus*. Due to their requirements for the bacterio-detritus suspension, this microphagous zooplankton occupied aphotic hypolimnion during the entire study period. Raptorials were typically represented by copepodites and adult copepods in the metalimnion, and were significantly and positively affected by temperature (r = 0.417, p = 0.001), dissolved oxygen (r = 0.463, p = 0.0001) and, particularly, phytoplankton biomass (r = 0.708, p < 0.00001). This is the first study in which the link between the lower and higher trophic levels is investigated in Lake Ohrid.

Keywords:
Copepods
Rotifers
Microphgous
Raptorials
Metalimnion Oligomictic lake

How to Cite

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INTRODUCTION

Zooplankton is an important link in the food webs between the primary producers and higher trophic levels in a lake. It is an efficient grazer on the suspended organic matter and phytoplankton, while also serves as food source for larger invertebrates and fish (González Sagrario and Balseiro, 2010; Špoljar et al., 2011; Compte et al., 2016; Celewicz-Goødyn and Kuczyńska-Kippen, 2017). Zooplankton species are sensitive to anthropogenic impacts, reflected in the alterations in their abundance and diversity as well as in water quality (Ejsmont-Karabin and Kuczyńska-Kippen, 2001; Jeppesen et al., 2011; Špoljar, 2013). The abundance and composition of zooplankton vary spatially and seasonally in large lakes due to both biotic and abiotic factors. The key factors are temperature (Voutilainen et al., 2016), oxygen (Ekau et al., 2010), nutrients (Conde-Porcuna et al., 2002), food resources (Špoljar et al., 2005), competition (Gilbert, 1989) and predation (Meerhoff et al., 2007; Basińska et al., 2010).

The role of zooplankton species in water bodies is generally analysed based on the variations in distribution of particular species or populations. More recently, their functional traits are considered, aggregating their species in groups (guilds) with similar roles in the ecosystems (Karabin 1985; Obertegger and Manca, 2011; Špoljar et al., 2011; Litchman et al., 2013). Various levels of zooplankton functions and types provide more detailed and complex information on functioning of natural food webs (France, 2012). Functional categories can be distinguished on the niche bases occupied by species in the food web including feeding (trophic) groups, *i.e.* bacterivorous, algivorous or predatory species (Špoljar et al., 2005, 2011), or in relation with the habitat within the water body, *i.e.* littoral species within different type of macrophytes (Celewicz-Goødyn and Kuczyńska-Kippen, 2017).

The deep oligotrophic lakes are characterised by low zooplankton biomass, abundance and biodiversity (Habdija et al., 2011). In these lakes, the bottom-up control is stronger than the top-down control of the zooplankton grazing on phytoplankton (Auer et al., 2004). Due to the opportunity to escape from predators with vertical migrations to the deeper aphotic layers, fish predation pressure on zooplankton is lower in deep lakes, whereas in shallow lakes (Jeppesen et al., 1997, 2003) it is considerable.

The study of freshwater zooplankton communities in Lake Ohrid has a long history (Georgević, 1907; Stanković, 1931; Serafimova-Hadžišče, 1959, 1986; Gušeska, 1998). Although there have been numerous surveys of the lake zooplankton with records about its composition, abundance, biomass, and spatial and temporal distribution (Kostoski et al., 2004, 2005; Tasevska et al., 2008; Gušeska et al., 2013, 2014), data concerning the relationships of the zooplankton assemblages with the range of physical and chemical characteristics of the lake and biotic factors are limited (Gušeska et al., 2005; Noveska and Tasevska, 2010; Tasevska et al., 2012a, 2012b). The aim of this study was to assess the spatio-seasonal patterns of the main zooplankton groups, Rotifera, Cladocera and Copepoda, and their relations in the functional feeding guilds with the environmental conditions.

MATERIALS AND METHODS

Study site

Lake Ohrid (41°2′19″N, 20°44′13″E) is the oldest lake in Europe and one of the oldest water systems in the world. Being formed tectonically 4 to 10 million years ago, the lake is situated in the Ohrid valley in the south-western part of Macedonia adjacent to Albanian border at an altitude of 693.17 m above the sea level. It has a surface area of 358.2 km^2, a maximum depth of 288.7 m, a water volume of 58.6 km^3 and a shoreline length of 87.53 km. Detailed morphometric and limnological attributes of the lake were recorded in the study of Matzinger et al. (2006, 2007). A main characteristic of Lake Ohrid's ecosystem is the scarcity of nutrients and consequently a low level of primary production. Its biodiversity richness, especially in relict and endemic species - as a result of its ancient origin, geographic isolation and the stability of its ecological conditions - has given it a global significance (Spirkovski et al., 2000; Matzinger et al., 2007). Results of a comprehensive study classified Lake Ohrid as oligomictic regarding the thermal combination and stratification. It has been discovered that the top ~150 m of its water column engages in annual thermal stratification, while the lower hypolimnion is stable due to the salinity gradient. The "complete overturn" takes place only roughly once every 7 years during the cold winters (Matzinger et al., 2006). In this study, the term 'mixolimnion' will be used, common for the meromictic lakes (Kalf, 2002), for annualy-mixed water column apart from the rarely- or unmixed deeper water layer.

Data collection and analysis

Sampling was conducted in 2010 in the pelagic zone of Lake Ohrid, on the vertical profile above the maximum depth of 245 m, during two months of each season: winter (January, March), spring (April, May), summer (July, September), autumn (October, December). The vertical layers were divided into epilimnion (1 and 10 m), metalimnion (20 and 30 m) and hypolimnion (40, 50, 75 and 100 m).

Zooplankton was collected by a 5-liter Ruttner sampler, filtered *in situ* through a sieve (45 μm mesh-size) and preserved in 4% formalin. The specimens were quantitatively analysed under a Laica DM IRB microscope (100 to 600× magnification). Identification of the species was undertaken according to the guides provided by Koste (1978), Amoros

(1984) and Einsle (1993).

Water temperature was measured in the field using a WTW probe. Dissolved oxygen (Winkler method, APHA-AWWA-WPCF, 1998), total nitrogen, TN (Solorzano, 1969) and total phosphorus, TP (Strickland and Parsons, 1972) were analysed in the laboratory. The concentration of chlorophyll *a* (Chl *a*), as an indicator of phytoplankton biomass, was determined by spectrophotometry, following its extraction in 90% ethanol (ISO 10260, 1992; Meyns et al., 1994).

The zooplankton taxa were separated into functional feeding guilds (FFG), according to their food-collecting mechanism and size of the food particles (Karabin, 1985; Špoljar et al., 2011), as microphagous - collect multiple food particles, mainly bacterio-detritus suspension and raptorials - show an active grasping and piercing to catch food, *i.e.* algae, protozoans or microfauna (Oberteger et al., 2011).

The obtained data were logarithmically transformed [log (x+1)], checked by the Shapiro–Wilk's test and, as they did not follow a normal distribution, were analysed by non-parametric tests using Statistica 13.0 software (Statsoft Inc., 2013). Kruskal-Wallis H test was conducted for the analysis of spatial and seasonal differences in the environmental parameters and zooplankton assemblage. The relationships between environmental variables and zooplankton abundance were tested by Spearman's correlations.

RESULTS

The summarized results of analysing water temperature, concentration of dissolved oxygen, TP, TN and Chl *a* are displayed in Table 1.

Table 1. Range and mean ± SD values of the environmental variables and abundances of the zooplankton groups (ind. L^{-1})

	Range	Mean		SD
T (°C)	6.1 – 24.6	8.67	±	0.449
O_2 (mg. L^{-1})	7.749 – 12.56	9.85	±	0.104
TP (µg. L^{-1})	2.48 – 11.935	6.372	±	0.279
TN (µg. L^{-1})	159.46 – 599.26	327.265	±	12.108
Chl *a* (µg. L^{-1})	0.007 – 1.78	0.654	±	0.052
Rotifera	0 – 40	7.820	±	9.167
Cladocera	0 – 9.5	1.180	±	2.206
Copepoda	0 – 66.5	15.633	±	14.856
Zooplankton total	0 – 86.5	24.633	±	22.030
Microphagous	0 – 54	14.188	±	12.252
Raptorials	0 – 47.5	10.336	±	13.050

T – temperature; O_2 – dissolved oxygen; TP – total phosphorus; TN – total nitrogen; Chl *a* - chlorophyll *a*

Configuration of the environmental parameters and zooplankton indices showed more pronounced spatial, *i.e.* vertical, than seasonal pattern (Table 2). Water temperature and phytoplankton biomass did not show significant seasonal oscillations (Kruskal-Wallis test, $p < 0.05$). As expected, concentration of dissolved oxygen was higher during winter (10.1 ± 0.7 mg O_2 L^{-1}) than in summer and autumn. Nutrients seasonality indicated a significant increase in summer so that the values of TP (8.64 ± 1.56 µg L^{-1}) and TN (370.81 ± 87.43 µg L^{-1}) were twice and triple their annual mean values, respectively (Table 1). In contrary, there was no significant difference in the vertical distribution of the nutrients (Kruskal-Wallis test, $p < 0.05$). Water temperature and phytoplankton biomass showed strong vertical differences with the highest values in the epilimnion (13.71 ± 5.1°C) and metalimnion (1.04 ± 0.31 µg Chl *a* L^{-1}), respectively (Table 2).

Pelagial zooplankton consisted of 16 species, including two endemic copepods, *Arctodiaptomus steindachneri* (Richard, 1897) and *Cyclops ochridanus* (Kiefer, 1932), and rotifers as the most diverse group presented by 8 species (Table 3). Mean annual abundance of zooplankton (25 ± 22 ind. L^{-1}) was very low (Table 1, Fig. 1). Copepods prevailed in all seasons (51% to 59%), except in summer when rotifers overtook a higher share (44%), reaching their peak with significant increase in abundance (Kruskal-Wallis test, $p < 0.05$, Table 1 and 2). Copepods seasonality pattern did not show significant oscillations (Kruskal-Wallis test, $p > 0.05$), although displayed notable variations. They achieved their peak in spring, caused mainly by higher abundance of nauplii of the calanoid *Eudiaptomus gracilis* (Sars, 1862) and cyclopoid *C. ochridanus* with an increased abundance in autumn due to the dominance of the cyclopoid *C. ochridanus* nauplii (Fig. 1, Table 3). Within zooplankton, the abundance of cladocerans was the lowest, although their contribution to the zooplankton assemblage increased slightly in autumn (Fig. 1).

In the vertical distribution, each zooplankton group developed the most abundant populations in thermocline - metalimnion (Fig. 1, Tables 2 and 3). Copepods prevailed in the entire mixolimnion layer, with the contributions from 47% up to 55% in the vertical gradient.

Functional feeding guilds contained microphagous and raptorial zooplankters.

The obligate predators among cladocerans, *Leptodora kindtii* (Focke, 1844), and rotifers, *Asplanchna priodonta* Gosse, 1850 and *Ploesoma truncatum* (Levander, 1894), were present very sparsely, individually and sporadically. Abundance of the microphagous and raptorials did not show seasonal fluctuations, and their vertical oscillations fitted to general zooplankton trend, maximizing in the metalimnion (Fig. 2, Tables 1 and 2). Microfilter-feeders comprised mainly of the most abundant rotifer, *Kellicottica longispina* (Kellicott, 1879), and copepod nauplii which,

Table 2. Seasonal and spatial oscillations of the environmental variables and abundances of the zooplankton groups (ind. L-[1]), Kruskal-Wallis test ($n = 64$, $p < 0.05$) with accompanying results of the post-hoc multiple comparison test. For abbreviations see Table 1.

	Seasonal oscillations			Spatial oscillations		
	H	*P*	Multiple comparison test	H	*P*	Multiple comparison test
			a) Environmental variables			
T (°C)	1.54	ns		46.22	0.0000	E, M > H
O_2 (mg.L^{-1})	16.65	0.0008	W, SP > A	12.05	0.002	M > H
TN (µg. L^{-1})	9.78	0.02	SU > A	0.1	Ns	
TP (µg. L^{-1})	40.70	0.0000	W, SP < SU, A	6.26	Ns	
Chl a (µg. L^{-1})	2.79	Ns		20.81	0.0000	E, M > H
			b) Zooplankton groups			
Rotifera	13.85	0.003	SU > W, A	16.20	0.0003	M > H
Cladocera	6.92	ns		23.10	0.0000	M > E, H
Copepoda	0.43	ns		12.99	0.002	M > E, H
Microphagous	4.65	ns		16.35	0.0003	M > E, H
Raptorials	1.26	ns		25.25	0.0000	M > E, H

ns - nonsignificant; W – winter; SP – spring; SU – summer; A – autumn

Table 3. Zooplankton composition and their feeding traits according to the spatio-seasonal species maxima. FFG: Functional Feeding Guilds, M: microphagous, R: raptorials

	FFG	J	M	A	M	J	S	O	D	
Bosmina longirostris (Müller 1785)	M					1 – 10				Epilimnion
Eudiaptomus gracilis copepodite	R			21 – 30						Epilimnion
Arctodiaptomus steindachneri (Richard, 1897)	R				1 – 10					Epilimnion
Ploesoma truncatum (Levander, 1894)	R					1 – 10				Epilimnion
Mesocyclops leuckarti (Claus, 1857)	R						1 – 10			Epilimnion
Mesocyclops leuckarti copepodite	R						1 – 10			Epilimnion
Asplanchna priodonta Gosse, 1850	R							1 – 10		Epilimnion
Eudiaptomus gracilis nauplius	M		11 – 20							Metalimnion
Eudiaptomus gracilis (Sars, 1862)	R			11 – 20						Metalimnion
Cyclops ochridanus copepodite	R			1 – 10						Metalimnion
Daphnia pulicaria Forbes, 1893	R				1 – 10					Metalimnion
Filinia terminalis (Plate, 1886)	M							1 – 10		Metalimnion
Arctodiaptomus steindachneri copepodite	R					31 – 40				Metalimnion
Arctodiaptomus steindachneri nauplius	M					1 – 10				Metalimnion
Mesocyclops leuckarti nauplius	M					1 – 10				Metalimnion
Kellicottia longispina (Kellicott, 1879)	M					31 – 40				Metalimnion
Leptodora kindtii (Focke, 1844)	R						1 – 10			Metalimnion
Cyclops ochridanus Kiefer, 1932	R						1 – 10			Metalimnion
Synchaeta pectinata Ehrenberg, 1832	R						1 – 10			Metalimnion
Diaphanosoma brachiurum (Liévin, 1848)	R							1 – 10		Hypolimnion
Keratella quadrata (Müller, 1786)	M									Hypolimnion
Polyarthra vulgaris Carlin, 1943	R						1 – 10			Hypolimnion
Trichocerca capucina (Wierzejski & Zacharias, 1893)	R						1 – 10			Hypolimnion
Cyclops ochridanus nauplius	M		11 – 20						21 – 30	Hypolimnion

o 1 – 10 0 11 – 20 0 21 – 30 0 31 – 40 ind. L-1

Table 4. Relationships between zooplankton abundances (ind. L-1) and environmental variables (Spearman correlation coefficient, $p < 0.05$)

	Rotifera	Cladocera	Copepoda	Microphagous	Raptorials
T (°C)			0.482		0.417
O_2 (mg. L^{-1})	0.430		0.437	0.410	0.463
Chl *a* (µg L^{-1})		0.531	0.652		0.708

besides metalimnion, occupied the hypolimnion (depths 40 - 75 m) during the entire study period (Fig. 2). Raptorials were represented mainly by copepodite and adult copepods and were limited to metalimnion. Microfilter-feeders were positively affected by dissolved oxygen, and raptorials by temperature, dissolved oxygen and, most significantly, by phytoplankton biomass ($r = 0.708$, $p < 0.00001$; Table 4). Similar interactions with environmental variables, as functional feeding guilds, also exposed the main zooplankton constituents (Table 4).

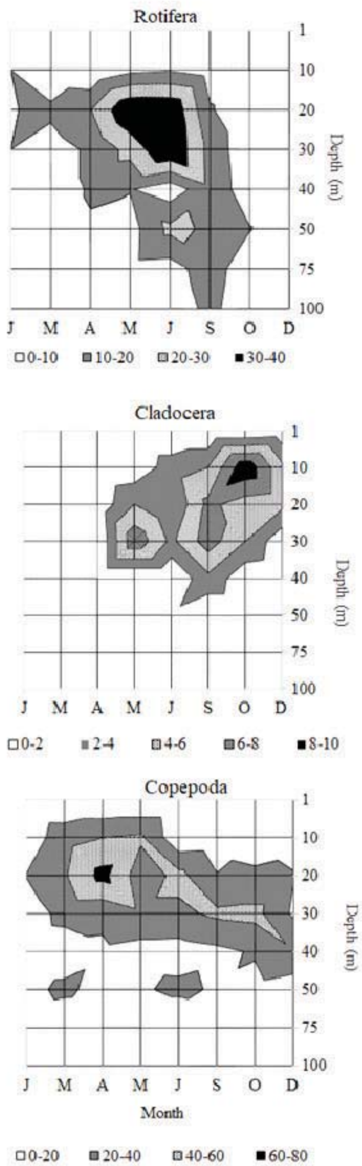

Fig 1. Spatio-seasonal distribution of Rotifera, Cladocera and Copepoda (ind. L-1) in the pelagic zone of Lake Ohrid

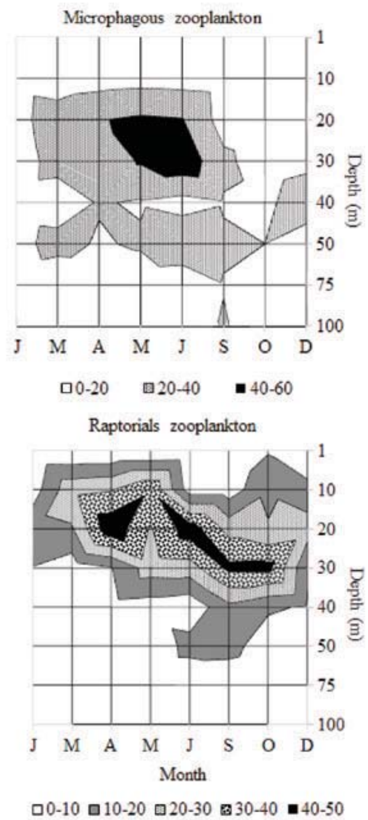

Fig 2. Spatio-seasonal distribution of microphagous and raptorial zooplankton (ind. L-1) in the pelagic zone of Lake Ohrid

DISCUSSION

Results of this study provide insights into the spatio-temporal distribution of the main zooplankton groups in Lake Ohrid nested within the functional-feeding guilds. In spring, the microphagous entities, consisting of the naupliar stage of *C. ohridanus* and *E. gracilis* which were not dependent upon the primary production, *i.e.* phytoplankton biomass, started to develop their populations. Abundance of the nauplii decreased in summer due to their further development to copepodite and adult stages, while in autumn the new generation gained the domination. Rotifers, as r-strategists, occupied the meta- and hypolimnion layers in summer chiefly by the microphagous species *K. longispina*. This small rotifer was one of the rare inhabitants of the deeper hypolimnion due to the availability of suspended bacterio-detritus food resources. Transparency enhanced the phytoplankton growth, resulting in the occupation of the metalimnion by raptorial copepod species both in copepodite and adult stages throughout the study period.

The abundance of zooplankton in the metalimnion could be argued from several points of view. The peculiar environmental conditions in this transitional layer have also been observed in other studies (Cantin et al., 2011; Karpowicz and Ejsmont-Karabin, 2017). For instance, the non-significant difference in vertical distribution of the nutrients was in compliance with the orthograde regime in oligotrophic lakes. During the thermal stratification, sharp negative vertical gradient of temperature in the metalimnion increases water density and nutrient concentration. In addition, due to the sufficient light availability, this is the most productive photosynthetic layer which concomitantly promotes the zooplankton growth. This was the case for Ohrid Lake where the maximum chlorophyll *a* concentration was measured in the metalimnion (0.31 ± 0.06 μg L^{-1}). In addition, sinking to the deeper layers protects the plankton against UV irradiation, thus only few species achieve their maximum abundances in epilimnion (Compte et al., 2016). Furthermore, high abundances of visual predators, zooplanktivorous fish, *i.e.* Ohrid trout *Salmo letnica* (Karaman, 1924), belvica *Salmo ohridanus* (Steindachner, 1892) and bleak-plasica *Alburnus alburnus arborella* (de Filippi, 1844), have probably reduced zooplankton in the epilimnion (Talevski et al., 2009).

According to the survey of rotifer succession in Lake Ohrid, the microphagous *Keratella cochlearis* (Goose, 1851) and *K. longispina* alternatively dominated from the year 2000 to 2008 (Tasevska et al., 2008). In our study conducted in 2010, the most abundant rotifer species in Lake Ohrid was *K. longispina* with similar abundance (7 ind. L^{-1}) to that in 2008 (6 ind. L^{-1}) (Tasevska et al., 2008). The presence of this species in the hypolimnion could be a result of its wide tolerance to oxygen depletion and its opportunistic nature that will allow it to quickly occupy empty ecological niches after the crustaceans nauplii decrease in summer (B rzi š and Pejler, 1989). Overall, higher abundances of the microphagous species rely upon the increase in concentration of the suspended organic matter, *i.e.* production, indicated eventually at the higher trophic levels (Malekzadeh-Viayeh and Špoljar, 2012; Špoljar, 2013).

Oligotrophic lakes are generally dominated by calanoid copepods because of their competitive advantage for algae over cladocerans (Bunnell et al., 2011). Their domination is also recorded for other lakes of low trophic levels, such as that of *Eudiaptomus hadzici* (Brehm, 1939) in karst Visovac Lake in Croatia (Bukvić et al., 1999) and in the shallow lakes of Uruguay with warmer waters (Meerhof et al., 2007). Freshwater planktonic copepods play an important role as feed for the planktivorous fish (Jeppesen et al., 2000). Cyclopoids are mostly omnivores and raptors upon algae, protozoans and small zooplankton. Calanoids, in turn, have a more algivorous diet and outcompete the early copepodite stages and cladocerans. Moreover, they have lower food threshold and are usually more abundant than cyclopoids in oligotrophic lakes (Anneville et al., 2007). Thus, low cladoceran abundance in Lake Ohrid could be the result of their competition with the copepods, while high risk of their predation by fish due to their reduced swimming velocity could also have an impact (Dodson et al., 1997).

Knowledge of nutrient flux through the complex dynamics of natural food webs can be useful for understanding the ecology of the oligomictic and oligotrophic lakes. Considering the functional role of zooplankton within the freshwater food webs, exploring their interactions with biotic and abiotic parameters can assist in the protection of water quality and biodiversity in such peculiar ecosystems such as Lake Ohrid.

Sažetak

ZOOPLANKTON U DREVNOM I OLIGOTROFNOM JEZERU OHRID (EUROPA) U INTERAKCIJI S UVJETIMA OKOLIŠA

Analiziran je sastav zooplanktona u geološki starom, tektonskom Ohridskom jezeru (Makedonija, jugoistočna Europa). Glavni cilj rada bio je utvrditi sezonske i prostorne značajke funkcionalnih hranidbenih skupina zooplanktona i njihovu povezanost s uvjetima okoliša. Najveća produkcija zooplanktona utvrđena je u metalimniju, u kojem su biomasa fitoplanktona i brojnost zooplanktona postigle najveće vrijednosti. Utvrđeno je 16 pelagičkih vrsta od kojih dvije endemične: *Arctodiaptomus steindachneri* (Richard, 1897) i *Cyclops ochridanus* (Kiefer, 1932). Zooplankton pelagijala bio je zastupljen s niskom brojnošću, 25 ± 22 ind. L^{-1}, a najveći udio, 60 %, postigli su veslonošci. Unutar trofičke skupine mikrofaga, prevladavali su tijekom ljeta kolnjaci s vrstom *Kellicottica longispina* (Kellicott, 1879), a naupliji veslonožaca prevladavali su u proljeće *Eudiaptomus gracilis* (Sars, 1862) and *C. achridanus* i jesen *C.achridanus.* Ova trofička skupina hrani se suspenzijom bakterija i detritusa, te je tijekom istraživanog razdoblja zauzimala afotički hipolimnij. Predatori su uglavnom bili zastupljeni s kopepoditima i odraslim veslonošcima u metalimniju. Na njihove populacije su značajno i pozitivno utjecali: temperatura (r = 0.417, p = 0.001), otopljeni kisik (r = 0.463, p = 0.0001) te najizraženije biomasa fitoplanktona (r = 0.708, p < 0.00001). Ovo istraživanje među prvima razmatra zooplankton Ohridskog

jezera kao važnu kariku unutar hranidbene mreže ovog oligotrofnog ekosustava.

Ključne riječi: veslonošci (Copepoda); kolnjaci (Rotifera); mikrofagi, predatori, metalimnij, oligomiktičko jezero

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