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RESEARCH ARTICLE

Zooplankton communities in Mediterranean temporary lakes: the case of saline lakes in Cyprus

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Abstract – Temporary saline lakes are diverse ecosystems mostly located in arid areas. In the Mediterranean region they are among the most remarkable, but also the most threatened habitats; thus, effective management and conservation plans need to consider their special hydrological and ecological features and requirements. They are mainly fishless systems and so zooplankton is the driver of the trophic cascade. Our aim was to determine zooplankton communities' composition and biomass in seven temporary saline lakes of Cyprus and investigate their relation with environmental variables. Salinity ranged between <2 and 300 ppt and was a key factor shaping zooplankton community. In hyposaline conditions zooplankton communities exhibited higher species diversity than in meso- and hypersaline conditions. Hyposaline lakes were dominated by *Arctodiaptomus salinus* (Daday, 1885)*, Daphnia magna* Straus, 1820 and *Moina brachiata* (Jurine, 1820) in terms of biomass, while meso- and hypersaline lakes by anostracans *Artemia salina* (Linnaeus, 1758) and *Phallocryptus spinosus* (Milne-Edwards, 1840) or *M. brachiata* and *D. magna* highlighting competition as another factor shaping the zooplankton community. We conclude that zooplankton reflects environmental pressures, such as salinity fluctuations which are closely related to water level fluctuations, in the mostly fishless Mediterranean temporary saline lakes. Moreover, salinity fluctuations should be considered a key factor for typological considerations in quality assessments, restoration and management plans in temporary saline systems since it can reflect the hydrological variations on the communities across different years and seasons by salinity gradient even for the same water body.

Keywords: Zooplankton / Mediterranean region / temporary shallow lakes / saline lakes / diversity

1 Introduction

Saline lakes range from small temporary ponds to large deep waterbodies like the Caspian Sea (Eugster and Hardie, 1978). They are diverse ecosystems with important aesthetic, cultural, economic, recreational, scientific, conservation and ecological values (Williams, 1993; Williams, 1998); moreover, they play an important role in the landscape including being biodiversity refugia (O'Connell *et al.*, 2006). Saline lakes are characterized by salinity levels higher than 3 ppt and have no direct connection to the marine environment (Williams, 2002). Although geographically widespread, they are located mostly in arid areas, where they tend to be more abundant than freshwater systems (Hammer, 1986). In the Mediterranean region, these ecosystems naturally fluctuate in both size and salinity because of natural changes in wet and drought cycles (Jarecki and Walkey, 2006); they are usually characterized by a flooding period in winter and spring, and a dry season in summer and autumn (Zacharias *et al.*, 2007). Yet, some of them may hold water for more than one year while others may remain dry for more than one season, depending on the amount of rainfall (Zacharias *et al.*, 2007). Consequently, ecosystem function and ecological equilibrium are mainly regulated by water level fluctuations and salinity which can differ each year according to each climatic pattern (Williams, 2002). Changes in water balance and, consequently, changes in physical and chemical characteristics of the water column are reflected in existing communities (Kirono *et al.*, 2012). The composition of the biota living in such habitats is remarkably distinguishable from other aquatic habitats (Williams, 2002) since these organisms have developed unique physiological and biochemical mechanisms for living in a hyperosmotic medium. Mostly, it comprises halotolerant species of freshwater habitats, but with increasing salinity these disappear and are replaced with species found only in saline lakes (Hammer, 1986).

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Several studies have been conducted regarding zooplankton in saline habitats (*e.g.,* Davis, 2000; Brucet *et al.*, 2010) and most of them have identified the strong effect of salinity on the distribution of zooplankton, while few of them also identified influence of other environmental factors too (Boronat *et al.*, 2001; Vieira and Bio, 2011). Zooplankton species possess several life history traits (diapause, encystment, production of resting eggs, short life-cycles, high reproduction rates, rapid development) that allow them to adapt in highly variable environments, in conditions of osmotic stress and desiccation (Williams, 1985; Hairston, 1996; Brock *et al.*, 2003). Among zooplankton species, crustaceans, such as Artemiidae which are able to survive in stressful conditions like extreme salinity, high or low temperature, and anoxia (Torrentera and Dodson, 2004), and certain species of copepods, which are able to respond to environmental changes, dominate in saline systems (*e.g.*, Alonso, 1990; Torrentera and Dodson, 2004; Khemakhem *et al.*, 2010). Thus, they can be considered as good indicators of saline conditions (Marques *et al.*, 2011). Although zooplankton community is a key component of the aquatic food webs (*e.g.,* Moss *et al.*, 2003; Jeppesen *et al.*, 2011; Haberman and Haldna, 2014), it is not included as a biological quality element in the water framework directive 2000/60/EE (WFD) (European Commission, 2000). Nonetheless, a number of zooplankton multimetric indices have been developed for the assessment of ecological water quality in European lakes (*e.g.*, Moss *et al.*, 2003; Boix *et al.*, 2005) and for the selection of priority conservation areas in the Mediterranean region (Gilbert *et al.*, 2014).

Temporary saline lakes are among the most remarkable, but also the most threatened habitats in the Mediterranean region (Zacharias and Zamparas, 2010). Intensive catchment activities (*e.g.*, pumping of surface/groundwater, dredging, inflow diversion) and human-induced climate change are major drivers of impact (Stenger-Kovács *et al.*, 2014). The European Union has included Mediterranean temporary saline lakes in its conservation plans (Habitats Directive, *e.g.*, Natura codes 1150, 3140 and 92D0, 92/43/EEC) (Council of the European Commission, 1992). Still, based on the criteria of the Habitats Directive (*i.e.* vegetation), not all the saline water bodies can be identified as “Habitats”. Moreover, such temporary aquatic habitats, same as all surface waters, should be protected, monitored and restored (if needed) following the guidelines of the WFD (European Commission, 2000).

In the Mediterranean island of Cyprus, saline lakes constitute the only natural lake asset of the island since all other lentic waters of significant size are freshwater reservoirs. Although for the majority of these lakes, physical and chemical data and available, studies on their biological component are rather limited. In particular, the study of zooplankton communities is limited to species-based approaches in both ecological and molecular aspects (*e.g.,* Mura and Hadjstephanou, 1987; Ketmaier *et al.*, 2008; Munoz *et al.*, 2008; Tziortzis *et al.*, 2014). New insights on the biota of such saline lakes, which are subjected to active conservation (*e.g.*, RAMSAR, NATURA 2000, *etc.*) will provide valuable ecological knowledge to be considered in their ecological and conservation management plans.

Thus, this is the first whole-community approached study on the zooplankton community of the saline lakes of Cyprus.

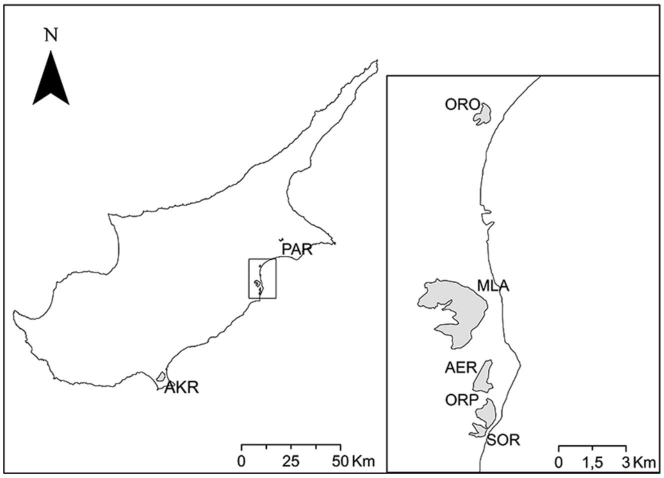

Fig. 1. Map of Cyprus showing the locations of the seven lakes included in the study. *Abbreviations* Megali Larnaka Lake (MLA), Airport Salt Lake (AER), Soros Salt Lake (SOR), Orphani Salt Lake (ORP), Akrotiri Salt Lake (AKR), Lake Paralimni (PAR), Lake Oroklini (ORO).

The objective of the present work was to study the zooplankton communities in seven temporary saline lakes of Cyprus, analyzing the taxonomic composition and biomass of the populations, with the aim of contributing to the knowledge of zooplankton communities across a salinity gradient in the Mediterranean area. More specifically, our aim was to:

- explore the diversity of the encountered zooplankton community;
- determine the principal environmental parameters that affect zooplankton community;
- provide valuable ecological knowledge to be considered in ecological and conservation management plans.

2 Materials & methods

2.1 Study site

Samples were collected from seven lakes in Cyprus (Fig. 1); Megali Larnaka Lake (MLA), Airport Salt Lake (AER), Soros Salt Lake (SOR), Orphani Salt Lake (ORP), Akrotiri Salt Lake (AKR), Lake Paralimni (PAR) and Lake Oroklini (ORO). All of them are temporary salt lakes, located in an arid to semi-arid areas at elevations below 200 m a.s.l. They are mainly fishless or the presence of fish populations is restricted to the peak of wet periods. They are characterized by shallowness (depth from 0.05 to 1 m), small surface area (0.4–9.4 Km^2) and varying salinity levels (<2–300 ppt). Although they are protected sites, they are susceptible to eutrophication since they are subjected to important anthropogenic pressures (agricultural and artificial land coverage in the basin >40%, (Dörflinger *et al.*, unpublished data) (LAWA, 2003). Moreover, elevated values of TP (maximum values: 83–260 μg/L) supporting eutrophic conditions (Smith, 2003) were recorded in all the lakes during 2014–2016 (Water Development Department of Cyprus, unpublished data).

Megali Larnaka Lake, Airport Sat Lake, Orphani Salt Lake and Soros Salt Lake, which are separated by natural and artificial embankments, constitute the Larnaka Salt Lakes complex. All of them except Soros Salt Lake are interconnected. Akrotiri Salt Lake is surrounded by saltwater and freshwater marshes. Both Larnaka Salt Lakes complex and Akrotiri Salt Lake are coastal lakes without natural outflow. Lake Paralimni is surrounded by an urbanized area and consists of a main lake body with outflow occurring through a channel that was, at least in its present state, constructed in the XX century. Lake Oroklini is a marshy coastal lake that, due to drainage works during the XX century, consists at present of a main lake body, which is impounded by an artificial embankment and an overflow weir, and of several drainage channels and small ponds downstream of the overflow weir.

2.2 Field work

Samplings were conducted during the period of 2014–2016, provided that water was present. The information concerning frequency and stations of samplings are given in Table 1. During each sampling physical and chemical parameters were measured and phytoplankton and zooplankton samples were collected. Water depth, water temperature, pH, conductivity and salinity were measured *in situ* using an Idronaut CTD 316 Plus. Due to the shallowness of the studied lakes, surface phytoplankton samples were collected using a 1 L plastic bucket; each sample was further separated in two 500 mL plastic flasks, one kept live for qualitative analysis and one preserved with Lugol for quantitative analysis. For zooplankton analysis, at least 30 L of water were filtered each time through mesh size of 50 μm and were preserved in 4% formalin (final concentration).

2.3 Phytoplankton analysis

Live and Lugol preserved samples were examined under a light inverted microscope (Carl Zeiss Axio Observer.A1), and species were identified using appropriate taxonomic keys (Huber-Pestalozzi, 1938; Tikkanen, 1986). Phytoplankton counts were performed using the sedimentation method of Utermöhl (1958). For biovolume estimation, the size of 30 individuals (cells, filaments or colonies) of each species was measured using tools of a digital microscope camera (Nikon DS-L1). Mean cell or filament volume estimates were calculated using appropriate geometric formulae (Hillebrand *et al.*, 1999). For the conversion of biovolume to biomass values, water density (*i.e.* 1 g/cm^3) was used (Rott, 1981)

2.4 Zooplankton analysis

Laboratory analysis included species identification and abundance and biomass estimates. For the species identification, at least 400 individuals per sample were examined under a light microscope. Zooplankton taxa were identified to the lowest possible taxonomic level using appropriate taxonomic keys [(for rotifers: Koste (1978), Nogrady *et al.* (1995), Segers (1995), Nogrady and Segers (2002); for cladocerans: Amoros (1984), Alonso (1996), Benzie (2005); for copepods: Dussart (1967), Kiefer (1971), Reddy (1994), Einsle (1996), Dussart and Defaye (2001); for anostracans: Alonso (1996), Brtek and Mura (2000)]; in most cases all the way down to species level, whereas harpacticoids (Copepoda, Harpacticoida) and ostracods (Ostracoda, Podocopa) were only identified to order level. For abundance analysis, for each sample (total volume of 50 or 100 mL), five counts of 1 mL subsamples were made on a Sedgwick-Rafter cell, using a light microscope (Leitz Laborlux S). In the cases where the subsample count was less than 60 individuals, the whole sample was counted. Biomass was calculated as approximations using mean individual dry weight values (Dumont *et al.*, 1975; Bottrell *et al.*, 1976; Maier, 1994; Michaloudi, 2005; Michaloudi unpublished; González *et al.*, 2008; Anh *et al.*, 2009; Azevedo *et al.*, 2012; Svetlichny *et al.*, 2012). Species and taxonomical groups comprising more than 20% of the total zooplankton abundance and biomass were considered to be dominant (Haberman, 1976a and b).

2.5 Data analysis

For the data analysis all lakes were classified into three categories according to their salinity values (0–10, 34–50 and 50–300 ppt) according to salinity spectra suggested by Hammer (1986). Moreover, for the better understanding of communities' biodiversity patterns the latter category (50–300 ppt) was divided further in two subcategories 50–70 ppt and >70 ppt.

In order to identify the similarity of the zooplankton communities among each sample, hierarchical cluster analysis based on the Bray–Curtis similarity index (Bray and Curtis, 1957) was performed on the zooplankton taxa's biomass matrix. Biomass data were transformed into log $(x+1)$ in order to reduce bias due to highly abundant groups. CLUSTER was run using group-average linking. The Similarity profile (SIMPROF) permutation test option (default settings of 999 permutations and significance level = 0.05) was applied to indicate significant groups in the resulting dendrogram. The similarity analysis routines, analysis of similarity (ANOSIM) and similarity percentage analysis (SIMPER) were used to test the significance levels and sources of variance between the various zooplankton assemblages associated with the different groupings identified in the hierarchical cluster analysis. The above analyses were conducted with the Plymouth Routine in Multivariate Ecological Research (PRIMER) v.6 software package (Clarke and Gorley, 2006).

Community diversity and evenness were determined according to Shannon (1948) and Pielou (1969), respectively. Differences between the means of the total number of zooplankton taxa (S), Shannon diversity index (H') and Pielou's Evenness (J) in each salinity category were tested by analysis of variance (One-way ANOVA) and a Fisher's least significant difference (LSD) procedure. Weight cases were used to reduce bias due to there being different number of samplings in each group. Analyses were performed using IBM SPSS Statistics 22.

Direct ordination analyses were used to assess significant relationships between biological and environmental data. Samplings with missing actual environmental data were excluded from the analysis. All variables, except pH, were log $(x+1)$ transformed, because of the occurrence of zero values. Previously, a detrended correspondence analysis (DCA) was performed and, as biological data showed a bell-shaped response with respect to environmental gradients, a canonical

Table 1. Physical and chemical characteristics, total phytoplankton biomass and total zooplankton abundance and biomass of the seven lakes in Cyprus used in the study. *Abbreviation*: Stations (St), Abb (Samplings abbreviations), Months (M), Total phytoplankton biomass (PhytoBio), Total zooplankton abundance (ZooAbu) and biomass (ZooBio), February (Feb), March (Mar), first and second half of March (Mar1 and Mar2, respectively), April (Apr), missing data (m.d.)

Lake				Temperature (°C)			Depth (cm)			Salinity (ppt)			pH			PhytoBio (mg/L)			ZooAbu (ind/L)			ZooBio (mg/L)		
	St	M	Abb	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016
Larnaka Salt Lakes																								
Megali Larnaka	St 1	Feb	MLAA1402	17.80	–	–	13	–	–	57.60	–	–	7.59	–	–	0.73	–	–	3.23	–	–	11.31	–	–
		May	MLAA1505	–	23.00	–	–	35	–	–	50.84	–	–	8.98	–	–	0.12	–	–	20.47	–	–	0.20	–
	St 2		MLAB1505	–	21.70	–	–	100	–	–	50.63	–	–	8.66	–	–	0.14	–	–	6.81	–	–	0.03	–
		Feb	MLAB1602	–	–	m.d.	–	–	35	–	–	m.d.	–	–	m.d.	–	–	0.76	–	–	13.50	–	–	100.66
		Mar	MLAB1603	–	–	24.87	–	–	32	–	–	48.69	–	–	7.43	–	–	0.02	–	–	19.54	–	–	125.55
		Apr	MLAB1604	–	–	23.30	–	–	25	–	–	228.80	–	–	6.75	–	–	0.02	–	–	16.75	–	–	162.41
		May	MLAB1605	–	–	27.20	–	–	16	–	–	300.00	–	–	7.28	–	–	1.40	–	–	1.50	–	–	7.79
Airport Lake	–	Feb	AERB1402	19.40	–	–	23	–	–	36.08	–	–	8.93	–	–	<0.01	–	–	8.79	–	–	76.57	–	–
		May	AERB1505	–	22.20	–	–	40	–	–	36.81	–	–	9.44	–	–	0.14	–	–	5.35	–	–	036	–
Soros Lake	–	Feb	SOR1402	23.17	–	–	18	–	–	50.60	–	–	8.29	–	–	41.60	–	–	4.66	–	–	4.47	–	–
		May	SOR1505	–	23.30	–	–	65	–	–	48.61	–	–	9.18	–	–	0.06	–	–	5.42	–	–	1.33	–
Orphani Lake	–	Feb	ORP1402	23.27	–	–	13	–	–	50.46	–	–	7.88	–	–	9.70	–	–	3.48		–	0.01	–	–
		May	ORP1505	–	24.30	–	–	40	–	–	49.37	–	–	8.17	–	–	0.06	–	–	3.24	–	–	1.55	–
		Mar	ORP1603	–	–	25.39	–	–	25	–	–	48.12	–	–	8.23	–	–	0.53	–	–	1.42	–	–	0.47
		Apr	ORP1604	–	–	26.70	–	–	15	–	–	161.00	–	–	7.50	–	–	2.85	–	–	0.29	–	–	0.08
Akrotiri Lake	St 1	Feb	AKRA1402	15.50	–	–	37	–	–	53.37	–	–	8.44	–	–	1.79	–	–	6.30	–	–	0.27	–	–
		Apr	AKRA1504	–	22.70	–	–	60	–	–	34.81	–	–	8.43	–	–	0.50	–	–	15.28	–	–	0.05	–
		Feb	AKRA1602	–	–	12.30	–	–	18	–	–	65.50	–	–	7.52	–	–	0.07	–	–	4.13	–	–	0.13
		Mar	AKRA1603	–	–	20.00	–	–	15	–	–	69.00	–	–	7.10	–	–	0.16	–	–	0.38	–	–	0.24
		Apr	AKRA1604	–	–	20.20	–	–	10	–	–	54.27	–	–	8.00	–	–	<0.01	–	–	2.94	–	–	1.54
	St 2	Apr	AKRB1504	–	23.50	–	–	45	–	–	35.96	–	–	8.91	–	–	0.43	–	–	2.69	–	–	<0.01	–
Lake Paralimni	St 1	Mar1	PARA1503a	–	25.90	–	–	5	–	–	3.99	–	–	9.08	–	–	0.35	–	–	73.16	–	–	0.10	–
		Mar2	PARA1503b	–	19.20	–	–	20	–	–	4.80	–	–	10.05	–	–	0.05	–	–	280.56	–	–	1.22	–
	St2	Feb	PARB1402	18.80	–	–	95	–	–	5.37	–	–	8.45	–	–	0.01	–	–	250.82	–	–	0.79	–	–
		Mar1	PARB1503a	–	21.20	–	–	20	–	–	3.59	–	–	10.11	–	–	0.05	–	–	168.65	–	–	0.19	–
		Mar2	PARB1503b	–	23.00	–	–	30	–	–	4.20	–	–	10.76	–	–	0.01	–	–	125.14	–	–	0.48	–
		Feb	PARB1602	–	–	m.d.	–		m.d.	–	–	m.d.	–	–	m.d.	–	–	m.d.	–	–	226.90	–	–	3.77
	St3	Mar1	PARC1503a	–	24.20	–	–	20	–	–	4.49	–	–	8.85	–	–	0.06	–	–	119.57	–	–	0.03	–
		Mar2	PARC1503b	–	22.00	–	–	10	–	–	5.80	–	–	9.54	–	–	0.05	–	–	291.48	–	–	0.08	–
Lake Oroklini	St 1	Feb	OROA1402	23.80	–	–	95	–	–	7.04	–	–	8.51	–	–	0.19	–	–	1253.33	–	–	6.37	–	–
		May	OROA1505	–	19.90	–	–	25		–	7.02	–	–	8.49	–	–	0.16	–	–	126.67	–	–	0.60	–
		Feb	OROA1602	–	–	m.d.	–	–	37	–	–	m.d.	–	–	m.d.	–	–	29.43	–	–	199.26	–	–	1.64

Table 1. (continued).

Lake	St	M	Abb	Temperature (°C)			Depth (cm)			Salinity (ppt)			pH			PhytoBio (mg/L)			ZooAbu (ind/L)			ZooBio (mg/L)		
				2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016	2014	2015	2016
		Mar	OROA1603	–	–	22.03	–	–	50	–	–	8.90	–	–	8.51	–	–	49.17	–	–	176.86	–	–	0.86
		Apr	OROA1604	–	–	22.70	–	–	40	–	–	9.29	–	–	8.39	–	–	48.33	–	–	1702.78	–	–	8.64
		May	OROA1605	–	–	22.92	–	–	20	–	–	<2.00	–	–	9.00	–	–	7.79	–	–	29.58	–	–	0.18
	St 2	Mar	OROB1503	–	12.30	–	–	m.d.		–	<2.00	–	–	8.34		–	3.88	–	–	155.28	–	–	3.86	–

correspondence analysis (CCA) was applied. All environmental parameters with an inflation factor <20 were included in the analysis as explanatory variables (Ter Braak and Verdonschot, 1995); the biomass of each zooplankton taxon was included as response variable. The statistical significance of the variation in the parameters and the overall significance of the ordination were tested with the Monte-Carlo permutation test (as default settings of 499 unrestricted permutations; $p < 0.05$). Ordination analyses were performed using CANOCO program, version 4.5 (Ter Braak and Smilauer, 2002).

3 Results

3.1 Environmental parameters

The values of the environmental parameters (depth, temperature, salinity, pH, estimated phytoplankton biomass) in the studied lakes are given in Table 1. Temperature ranged from 12.30 °C (AKRA1602 and OROB1503) to 27.20 °C (MLAB1605). Maximum depth was low, less than 1 m for all the studied systems. Salinity ranged from <2 ppt (OROB1503 and OROA1605) to 300 ppt (MLAB1605), and pH from 6.75 to 10.76 (MLAB1604 and PARB1503b, respectively). Total phytoplankton biomass ranged from <0.01 mg/L (AERB1402 and AKRA1604) to 49.17 mg/L (OROA1603) (Tab. 1).

3.2 Community composition and structure

A total of 57 zooplankton taxa were identified in the studied lakes; 36 Rotifera, 13 Cladocera, five Copepoda, two Anostraca and some unidentified Ostracoda. The lowest species richness was recorded in Airport Lake (five taxa) and the highest in Lake Paralimni (35 taxa) (Fig. 2, Appendix). In hyposaline conditions (0–10 ppt), zooplankton communities were more diverse than in meso- and hyper- saline conditions (>70 ppt) (Fig. 3; Supplementary material, Tab. S1). More specifically, rotifers were more diverse in hyposaline conditions (0–10 ppt), compared to mesosaline (30–50 ppt) and slightly hypersaline (50–70 ppt), while no rotifer was recorded in hypersaline conditions (>70 ppt) (Fig. 3). In hyposaline conditions (0–10 ppt), crustacean communities were more diverse compared to meso- and slightly hypersaline conditions (30–70 ppt), mainly due to Cladocera, while no Cladocera were recorded in hypersaline conditions (>70 ppt) (Fig. 3). Among Copepoda, *Arctodiaptomus salinus* (Daday, 1885) was recorded at all salinity spectra (Fig. 3). In hyposaline conditions it co-existed with the cyclopoids *Metacyclops minutus minutus* (Claus, 1863) and *Diacyclops bicuspidatus odessanus* (Shmankevich, 1875), and unidentified harpacticoids (Fig. 3). For higher salinity values, *A. salinus* co-existed mostly with harpacticoids (Fig. 3). Anostraca were recorded only in sites with meso- hyper saline conditions (Fig. 3).

Total biomass ranged from <0.01 to 162.41 mg/L, in Akrotiri Lake (AKRB1504) and Megali Larnaka (MLAB1604), respectively (Tab. 1). The crustacean community contributed at least 96% to the total biomass, given the low rotifer biomass (Fig. 4a). In Lake Paralimni and Lake Oroklini, where hyposaline conditions are occurring mainly, the crustacean community consisted mainly of copepods and cladocerans (Fig. 4a) and biomass ranged from 0.03 mg/L to

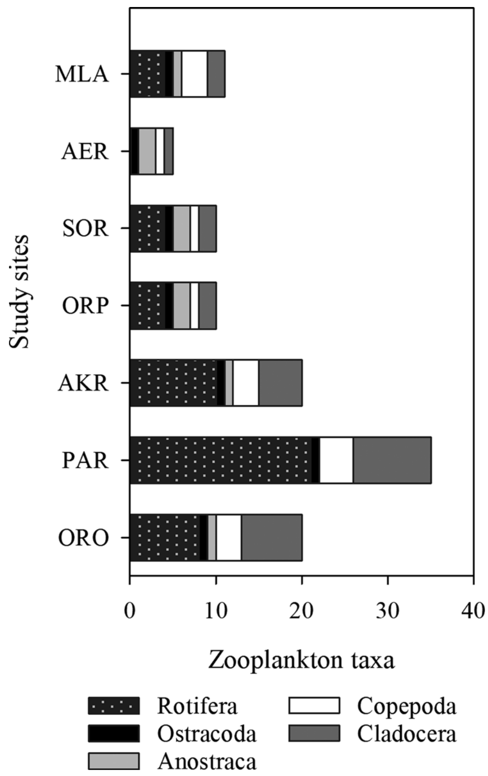

Fig. 2. Contribution of the zooplankton groups in the communities of seven lakes of Cyprus. Study sites abbreviations as shown in Figure 1.

6.37 mg/L, respectively (Tab. 1). The copepod community consisted almost exclusively of *A. salinus* in Lake Oroklini while in Lake Paralimni the cyclopoid *M. minutus minutus* was also dominant (Fig. 4a). The cladoceran community consisted almost exclusively of *Daphnia* (*Ctenodaphnia*) *magna* Straus, 1820 and *Moina brachiata* (Jurine, 1820) in Lake Oroklini while in Lake Paralimni *Bosmina* (*Bosmina*) *longirostris* (O.F. Müller, 1776) was also dominant (Fig. 4a).

In Larnaka Salt Lakes and Akrotiri Salt Lake, where meso- and hyper- saline conditions were occurring, in the cases where the anostracans *Artemia salina* (Linnaeus, 1758) and *Phallocryptus spinosus* (Milne-Edwards, 1840) were recorded their relative biomass was high from 44% to almost 100% in Megali Larnaka Lake (MLAA1505 and MLAA1402, MLAB1602, MLAB1604) and Airport Salt Lake (AERB1402) (Fig. 4a). When anostracans were not recorded, the crustacean community consisted mainly of the cladoceran *M. brachiata* in Megali Larnaka Lake (MLAB1505) and Akrotiri Salt Lake (AKRA1504) and of unidentified ostracods and the cladocerans *D. magna* and *M. brachiata* in Orphani Salt Lake (ORP1402 and ORP1604) and Akrotiri Salt Lake (AKRB1504), respectively (Fig. 4a).

The hierarchical cluster analysis (Fig. 4b) revealed that the zooplankton community structure differed significantly between samplings with varying salinity. Five groups were generated (ANOSIM, $R = 0.92$, $p = 0.01$). Samplings with low salinity fell in the upper band of cluster of sites (Group A; Fig. 4b), while those with medium and high salinity fell in the rest of the groups with no apparent pattern (Groups B, C, D, E; Fig. 4b). Groups A and E were significantly separated with each other and the rest of the groups as was shown by the pairwise comparison (ANOSIM, $R \geq 0.81$, $p < 0.02$; Tab. S2). Their similarity is due mainly to the contribution of *A. salinus* and *D. magna* in Group A and in *A. salina* in Group E (Tab. S2).

The Species richness (S), Pielou's evenness index (J) and Shannon's diversity index (H') for the zooplankton communities are shown in Figure 5. Indices S, J and H' differentiated significantly between the categories of salinity (ANOVA, $F = 14.55$, $p < 0.01$, $F = 5.75$, $p < 0.01$ and $F = 7.21$, $p < 0.05$, respectively) (Fig. 5). Pairwise test indicated that differences in S, J and H' between the hyposaline lakes and the rest with higher salinity values were significant ($p < 0.05$) (Fig. 5).

3.3 Relationships between physical and chemical parameters and zooplankton communities' structure

To assess significant relationships between environmental data and zooplankton's community structure, ordination analysis of taxa assemblages, expressed in terms of biomass was conducted (Fig. 6). In the diagnostic DCA the highest value of the length of gradient of axis was 4.28, which indicates that the relationship between the zooplankton and environmental variables was unimodal (Ter Braak and Smilauer, 2002), and a CCA was performed. The significant environmental variables ($p < 0.05$) included in the CCA were salinity, total phytoplankton biomass and water depth (Fig. 6). The Monte Carlo test confirmed that the selected CCA model was significant with F ratio $= 5.55$ ($p < 0.01$). The eigenvalues of the first two axes were 0.63 and 0.47, and both of them together explained 88.60% of the variation in species-environment relation. The first axis, which accounted for a total variance of 51%, was positively and strongly correlated with salinity ($r = 0.95$). Axis 2 showed 37.30% variation, and it was positively and strongly correlated with total phytoplankton biomass ($r = 0.95$). Depth was negatively and strongly correlated with the third axis ($r = -0.96$), which accounted for a total of 11.40% variation.

4 Discussion

Saline lakes were largely being ignored by limnologists since few studies existed on the biota and associated processes of such lakes (Moss, 1994). Lately, though, there is an increase of interest to understand these ecosystems where life reaches its extremes. In the present study we investigated the structure of zooplankton community of seven saline Mediterranean lakes in relation to certain environmental parameters. As our data indicated, salinity was a key factor shaping both composition and structure of the zooplankton community in the studied lakes. Undoubtedly, the trophic state is an important factor affecting zooplankton community structure (Benndorf *et al.*, 2002); in such systems though, salinity seems to play a more crucial role as a predominant driving force. Moreover, zooplankton communities differentiated across different years and seasons by salinity gradient even for the same water body. A crucial factor affecting the biological elements of saline lakes, and thus zooplankton is the hydrological budget (Williams, 2002). Still, differences in hydrological patterns are usually reflected in long-term or seasonal changes in salinity (Williams, 2002). Although, in our

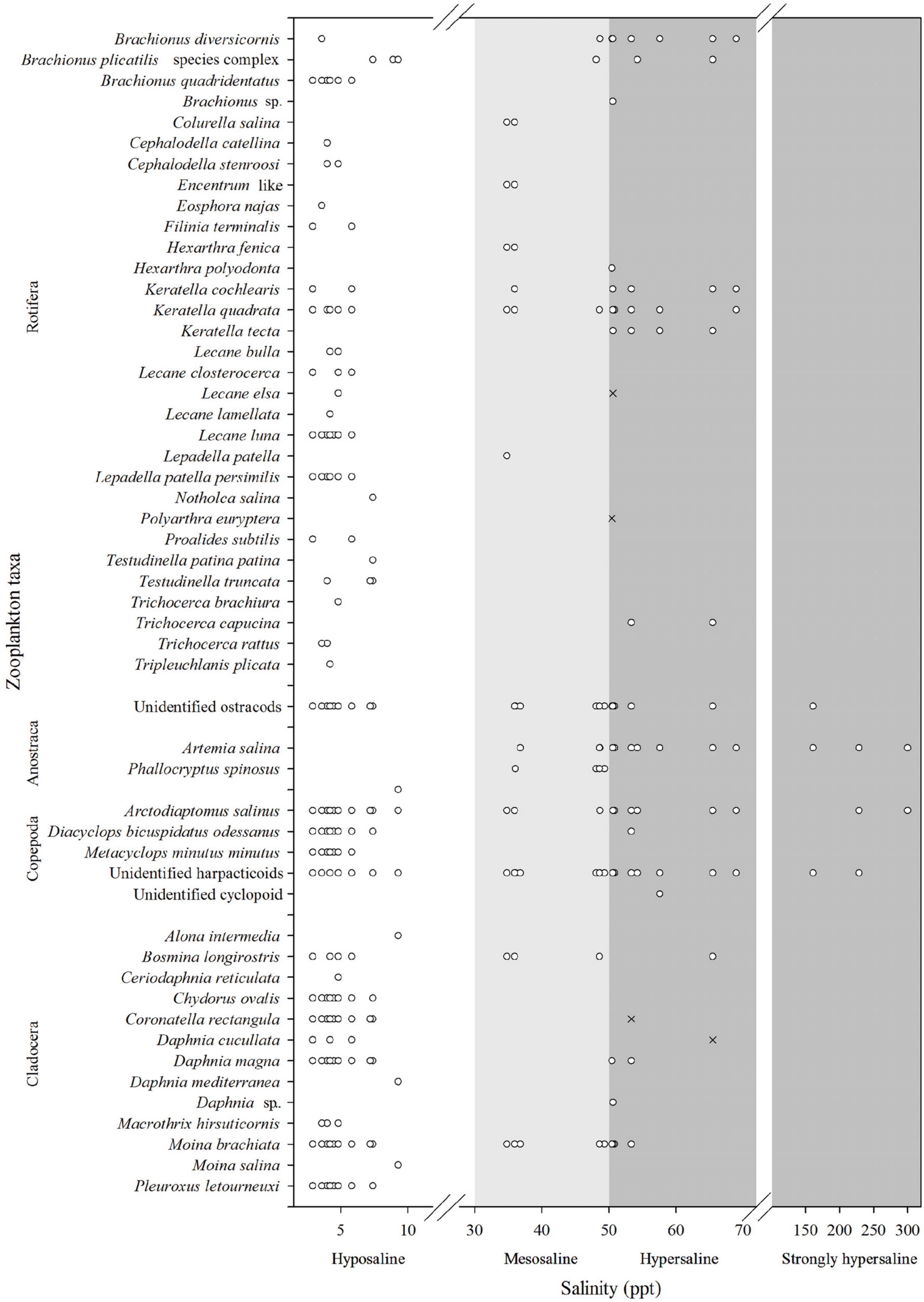

Fig. 3. Zooplankton taxa records in the recorded salinity gradient. Open circles indicate presence of each taxon in the seven studied lakes according to the *in situ* salinity values. White, light gray and dark gray areas indicate hyposaline, mesosaline and hypersaline conditions, respectively. X mark indicates typically freshwater taxa recorded.

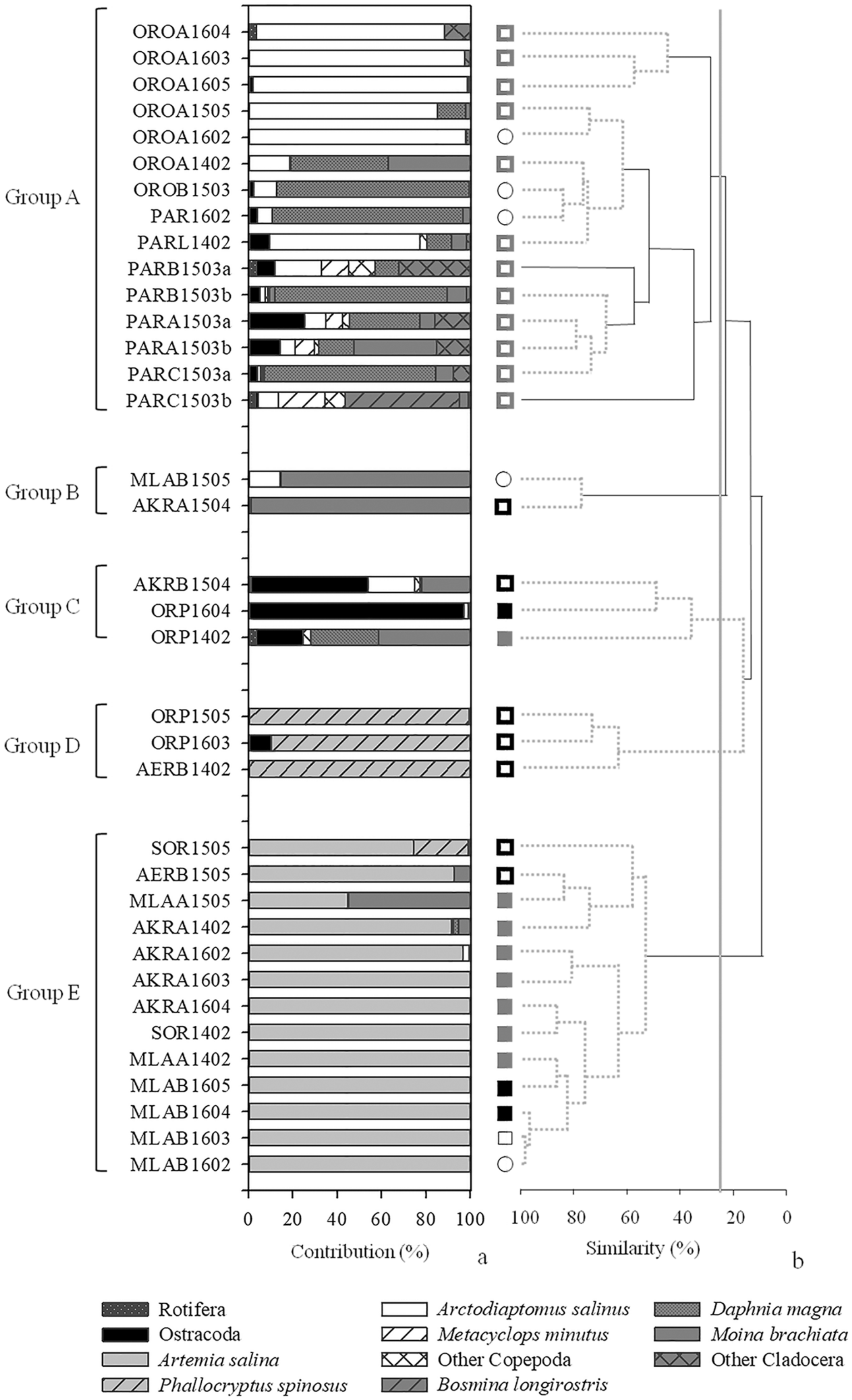

Fig. 4. (a) Percentage contribution of dominant zooplankton taxa to total biomass in the studied lakes in Cyprus. (b) Dendogram of Bray-Curtis similarity index of zooplankton community among samplings in the studied lakes of Cyprus from hierarchical agglomerative cluster analysis in $\log x + 1$ transformed data of zooplankton taxa's biomass at level of similarity 25%, as indicated by the solid gray line. Solid black lines indicate significant branches based on SIMPROF permutation tests, while dashed gray lines indicate non-significant divisions. Symbols coded for salinity category open gray square for hyposaline (0–10 ppt), open black square for mesosaline (30–50 ppt), gray filled square for slightly hypersaline (50–70 ppt) and black filled square for strongly hypersaline (>70 ppt) conditions. Samplings abbreviations as shown in Table 1.

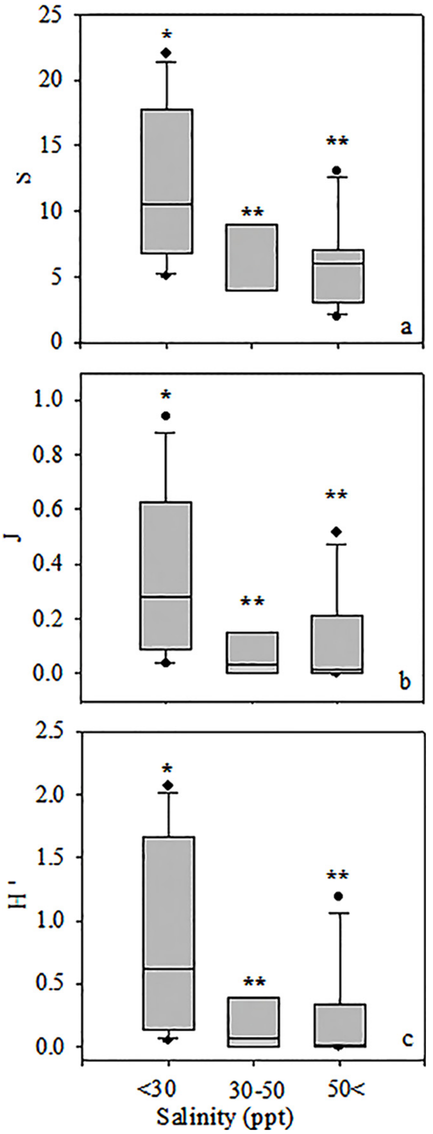

Fig. 5. Box plots of Species richness (S), Pielou's eveness index (J) and Shannon diversity index (H') for the zooplankton community of the seven lakes in Cyprus calculated for biomass data grouped by salinity ($p < 0.05$). *, **Significant differences (Fisher's LSD test).

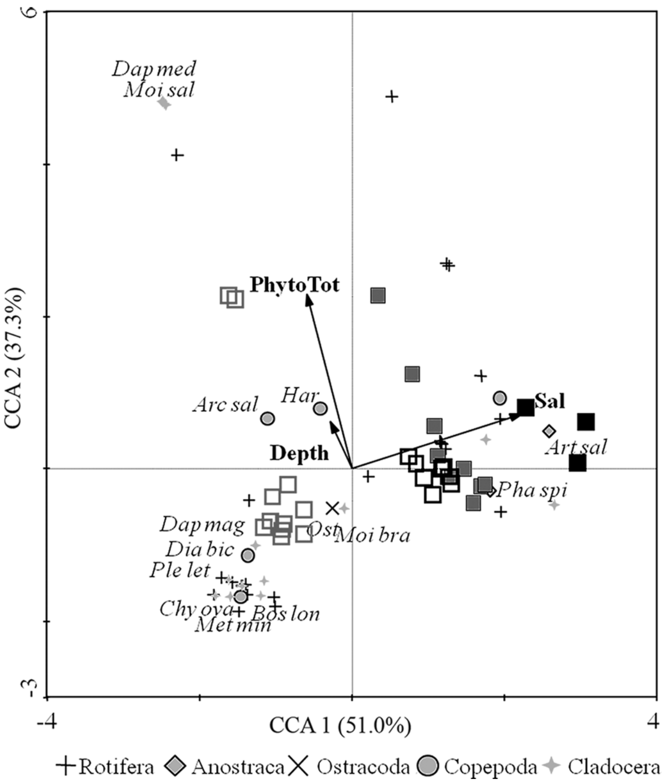

Fig. 6. Triplot diagram of zooplankton species, explanatory variables and samples in a canonical correspondence analysis (CCA) of the first and second canonical axis illustrating the relationships among communities in the studied lakes in Cyprus. Square points indicate the position of zooplankton communities in relation to environmental parameters (solid arrows) and species composition (data points) based on taxa's biomass. Samplings were coded based on salinity categories same as in Figure 4b. Labelled taxa indicate the taxa that contributed in similarity and dissimilarity among samplings according to SIMPER analysis (Supplementary Tab. S2); *Artemia salina* (Art sal), *Arctodiaptomus salinus* (Arc sal), *Bosmina longirostris* (Bos lon), *Chydorus ovalis* (Chy ova), *Daphnia magna* (Dap mag), *Daphnia mediterranea* (Dap med), *Diacyclops bicuspidatus odessanus* (Dia bic), Unidentified harpacticoids (Har), *Metacyclops minutus minutus* (Met min), *Moina brachiata* (Moi bra), *Moina salina* (Moi sal), unidentified ostracods (Ost), *Phallocryptus spinosus* (Pha spi), *Pleuroxus letourneuxi* (Ple let).

study, the snapshot samplings did not provide enough data concerning the hydrological budget in order to reach sound conclusions related to this parameter, our data share the major patterns that have been described in shallow temporary lakes with high salinity (*e.g.*, Alonso, 1990; Brucet *et al.*, 2005, Waterkeyn *et al.*, 2008).

Regarding zooplankton composition, the distribution of some taxa is largely explained by their physiological adaptations to salinity (Derry *et al.*, 2003). For example, the rotifers encountered in the studied lakes, based on the categories of Fontaneto *et al.* (2006), were mainly euryhaline species [*e.g.*, *Brachionus quadridentatus* Hermann, 1783; *Keratella quadrata* (Müller, 1786)], haloxenous [*e.g.*, *Brachionus diversicornis* (Daday, 1883); *Colurella salina* Althaus, 1957; *Hexarthra polyodonta* (Hauer, 1957)], strictly saline [*e.g., Brachionus plicatilis* species complex; *Lecane lamellata* (Daday, 1893); *Notholca salina* Focke, 1961] or freshwater stenohaline species (*e.g.*, *Cephalodella intuta* Myers, 1924) depending on the recorded salinity (Fig. 3). According to Ruttner-Kolisko (1971), for rotifers, after the salinity threshold of 1.50 ppt, the biocenosis is changing characteristically and this adaptation is reflected in the taxonomic composition of zooplankton communities of Mediterranean arid regions as was also shown in our study. In the crustacean communities, species with high salinity tolerance were mainly recorded. Among cladocerans, most species that have been recorded in the studied lakes are typical of temporary saline lakes in the Mediterranean arid regions [*e.g.*, *Alona intermedia* Sars, 1862; *Daphnia* (*Ctenodaphnia*) *mediterranea* Alonso, 1985; *Ceriodaphnia reticulata* (Jurine, 1820); *Coronatella rectangula* (Sars, 1862); *Macrothrix hirsuticornis* Norman & Brady, 1867; *M. brachiata*; *Moina salina* Daday, 1888; *Pleuroxus letourneuxi* (Richard, 1888)] (Alonso, 1990; Eitam *et al.*, 2004; Marrone *et al.*, 2006; Benvenuto *et al.*, 2015) and also typical of freshwater habitats, such *Daphnia cucullata* Sars, 1862; while the Copepoda community was less diverse, comprising the calanoid copepod *A. salinus*, unidentified harpacticoids and two cyclopoid copepods which are typically found in temporary ponds, (Alonso, 1990; Benvenuto *et al.*, 2015). *A. salinus* was recorded in all salinity spectra in the present study, reflecting its adaptation in a wide range of salinity conditions (Svetlichny *et al.*, 2012). Finally, the anostracan genera *Artemia* and *Phallocryptus* were recorded only in sites with meso- hyper saline values, reflecting their adaptation in hypersaline water bodies (Alonso, 1990). In total, hyposaline lakes were more diverse not only in terms of species richness, but also in terms of Pielou's eveness index (J) and Shannon diversity index (H') in agreement with Moss (1994) and Brucet *et al.* (2009).

Likewise, salinity was an important shaping factor in zooplankton community structure. Regardless of salinity range, rotifer contribution to total biomass was low, due to their small size. Thus in terms of biomass crustaceans dominated. In hyposaline conditions, biomass was dominated by *A. salinus, D. magna* and *M. brachiata*. *A. salinus* dominance may be linked to its ability to better exploit available food. In particular, this copepod has been commonly described as herbivorous (Tolomeyev, 2002) and as a predator of small zooplankters, such as *Brachionus* species in adult stages (Lapesa *et al.*, 2004). Compared to *D. bicuspidatus odessanus*, which co-existed with *A. salinus* in the present study, it is a more efficient and less selective predator (Lapesa *et al.*, 2004). The large sized *D. magna* dominated in total biomass under hyposaline conditions due to its optimal individual growth rate, reproductive output and population growth rate, which are high at salinities near 4 ppt (Arnér and Koivisto, 1993) and its high filter feeding efficiency consuming both bacteria and algae (Gophen, 1977; Geller and Müller, 1981) outcompeting the rest of the filter feeders. Based on investigation of life history traits (development, reproduction and growth pattern) in *M. brachiata*, Maier (1992) concluded that the species has a relatively short egg development period and high egg production rates that are advantageous in fluctuating environments. Thus, *M. brachiata* was favored by the hydrological conditions of the studied systems. In meso- and hypersaline conditions (>70 ppt), in some cases communities were dominated by anostracans (mostly over 90% in total biomass). In general, Anostraca tend to dominate temporary water bodies in early successional phases (Jocque *et al.*, 2010) because of their effective feeding strategy (Dumont and Ali, 2004). In the cases that anostracans were absent in the studied lakes, dominance of *A. salinus, M. brachiata* and ostracods (Fig. 4a) indicated a reverse relationship between anostracans and other filter feeders. This could be due to the competitive dominance of anostracans that suggests that they may be able to outcompete cladocerans and other filter feeders (Jocque *et al.*, 2010).

Competitive interactions seem to be the drivers affecting zooplankton community structure in these systems as opposed to freshwater lakes where fish predation is the major driving factor (Lampert and Sommer, 2007). In fishless aquatic habitats, competition for resources among zooplankton is stated as the rapid exclusion of competitively inferior species, which leads to dominance of a single or a few large body-sized species size, such as the cladoceran *Daphnia* and/or the anostracan *Artemia* in higher densities than in habitats with the presence of fish (Gliwicz *et al.*, 2010). Temporary and/or highly saline lakes are mostly unsuitable habitats for fish; thus, Mediterranean temporary saline lakes are either entirely fishless or fish presence is limited during the flood period (Gutiérrez-Yurrita *et al.*, 1998) or they serve as pathways for fish migration towards more suitable habitats, as is the case in *e.g.* Akrotiri lake.

Overall, the presence and dominance of specific zooplankton taxa in a wide range of salinity was recorded in the studied lakes. This may be either due to the physiological adaptation of species in fluctuating salinity of temporary lakes or/and to the presence of cryptic species complexes with different halopreferenda. For example, genetic research on *M. brachiata* recently revealed that under this binomen might actually be included four cryptic species contistuting the *M. brachiata* complex, and difference in species occurrences are associated with salinity and hydroperiod (Nédli *et al.*, 2014). Moreover, despite the fact that *A. salinus* is thought to be an euryhaline species (Svetlichny *et al.*, 2012), indications exist for the presence of cryptic species under this binomen (Anufriieva and Shadrin, 2014). Thus, more attention needs to be paid to study the phenotypic and genetic diversity in these zooplankton populations.

This is the first detailed study on the structure and dynamics of the zooplankton community of saline lakes in Cyprus. One more study exists by Balık *et al.* (2008), but their research was limited in the northern part of the island and dealt with freshwater reservoirs. In certain regions, such as the sensitive to climate change arid Mediterranean, many seasonally-filled saline lakes are likely to experience dryness for longer periods in the future (Williams, 2002). This will probably be the case for saline lakes of Cyprus. The implementation of effective management and conservation measures has to consider the special ecological features and requirements of these unique ecosystems; thus a solid basis built on ecological knowledge is required.

Our results support the importance of salinity as a major driver of zooplankton community composition and structure in saline lakes. Therefore, we propose that salinity should be considered a key factor for typological considerations in quality assessments, restoration and management plans, the development of indices indicating the water quality and even the establishment of reference conditions according to the WFD in these temporary saline systems. Moreover, despite the fact that zooplankton is not a standard biological element according to the WFD (European Commission, 2000), it should be considered as one, since it reflects environmental pressures (Bagella *et al.*, 2010), is a key shaping factor in the fishless Mediterranean temporary saline lakes; and is largely affected by the salinity gradient.

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Table A1. List of recorded taxa per study site in seven lakes of Cyprus. Open cycles indicate absence and solid black cycles presence of taxa. Study sites abbreviations as shown in Figure 1.

	MLA	AER	SOR	ORP	AKR	PAR	ORO
Rotifera	4	0	4	4	10	21	8
Brachionus diversicornis (Daday, 1883)	●	○	●	●	●	●	●
Brachionus ibericus Ciros-Pérez, Gómez and Serra, 2001	○	○	○	○	○	○	○
Brachionus plicatilis species complex	○	○	○	●	●	○	●
Brachionus quadridentatus Hermann, 1783	○	○	○	○	○	●	○
Brachionus sp. Pallas, 1766	○	○	●	○	○	○	○
Brachionus variabilis Hempel, 1896	○	○	○	○	○	●	○
Bdelloidea Hudson, 1884	○	○	○	○	○	○	●
Colurella salina Althaus, 1957	○	○	○	○	●	○	○
Cephalodella catellina (Müller, 1786)	○	○	○	○	○	●	○
Cephalodella stenroosi Wulfert, 1937	○	○	○	○	○	●	○
Cephalodella intuta Myers, 1924	○	○	○	○	○	●	○
Encertum like	○	○	○	○	●	○	○
Eosphora najas Ehrenberg, 1830	○	○	○	○	○	●	○
Filinia terminalis (Plate, 1886)	○	○	○	○	○	●	○
Hexarthra fenica (Levander, 1892)	○	○	○	○	●	○	○
Hexarthra polyodonta (Hauer, 1957)	○	○	○	●	○	○	○
Keratella cochlearis (Gosse, 1851)	○	○	●	○	●	●	●
Keratella quadrata (Müller, 1786)	●	○	●	○	●	●	●
Keratella tecta (Gosse, 1851)	●	○	○	○	●	○	○
Lecane bulla (Gosse, 1851)	○	○	○	○	○	●	○
Lecane closterocerca (Schmarda, 1859)	○	○	○	○	○	●	○
Lecane elsa Hauer, 1931	●	○	○	○	○	●	○
Lecane lamellata (Daday, 1893)	○	○	○	○	○	●	●
Lecane luna (Müller, 1776)	○	○	○	○	○	●	○
Lepadella patella (Müller, 1773)	○	○	○	○	●	○	○
Lepadella patella persimilis De Ridder, 1961	○	○	○	○	○	●	○
Notholca salina Focke, 1961	○	○	○	○	○	○	●
Polyarthra euryptera Wierzejski, 1891	○	○	○	●	○	○	○
Proalides subtilis Rodewald, 1940	○	○	○	○	○	●	○
Testudinella patina (Hermann, 1783)	○	○	○	○	○	○	●
Testudinella truncata (Gosse, 1886)	○	○	○	○	○	●	○
Trichocerca brachiura (Gosse, 1851)	○	○	○	○	○	●	○
Trichocerca capucina (Wierzejski and Zacharias, 1893)	○	○	○	○	●	○	○
Trichocerca rattus (Müller, 1776)	○	○	○	○	○	●	○
Tripleuchlanis plicata (Levander, 1894)	○	○	○	○	○	●	○
Ostracoda (unidentified ostracods)	1	1	1	1	1	1	1
Anostraca	0	2	2	2	1	0	1
Artemia salina (Linnaeus, 1758)	●	●	●	●	●	○	●
Phallocryptus spinosus (Milne-Edwards, 1840)	○	●	●	●	○	○	○
Copepoda	3	1	1	1	3	4	3
Arctodiaptomus salinus (Daday, 1885)	●	○	○	○	●	●	●
Diacyclops bicuspidatus odessanus (Shmankevich, 1875)	○	○	○	○	●	●	●
Metacyclops minutus minutus (Claus, 1863)	○	○	○	○	○	●	○
Unidentified harpacticoids	●	●	●	●	●	●	●
Unidentified cyclopoid	●	○	○	○	○	○	○
Cladocera	2	1	2	2	5	9	7
Alona intermedia Sars, 1862	○	○	○	○	○	○	●
Bosmina (Bosmina) longirostris (O.F. Müller, 1776)	○	○	●	○	●	●	○
Chydorus ovalis Kurz, 1875	○	○	○	○	○	●	○
Ceriodaphnia reticulata (Jurine, 1820)	○	○	○	○	○	●	○
Coronatella rectangula (Sars, 1862)	○	○	○	○	●	●	●
Daphnia (Daphnia) cucullata Sars, 1862	○	○	○	○	●	●	○
Daphnia (*Ctenodaphnia*) *magna* Straus, 1820	○	○	○	●	●	●	●
Daphnia (*Ctenodaphnia*) *mediterranea* Alonso, 1985	○	○	○	○	○	○	●
Daphnia sp. O. F. Müller, 1785	●	○	○	○	○	○	○

Table A1. (continued).

	MLA	AER	SOR	ORP	AKR	PAR	ORO
Macrothrix hirsuticornis Norman and Brady, 1867	○	○	○	○	○	●	○
Moina brachiata (Jurine, 1820)	●	●	●	●	●	●	●
Moina salina Daday, 1888	○	○	○	○	○	○	●
Pleuroxus letourneuxi (Richard, 1888)	○	○	○	○	○	●	●