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Spatio-temporal variation in the zooplankton community of the Zahara-El Gastor Reservoir (Cádiz, Spain)

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ABSTRACT

Spatio-temporal variation in the zooplankton community of the Zahara-El Gastor Reservoir (Cádiz, Spain).

Reservoirs play a crucial role in providing essential social and economic services at different scales. However, in recent years, anthropogenic impacts such as climate change and pollution have increased, affecting this type of ecosystem. Zooplankton communities are fundamental for regulating the biological balance in these environments, so it is essential to understand the processes that affect their dynamics. This study investigated the seasonal and spatial variation in species abundance of the zooplankton community of the Zahara- El Gastor Reservoir, Cádiz, Spain. This reservoir is located in the Guadalete-Barbate River basin and is included in the Sierra de Grazalema Natural Park, the area with the highest rainfall in the Iberian Peninsula. Water and zooplankton samples were collected monthly over a year at four sampling sites located along the reservoir's long-axis to determine its physicochemical characteristics and zooplankton species composition. The reservoir presented a mesotrophic state and a monomictic thermal cycle, with the mixing period occurring in winter. Temperature, water depth and volume, phosphates, carbonates, pH, and conductivity were the main environmental variables that affected the seasonal and spatial patterns of the zooplankton community. Rotifers presented the highest number of species and were predominant at the tail of the reservoir, especially in autumn, where *Polyarthra* spp. reached high densities. Relatively low densities of copepods were found throughout the year. Small branchiopods and cyclopoids were predominant in summer, while *Daphnia longispina* was linked to the colder seasons. The zooplankton community of the Zahara-El Gastor Reservoir reflected changes in the trophic state of the reservoir both in space and time.

KEYWORDS: zooplankton community, physicochemical parameters, spatio-temporal variation, Mediterranean Reservoir, Zahara-El Gastor.

RESUMEN

Variación espacio-temporal en la comunidad zooplanctónica del embalse de Zahara-El Gastor (Cádiz, España).

Los embalses desempeñan un papel esencial proporcionando servicios socioeconómicos a diferentes escalas. Sin embargo, en los últimos años, los impactos antropogénicos como el cambio climático y la contaminación han aumentado de manera importante, afectando a este tipo de ecosistemas. Las comunidades de zooplancton juegan un papel fundamental en la regulación del equilibrio biológico en estos ambientes, por lo que es esencial comprender los procesos que les afectan. Este estudio analiza la variación estacional y espacial en la abundancia de especies de la comunidad de zooplancton del embalse de Zahara-El Gastor, Cádiz, España. Este embalse se encuentra en la cuenca del río Guadalete-Barbate y está incluido en el Parque Natural Sierra de Grazalema, la zona con mayores precipitaciones en la Península Ibérica. Se tomaron muestras de agua y zooplancton mensualmente durante un año en cuatro puntos de muestreo ubicados a lo largo del eje longitudinal del embalse, para determinar sus características fisicoquímicas y la composición de especies de zooplancton. El embalse mostró un estado mesotrófico caracterizado por una estacionalidad y un ciclo térmico monomíctico, con el período de mezcla durante el invierno. La temperatura, *profundidad, volumen embalsado, fosfatos, carbonatos, pH y la conductividad fueron las principales variables ambientales que afectaron los patrones estacionales y espaciales de la comunidad de zooplancton. Los rotíferos presentaron el mayor número de especies y fueron predominantes en la cola del embalse, especialmente en otoño, donde* Polyarthra *spp. alcanzó densidades elevadas. Se encontraron densidades relativamente bajas de copépodos durante todo el año. Branquiópodos pequeños y ciclopoides fueron los predominantes en verano, mientras que* Daphnia longispina *estuvo asociada a las estaciones más frías. La comunidad de zooplancton del embalse Zahara-El Gastor reflejó cambios en el estado trófico del embalse tanto en espacio como en tiempo.*

PALABRAS CLAVES: *comunidad zooplanctónica, parámetros físico-químicos, variación espacio-temporal, embalse mediterráneo, Zahara-El Gastor.*

INTRODUCTION

Reservoirs provide very important services, such as drinking and irrigation water, hydroelectric power, fishing, and recreational use areas (Eekhout et al., 2020). However, in the past few decades, the exploitation of natural water resources, contamination, habitat degradation, and invasion by alien species induced by anthropogenic activities have put these environments at risk, affecting biodiversity, among many other ecological functions (Dudgeon et al., 2006). To protect and preserve freshwater environments it is essential to comprehend how diverse stressors can affect species diversity and alter ecosystem functioning, especially under intense anthropogenic pressure (Altshuler et al., 2011).

Zooplanktonic communities play an essential role in the regulation of the biological balance in aquatic ecosystems (Lampert & Sommer, 2007). In particular, the structure and dynamics of zooplankton communities are of interest because this group of small invertebrates plays a central role in the pelagic food chain (Jeppesen et al., 2011), transferring energy from lower trophic levels to higher ones (Li et al., 2019; Shayestehfar et al., 2010) as well as representing an essential food source for upper trophic levels such as fish (Chase, 2003). Understanding the processes and mechanisms that impact the variation of their communities is an important tool for an efficient management of freshwater ecosystems and thus maintain their balance (Loick-Wilde et al., 2016; Paerl et al., 2003; Tan et al., 2011). This is especially complicated in ecosystems that do not exhibit natural behavior and are strongly marked by anthropic management, such as reservoirs. Distribution and abundance of zooplanktonic communities in a reservoir are the result of the interaction of several factors, including the management of the reservoir, seasonal changes in water characteristics, interactions between species, or the mobility of those species, among others (Bonecker et al., 2013; Li et al., 2019; Seegers, 2008).

Zooplankton communities in Spanish reservoirs have been widely investigated, including numerous studies dealing with zooplankton reservoir colonization, systematics, and zoogeography, as well as species variations with physical-chemical, and biological variables (J. Armengol, 1978; De Manuel Barrabin, 2000). Recent studies have shown that zooplankton abundance and community composition could be good indicators of water quality in reservoirs (García-Chicote et al., 2019; Montagud et al., 2019; Almeida et al., 2020; Pinto et al., 2023).

In the present study, the zooplankton community and the associated environmental factors of the Zahara-El Gastor Reservoir were investigated. Situated in the province of Cadiz, south-western Spain, this reservoir was formed by the construction of a dam across the Guadalete River in 1992, although it did not become operational until 1995. The reservoir covered the Triassic saline springs of Ventas Nuevas, located on the right bank of the Guadalete River (Rodríguez-Ruiz, 1998). It is mainly used to regulate the water flow into the Guadalete River for agricultural irrigation and recreational use. The relevance of this study lies in the unique characteristics of this reservoir, which is located in the Guadalete-Barbate River Basin, a small independent hydrographical basin in the south of the Iberian Peninsula. This basin is included in the Sierra de Grazalema Natural Park, a region primarily characterized by irregular seasonal rainfall distribution. The area simultaneously experiences high temperatures and low rainfall during the summer, leading to severe water scarcity towards the end of the season. However, the recorded precipitation in the region represents an exceptional situation within the context of Mediterranean-Iberian climate characteristics, with total annual values sometimes approaching or even surpassing 2000 mm (Fuster, 2007).

The objective of the present study was to assess, for the first time, the spatial and temporal variation in both density and species composition of the zooplankton community in the Zahara-El Gastor Reservoir, and to investigate its response to changes in environmental variables. This study contributes to the understanding of the structure and dynamics of the zooplankton community in this reservoir, with an emphasis on the main species which could serve as indicators of its trophic status. The findings from this study are expected to offer valuable insights for the effective management and conservation of the reservoir.

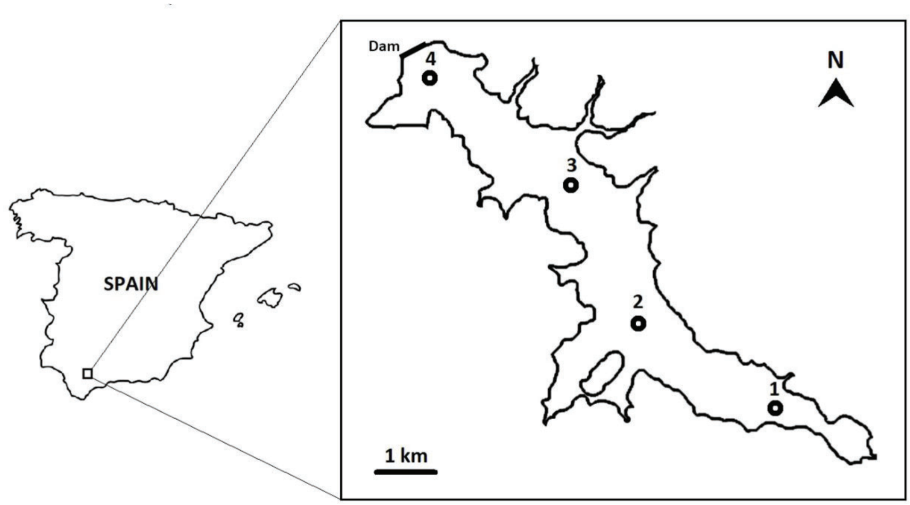

Figure 1. Sampling sites of the Zahara-El Gastor Reservoir. S1: tail of the reservoir at 7 km from the dam. S2: site at 6 km from the dam. S3: site at 4 km from the dam. S4: dam of the reservoir. *Puntos de muestreo en el embalse de Zahara-El Gastor. S1: cola del embalse a 7 km de la presa. S2: punto a 6 km de la presa. S3: punto a 4 km de la presa. S4: punto en la presa del embalse.*

MATERIALS AND METHODS

Sampling design and data collection

The reservoir has a maximum storage capacity of 223 hm^3 and a surface area of 723 ha. In this study, four sampling sites were selected to represent the reservoir spatial heterogeneity from the tail end to the dam (Fig. 1). Sampling site S1 was located 7 km from the dam, representing the tail of the reservoir, and was the shallowest site. Its location was chosen to guarantee the viability of the study in case of drought during the summer months. Sampling sites S2 and S3 were located 6 and 4 km from the dam, respectively. Sampling site S4 represented the deepest point and was in proximity to the dam. Surveys were performed monthly, during a whole year, from October 2019 to September 2020. For subsequent analyses, the monthly data were grouped into four climatic seasons: autumn (October, November, December 2019), winter (January, February, March 2020), spring (April, May, June 2020), and summer (July, August, September 2020).

For the limnological characterization of each sampling site, various in situ measurements were conducted. Depth was measured with a sonar-based DIVE-SCANT gauge. Temperature (^{o}C), dissolved oxygen (mg/l), pH, conductivity (µS/cm), Total Dissolved Solids (TDS; mg/l), and turbidity (NTU), were profiled with a multiparametric probe (HANNA HI9829) up to a depth of 20 m. Secchi depth (SD; m), a measure of water transparency, was determined using a Secchi disk. Simultaneously, we collected water surface samples from each sampling site for analytical determination of nitrates (NO_3; mg/l), phosphates (PO_4^{3-}; mg/l), and dissolved ammonia (NH_4^+; mg/l), using colorimetric tests. Moreover, to determine the concentration of the carbonates (HCO_3^-; mg/l), we carried out a Phenolphthalein Alkalinity test (AQUAMERCK, Spectroquant and MERCK). The photic zone (Zeu) was calculated as 2.5 times the Secchi disk depth (SD) (Poikane, 2009). Then, to determine chlorophyll-*a* concentration (mg/m^3), water samples were collected from the photic zone with a Van Dorn water sampling bottle. We extracted pigments and determined the absorbance using a spectrophotometer Genesys 10S UV-Vis, following the methodology published by Arar, 1997. The concentration of the pigment was calculated using the generalized equation described by Talling & Driver, 1963. Monthly measurements of precipitation (mm) and volume of dammed water (hm^3) for the study period were retrieved from the Automatic System of Hydrological Information (SAIH) of the Ministry for the Ecological Transition and Demographic Challenge of the Government of Spain.

Zooplankton samples were collected at each sampling site using a conical net of 30 cm diameter and nytal filter with 50 µm pore diameter, equipped with a unidirectional flowmeter (General Oceanics Inc, FL, USA) to calculate the filtered volume (McKinstry & Campbell, 2018; Ramírez García et al., 2002). Surveys were performed vertically from the bottom to the surface, filtering the whole water column. This method allows minimizing the vertical migration effect of zooplankton, a widely observed phenomenon in zooplankton of both continental and marine ecosystems (Armengol & Miracle, 2000). Samples obtained from each survey were preserved in 70% ethanol for subsequent laboratory analysis. Zooplankton abundance estimates were obtained by quantifying the average number of individuals of each species counted in several aliquots of the sample through a binocular microscope (Leica 020-507.010). Species were identified using specialised publications (Alonso, 1996; Dussart, 1967, 1969; Koste & Voigt, 1978) and the identification effort stopped until the species accumulation curve reached stabilisation (Bonecker et al., 2013). Copepod nauplii were quantified separately and identified up to the family level.

Data analyses

The trophic state of the reservoir was determined using the Carlson Trophic State Index (TSI') which classifies lakes into four types: oligotrophic (< 40), mesotrophic (40-50), eutrophic (50-70), and hypereutrophic (> 70) (Carlson, 1977; Carlson & Simpson, 1996). The index is calculated using the following formula: TSI' = [(TSI (SD) + TSI (Chl-*a*) + TSI (TP)) / 3], where each parameter is calculated from a specific equation including the annual mean value of the Secchi Disk depth (TSI (SD) = 60 – 14.41 ln (SD); m), the chlorophyll-*a* concentration (TSI (Chl-a) = 9.81 ln (Chl-*a*) + 30.6; mg/m^3) and the total phosphorus concentration in the reservoir (TSI (TP) = 14.42 In (TP) + 4.14; mg/m^3).

A Principal Component Analysis (PCA) was performed to identify the most important environmental variables determining patterns of spatio-temporal variation. Environmental variables included: nitrates, carbonates, phosphates, ammonia, chlorophyll-*a*, water transparency, water depth, pH, conductivity, temperature, dissolved oxygen, total dissolved solids, volume, precipitation and turbidity.

The zooplankton community diversity was described using the Shannon-Wiener (H´) index: $H' = -\Sigma p^s_i \log p_i$, where s is the total number of species, i is the total number of individuals for one species and p_i is the number of individuals for one species in relation to the number of individuals in the population. Moreover, we calculated the heterogeneity or β-diversity index (β), as a measure of species diversity in space: $\beta = \gamma/\alpha$, where α is the average diversity of different sites and γ is the total number of species of pooled sites.

To evaluate spatio-temporal differences in the zooplankton abundance we performed a Kruskal-Wallis (H) test comparing the abundance of each species among different seasons and sampling sites. We used this non-parametric test since the data did not meet the assumptions of normality and homogeneity, previously tested using the Shapiro-Wilk and Levene's tests, respectively.

Relationship between zooplankton species

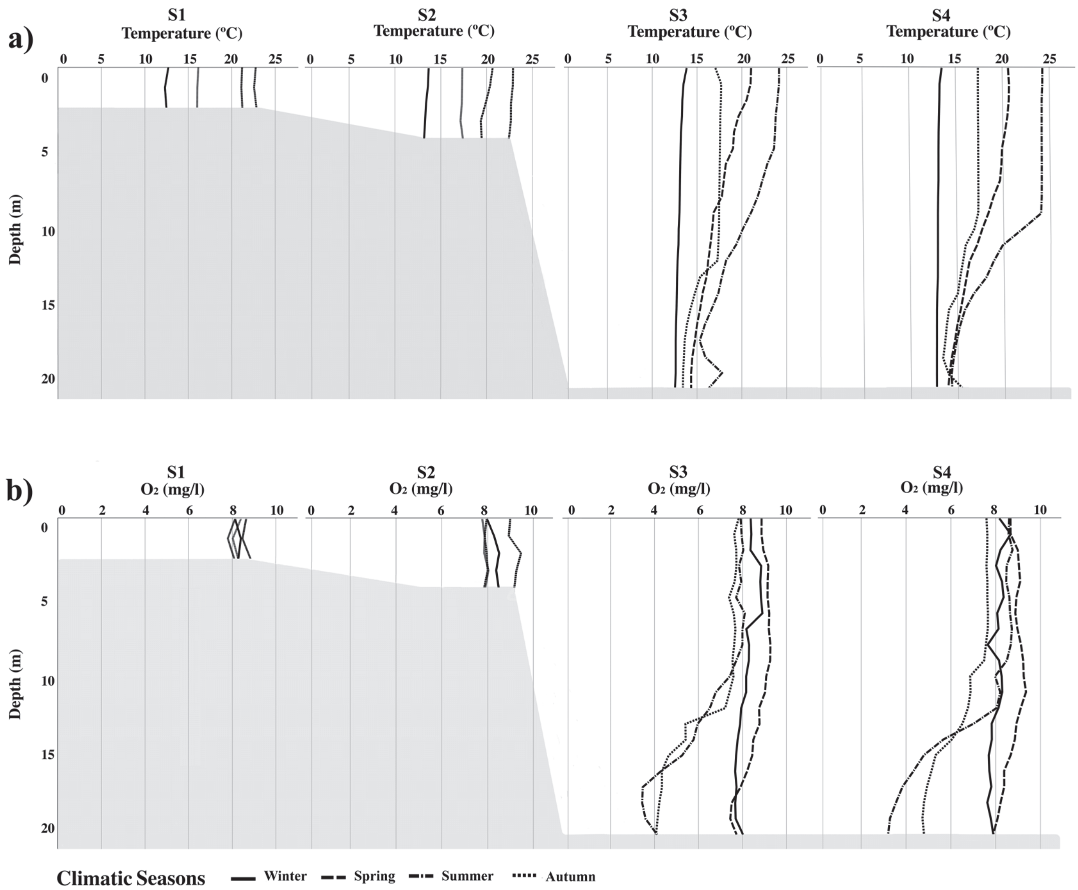

Figure 2. Depth profile of average temperature (a) and oxygen (b) measured monthly for each season at the four sampling sites (S1, S2, S3 and S4) in the Zahara-El Gastor Reservoir. *Perfiles de temperaturas (a) y concentraciones de oxígeno (b) medias mensuales para cada estación en los cuatro puntos de muestreo (S1, S2, S3 y S4) en el embalse de Zahara-El Gastor.*

densities and each spatio-temporal factor was tested by performing two separate discriminant function analyses (DFA) with Season and Sampling site as grouping variables. A Canonical Correspondence Analysis (CCA) was performed to relate zooplankton species abundance to the environmental variables (Legendre & Legendre, 2012). In order to exclude species representing rare observations, only zooplankton taxa which occurred with more than 0.5% of the total density were included in the analysis. Moreover, densities were log(x+1)-transformed to down-weigh the influence of outliers presenting very high values. Analyses were performed with IBM SPSS Statistics 26 (IBM Corp, 2019) and the CCA in the package "vegan" of R software (R Core Team, 2022).

RESULTS

Environmental structure

The Zahara-El Gastor Reservoir presented a warm monomictic thermal cycle, characterized by a mixing period from late autumn to early spring, followed by stratification in summer (Fig. 2). Autumn precipitations favored the mixing of the water column, resulting in lower temperatures and an increase in dissolved oxygen in the upper layer. During the mixing period in winter, both parameters showed practically uniform values along the water column (Fig. 2). The initial rainfall led to surface runoff into the hydrographic basin, triggering an increase in dissolved solids,

Table 1. Mean pH, conductivity (Con.), Total Dissolved Solids (TDS), turbidity (Turb.), nitrates (NO_3), dissolved ammonia (NH_4^+), carbonates (HCO^{3-}), phosphates (PO_4^{3-}), Secchi depth (SD) and chlorophyll-*a* (mg/m^3) recorded monthly from October 2019 to September 2020 in the Zahara-El Gastor Reservoir for each Season and Sampling Site. *Valores medios de pH, conductividad (Con.), Solidos Disueltos Totales (TDS), turbidez (Turb.), nitratos (NO_3), amonio (NH_4^+), carbonatos (HCO^{3-}), fosfatos (PO_4^{3-}), profundidad de Secchi (SD) y clorofila-*a *(mg/m^3) registrados desde octubre de 2019 hasta septiembre de 2020 en el embalse de Zahara-El Gastor en cada punto de muestreo.*

Season	Site	pH	Con. (µS/cm)	TDS (mg/l)	Turb. (NTU)	NO_3 (mg/l)	NH_4^+ (mg/l)	HCO_3^- (mg/l)	PO_4^{3-} (mg/l)	SD (m)	Chl-*a* (mg/m^3)
Winter	S1	7.78	653.3	428.7	5.6	7	0.008	248.1	0.015	1.2	4.606
Winter	S2	8.01	858.3	548.3	9.3	10	0.008	185.1	0.020	1.1	3.677
Winter	S3	8.12	843.7	537.7	3.4	3	0.008	142.5	0.015	1.8	3.028
Winter	S4	8.10	867.7	555.7	2.7	0	0.008	158.7	0.005	2.6	3.487
Spring	S1	8.19	696.3	380.3	26.2	15	0.150	252.2	0.015	0.8	6.768
Spring	S2	8.32	750.7	411.0	9.7	15	0.100	160.7	0.010	1.2	4.036
Spring	S3	8.48	813.3	440.0	4.5	15	0.025	162.7	0.015	1.9	2.622
Spring	S4	8.19	867.0	475.0	21.5	25	0.025	152.6	0.025	2.7	2.155
Summer	S1	8.34	1066.3	556.7	32.6	20	0.083	142.4	0.005	0.5	4.300
Summer	S2	7.90	1051.0	546.7	13.3	10	0.200	152.6	0.000	1.0	3.582
Summer	S3	8.25	1078.7	548.0	6.5	10	0.017	138.3	0.000	1.5	2.324
Summer	S4	8.32	1086.7	550.3	3.2	10	0.025	130.2	0.000	2.4	1.770
Autumn	S1	7.26	1258.7	763.0	28.0	10	0.171	207.5	0.031	0.5	4.679
Autumn	S2	7.44	1154.7	675.7	11.9	10	0.054	146.4	0.045	0.8	1.840
Autumn	S3	7.39	1154.7	680.0	20.1	10	0.021	148.5	0.015	1.6	1.786
Autumn	S4	7.43	1144.0	668.3	2.1	10	0.025	146.4	0.030	2.6	1.737

conductivity, turbidity, carbonates, and dissolved ammonia in the water body (Table 1). On the opposite, the onset of the stratification period was characterized by a rise in temperatures which, together with increasing concentrations of organic matter and nutrients, contributed to higher chlorophyll-*a* values. During summer, we observed a variation in nutrient concentrations, specifically a decrease in carbonates and phosphates. In addition to seasonality, we observed spatial variation in the physical-chemical characteristics of the reservoir along the tail-dam axis. Dissolved solids entering the reservoir through the tail resulted in the highest turbidity, carbonates and chlorophyll-*a* values being recorded at sampling site 1, corresponding to the tail. Meanwhile, water transparency increased with depth, reaching the highest values at sampling site 4, corresponding to the dam (Table 1).

The Carlson Trophic State Index (TSI) was 46.52, which indicates that the Zahara - El Gastor Reservoir can be considered as a mesotrophic system (40-50), characterized by a moderate water clarity with increasing probability of hypoxia in summer.

Principal Component Analysis results showed that the first two components together explained 40.15% of the variance (Fig. S1 and Table S1. Supplementary information, available at https://www.limnetica.net/en/limnetica). The first axis explained 20.93% of the variance and was related positively with conductivity and TDS and negatively with nitrates and water volume. This axis clearly separated sites sampled in summer and autumn, located in the positive zone of component 1, from winter and spring, located in the negative zone, describing differences in water chemistry during the year. The second axis explained 19.22% of the variance and was positively associated with chlorophyll-*a* concentration and turbidity, and negatively with depth and water transparency. Sampling sites grouped along the second

Table 2. Zooplankton taxa identified in the Zahara-El Gastor Reservoir during the study period. *Taxones de zooplancton identificados en el embalse de Zahara-El Gastor registradas durante el periodo del estudio.*

ROTIFERA PHYLUM	**ARTHROPODA PHYLUM**
Rotatoria Class	**Branchiopoda Class**
Ploimida Order	**Ctenopoda Order**
Fam *Asplanchnidae*	Fam *Sididae*
Asplanchna priodonta (Gosse, 1850)	*Diaphanosoma mongolianum*
Fam *Brachionidae*	**Anomopoda Order**
Anuraeopsis fissa (Gosse, 1851)	Fam *Bosminidae*
Brachionus angularis (Gosse, 1851)	*Bosmina longirostris* (Müller, 1776)
Brachionus calcyflorus (Pallas, 1766)	Fam *Daphniidae*
Keratella cochlearis (Gosse, 1851)	*Ceriodaphnia quadrangula* (Müller, 1785)
Keratella quadrata (Müller, 1786)	*Daphnia longispina* (Müller, 1776)
Keratella tropica (Apstein, 1907)	*Daphnia pulicaria* (Forbes, 1893)
Notholca acuminata (Ehrenberg, 1832)	Fam *Eurycercidae*
Notholca squamula (Müller, 1786)	*Chydorus sphaericus* (Müller, 1776)
Fam *Lecanidae*	Fam *Macrotrichidae*
Lecane hastata (Murray, 1913)	*Macrothrix laticornis* (Jurine, 1820)
Lecane luna (Müller, 1776)	**Hexanauplia Class**
Monostyla bulla (Gosse, 1851)	**Copepoda Subclass**
Gnesiotrocha Order	**Calanoida Order**
Fam *Filinidae*	Fam *Diaptomidae*
Filinia longiseta (Ehrenberg, 1834)	*Copidodiaptomus numidicus* (Gurney, 1909)
Fam *Hexarthridae*	**Cyclopoida Order**
Hexarthra fennica (Levander,1892)	Fam *Cyclopidae*
Fam *Lepadellidae*	*Acanthocyclops robustus* (G.O.Sars, 1863)
Colurella adriatica (Ehrenberg, 1831)	*Acanthocyclops vernalis* (Fischer, 1853)
Colurella obtusa (Gosse, 1886)	
Fam *Lepidellidae*	
Lepidella ovalis (Müller, 1786)	
Fam *Notommatidae*	
Eosphora anthadis (Harring & Myers, 1922)	
Monommata grandis (Tessin, 1890)	
Monommata longiseta (Müller, 1786)	
Fam *Synchaetidae*	
Polyarthra vulgaris (Carlin, 1943)	
Polyarthra dolichoptera (Idelson, 1925)	
Synchaeta pectinata (Ehrenberg, 1832*)*	
Fam *Testudinellidae*	
Testudinella patina (Hermann, 1783)	
Fam *Trichotriidae*	
Macrochaetus altamirai (Arévalo, 1918)	
Trichotria tetractis (Ehrenberg, 1830)	

axis according to the reservoir area, being sites 1 and 2 in the positive zone of component 2 and sites 3 and 4 in the negative one. This axis described variation in water depth and transparency, as sampling sites 1 and 2 were close to the reservoir tail and presented higher turbidity and chlorophyll-*a* and lower depth and water transparency compared to sites 3 and 4.

Zooplankton community structure

A total of 36 zooplankton species were identified in the Zahara-El Gastor Reservoir during the study period (Table 2). 26 species belonged to the phylum Rotifera, class Rotatoria while 10 species belonged to the phylum Arthropoda, including 7 species from the Branchiopoda class and 3 species from the Hexanauplia class (Copepoda subclass).

The zooplankton community from the Zahara-El Gastor Reservoir presented a Shannon-Wiener diversity index (*H’*) ranging from 1.49 in spring, S1 to 2.05 in autumn, S3 (Table 3). Overall, diversity index (*H’*) values were similar among the different sampling sites, with the highest value in S3 (2.07). As for the season, the highest values were found in winter (2.06) and summer (1.97). Heterogeneity (β) index showed a similar pattern to diversity index, presenting the lowest value in S1 (0.82) and the highest in S3 (0.91), while results were very similar across the different seasons.

Total zooplankton density showed large spatio-temporal variation. Autumn presented the highest density, while the other seasons had similar values (Fig. 3). As for the sampling site, density decreased from the tail towards the dam, showing S1 always the highest values. In particular, the highest density was reached in autumn at S1 (345 ind/l). This site was dominated by the phylum Rotifera both in total and relative density, while at the sampling stations 2, 3, and 4 Branchiopoda and Copepoda made up the majority of zooplankton density (Fig. 3d; Table S2, see supplementary information available at https://www.limnetica.net/en/limnetica). Zooplankton relative density at the different stations during spring followed a similar pattern to autumn, although with lower total density at S1 (Fig. 3b). In winter, Rotifera and Branchiopoda presented the highest densities at S1, while Branchiopoda y Copepoda were dominant at the other sampling sites (Fig. 3a). Finally, during summer, Brachiopoda were dominant at S1, while Copepoda made up the highest proportion of zooplankton at the other sites (Fig. 3c).

In terms of the variation in abundance of individual zooplankton species, six species in the phylum Rotifera exhibited significant differences in density among seasons, while two among sampling sites (Table S3 and S4, see supplementary information, available at https://www.limnetica.net/en/limnetica). At S1, *Polyarthra vulgaris* presented the highest mean density value in spring (39.0 ind/l), summer (15.2 ind/l) and autumn (94.3 ind/l), while *Polyarthra dolichoptera* presented the highest values in winter (26.5 ind/l) and autumn (148.7 ind/l) (Table S2). *Asplancha priodonta* (7.1 ind/l), *Keratella cochlearis* (13.5 ind/l) and *Keratella tropica* (6.2 ind/l) also showed high density in autumn at S1, although with lower values compared to *Polyarthra* spp.

In general, the Branchiopoda class presented a low density. The highest densities were registered in autumn at S1 for *Bosmina longirostris* (27.3 ind/l) and in summer at S1 for *Ceriodaphnia quadrangula* (22.8 ind/l) and *Daphnia longispina* (16.0 ind/l) (Table S2). *B. longirostris*, *D. longispina* and *Chydorus sphaericus* showed significant differences in their densities among seasons (Table S3) and only *B. longirostris* among sampling sites (Table S4).

As for the Copepoda, all species presented the highest density in autumn at S1, being *Copidodiaptomus numidicus* and the Diaptomidae nauplii the most abundant over the study period (Tables

Table 3. Shannon-Wiener (H´) index and heterogeneity (β) index of the zooplankton community from the Zahara-El Gastor Reservoir for the four seasons and sampling sites. *Índices de Shannon-Wiener (H`) y heterogeneidad (β) de la comunidad de zooplancton en el embalse de Zahara-El Gastor durante las cuatro temporadas y puntos de muestreo.*

	S1		S2		S3		S4		Annual	
	H’	*β*	*H’*	*β*	*H’*	*β*	*H’*	*β*	*H’*	*β*
Winter	1.58	0.77	1.98	0.96	1.86	0.90	2.01	0.98	2.06	0.90
Spring	1.49	0.79	1.62	0.86	1.77	0.94	1.83	0.97	1.88	0.89
Summer	1.87	0.99	1.62	1.00	1.83	0.97	1.73	0.92	1.97	0.89
Autumn	1.75	0.89	1.65	0.84	2.05	1.00	1.53	0.78	1.88	0.92
H’ Reservoir	2.05	0.82	2.02	0.85	2.07	0.91	2.05	0.87	2.24	0.87

S2). *Acanthocyclops robustus* and *Acanthocyclops vernalis* showed significant differences among seasons (Table S3) while *C. numidicus* among sampling sites (Table S4).

DFA produced three significant axes differentiating between seasons, where DF1 and DF2 accounted for 54.4% and 34.0% of the variance, respectively. Species collected in Summer and Winter were generally correctly classified (≥90%), while species collected in Spring and Winter were more frequently classified as each other (83.3%) (Fig. S2a, and Table S5. Supplementary information, available at https://www.limnetica.net/en/limnetica). Overall, 89.1% of observations originally in a given season could be correctly classified in their respective group. Zooplankton species presenting the highest correlation with the first canonical discriminant function included *A. priodonta*, *Brachionus calcyflorus*, *Diaphanosoma mongolianum*, *Daphnia pulicaria*, and *Macrothrix laticornis*, while species presenting high correlation with the second

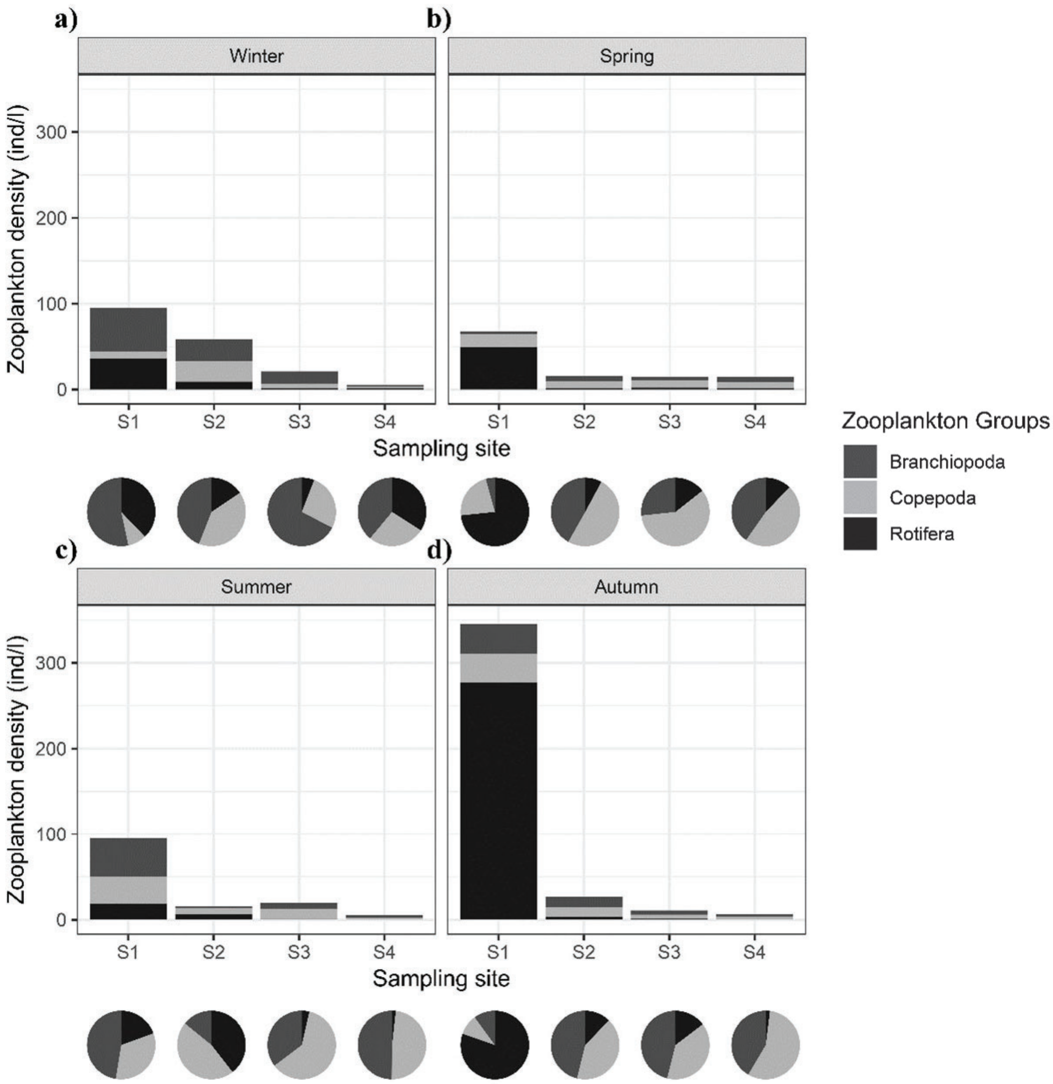

Figure 3. Spatio-temporal variation in absolute and relative density of the different zooplankton groups at the sampling station S1, S2, S3 and S4 in winter (a), spring (b), summer (c) and autumn (d) in the Zahara-El Gastor Reservoir during the study period. *Variación espacial en la densidad absoluta y relativa de los diferentes grupos de zooplancton en invierno (a), primavera (b), verano (c) y otoño (d) en el embalse de Zahara-El Gastor durante el periodo de estudio.*

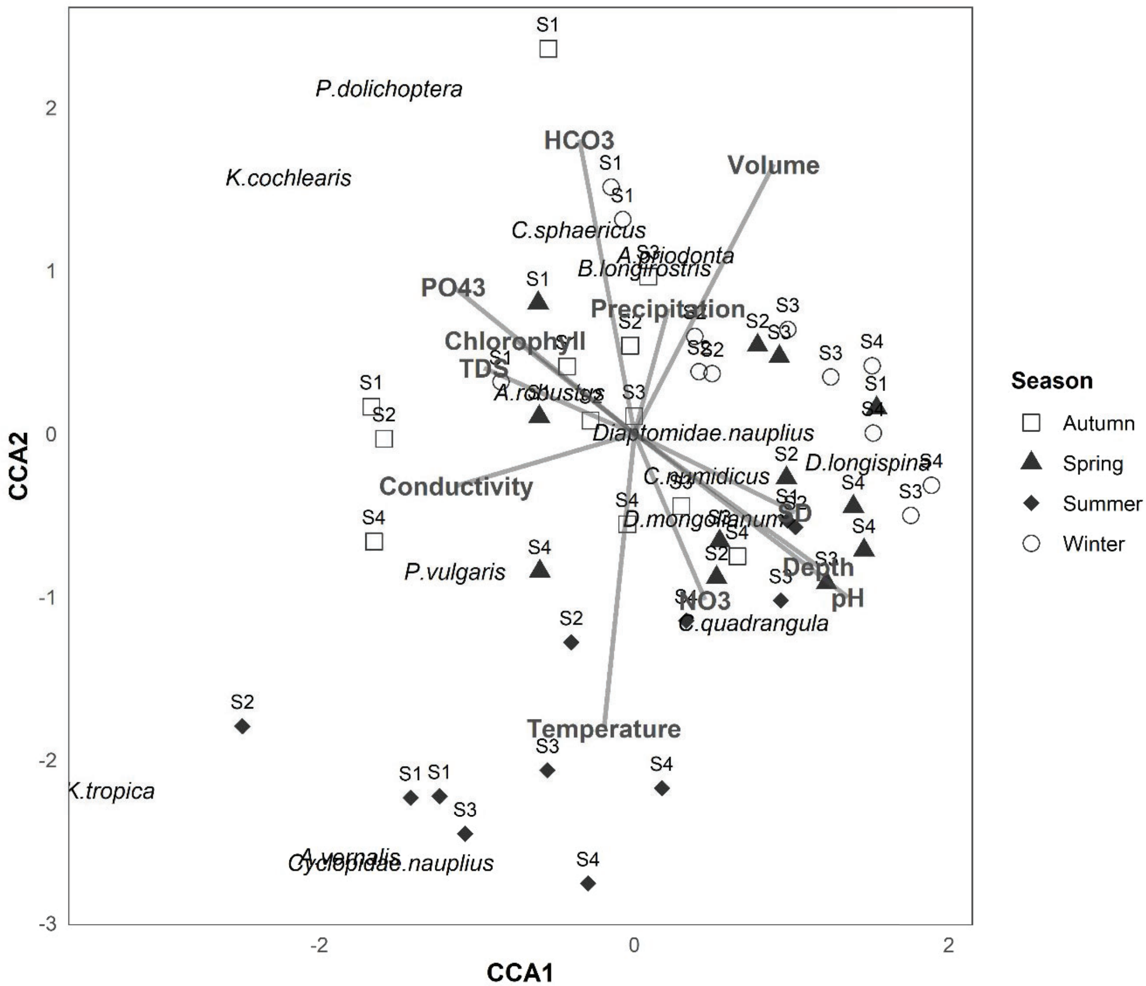

Figure 4. Scatterplot of Canonical Correspondence Analysis (CCA) of sampling sites, zooplankton species, and environmental variables collected in the Zahara-El Gastor Reservoir during the study period. Only environmental variables (arrows) with correlation >0.3 are shown. *Resultados del Análisis de Correspondencia Canónica (ACC) de los distintos puntos de muestreo, especies de zooplancton y variables ambientales registradas en el emblase de Zahara-El Gastor durante el periodo de estudio. Solo se muestran las variables ambientales (flechas) con correlación >0.3. A. vernalis = Acanthocyclops vernalis, P. vulgaris = Polyarthra vulgaris, P. dolychoptera= Polyarthra dolichoptera, K. tropica = Keratella tropica, K. cochlearis = Keratella cochlearis, A. robustus = Acanthocyclops robustus, C. sphaericus = Chydorus sphaericus, A. priodonta = Asplanchna priodonta, B. longirostris = Bosmina longirostris, D. mongolianum = Diaphanosoma mongolianum, C. numidicus = Copidodiaptomus numidicus, D. longispina = Daphnia longispina, C. quadrangula = Ceriodaphnia quadrangula.*

canonical discriminant function were rotifers *K. cochlearis*, *K. tropica*, *Anuraeopssis fissa*. *Notholca* sp., *Polyarthra* sp. and *Testudinella patina* as well as *D. mongolianum*, *Acanthocyclops* sp., and Cyclopidae naupilii. DFA of zooplankton species between sampling sites produced three significant axes, where DF1 and DF2 explained 85.1% and 10.3% of the variance, respectively. Zooplankton species from sites 1 and 4 were correctly classified (100%), while sites 2 and 3 showed 63.6% and 83.3% of accuracy, respectively, being sometimes classified as site 4 (Fig. S2b, and Table S5. Supplementary information, available at https://www.limnetica.net/en/limnetica). Overall, 87% of the original observations could be correctly classified. *Colurella obtusa*, *Monommata grandis*, *Keratella quadrata*, *Daphnia pulicaria*, *A. fissa*, and *Brachionus angularis* were among the best discriminating species between sampling sites.

Relating zooplankton community and environmental structure

The results of the CCA showed the relationship between the selected environmental variables and the dominant zooplankton species (Fig. 4 and Table 4). The first two canonical axes together explained 32.2% of the variance. The first axis accounted for 19.7% of the variance and was correlated negatively with phosphates and conductivity and positively with pH and water depth, representing water chemical properties. This axis separates the autumn and summer stations, in the negative zone of the component, from the spring and winter stations, in the positive zone. The second axis explained 12.5% of the variance and was correlated negatively with temperature and positively with carbonates and volume. This axis clearly grouped the summer stations in the negative zone of the component, which presented higher temperature and lower carbonates and water volume compared to the other seasons. The major source of variation in the zooplankton species ordination was determined by environmental differences among seasons. *K. tropica*. *A. vernalis*, and Cyclopidae naupilii dominated in summer at high temperature values, while rotifers *P. dolichoptera* and *K. cochlearis* were dominant at shallow stations, mainly in autumn, when conductivity, as well as phosphates and carbonates presented the highest values. To the right of the first axis, Branchiopod species such as *D. longispina*, *C. quadrangula* and *D. mongolianum* occurred at high pH and water depth. *A. robustus*, *C. numidicus*, and Diaptomidae nauplii were located in the center of the graph and represent copepod species without strong seasonal patterns in abundance.

Table 4. Summary of Canonical Correspondence Analysis (CCA) results among sampling sites, months, environmental variables, and community structure. *Resumen del Análisis de Correspondencia Canónica (ACC) entre puntos de muestreos, meses, variables ambientales y estructura de la comunidad.*

	Axis 1	Axis 2
Eigenvalue	0.633	0.253
Variance explained	19.7 %	12.5 %
Correlation with environmental variables		
Nitrates (NO_3)	0.179	-0.408
Carbonates (HCO_3)	-0.140	0.721
Phosphates (PO_4)	-0.460	0.360
Ammonia (NH_4)	-0.004	0.264
Chlorophyll-a (Chl-*a*)	-0.302	0.229
Water transparency (SD)	0.407	-0.193
Depth	0.467	-0.326
pH	0.542	-0.401
Conductivity	-0.453	-0.128
Temperature	-0.078	-0.722
Dissolved Oxygen	0.141	0.123
Total dissolved solids (TDS)	-0.382	0.161
Turbidity	-0.099	-0.027
Precipitation	0.086	0.308
Volume	0.354	0.661

DISCUSSION

The zooplankton community of the Zahara-El Gastor Reservoir presented variation in species composition and abundance among different seasons and sampling sites which reflected the temporal and spatial heterogeneity of its limnological characteristics.

Seasonal fluctuations of zooplankton populations are a well-known phenomenon and zooplankton typically exhibits a bimodal oscillation with spring and autumn peaks in density in temperate lakes and reservoirs (Wetzel, 2001). However, the density values recorded in our study can be considered relatively low, being typical of environments with low nutrient concentration (de Zaburlín et al., 2010). The zooplankton abundance from our study reflected the trophic state of the reservoir, presenting typical values found in Mesotrophic systems of the Mediterranean region (García-Chicote et al., 2018).

The physical-chemical characteristics of the tail area showed a completely different behavior compared to the rest of the reservoir, determining a clear decreasing gradient in zooplankton density from the tail to the dam, independently from the season. The existence of spatial heterogeneity along the reservoir's long-axis is common in reservoirs (Betsill & van den Avyle, 1994). In particular, the highest density was reached in the tail area during autumn (345 ind/l). Precipitations cause surface runoff generating water movements that dilute transported materials and nutrients as they move through the reservoir. These phenomena mainly affect the tail, and may explain the longitudinal variation in the zooplankton abundance (Perbiche-Neves & Nogueira, 2013; Sabater et al., 1988), especially in autumn when the precipitation and river inflow are higher.

The zooplankton species identified in this study are typical of water bodies from the Iberian Peninsula (Alonso, 1996; J. Armengol, 1978; De Manuel Barrabin, 2000). In general, Rotifera presented the highest number of species followed by Branchipoda and Copepoda, similarly to other reservoirs at similar latitudes in the Mediterranean region (Dorak et al., 2019; García-Chicote et al., 2019).

A set of physico-chemical variables played a decisive role in determining the species composition of the zooplankton community in the reservoir. Rotifers, which have a greater capacity for colonizing altered and unstable environments provided by their reproductive and feeding strategy (de Zaburlín et al., 2010), were always dominant in absolute and relative density in the tail area, with the exception of the summer season where Brachiopoda prevailed (de Zaburlín et al., 2010). In particular, in autumn, *P. dolichoptera*, was the species which presented the highest abundance, and together with *P. vulgaris*, *K. cochlearis*, and small Cladocera such as *B. longirostris* was dominant at sites characterized by low depth and high total phosphates, chlorophyll-*a*, carbonates and conductivity levels such as the tail area. *Polyarthra* spp. are widespread and abundant taxa due to their high tolerance to changing environmental conditions (Dorak et al., 2019; Muñoz-Colmenares et al., 2021b). A gradient in *Polyarthra* spp density decreasing from tail to damn and coinciding with chlorophyll concentrations was also found in a reservoir in southern Spain (Fernández-Rosado & Lucena, 2001). These results are in line with other studies showing that rotifers presence is linked to higher trophic state and respond quickly to alteration in abiotic conditions while large zooplankton species decay (Jeppesen et al., 2000; Arora & Mehra, 2003b; a; Pinto-Coelho et al., 2005), especially at the start of the mixing period, when the first rainfall causes surface runoff into the hydrographic basin, triggering an increase in dissolved solids, conductivity, turbidity, carbonates, and dissolved ammonia in the water body (Glé et al., 2008; Valencia, 2004). In addition, higher levels of suspended inorganic solids may act against the selection of large filter feeders, allowing small-sized zooplankton species to be dominant under these conditions (De Manuel Barrabin, 2000; Lougheed & Chow-Fraser, 1998).

In general, sampling sites 2, 3 and 4 presented a larger proportion of Branchiopoda and Copepoda. Systems with a longer water retention time can provide a more stable environment for copepods and larger cladocerans (Perbiche-Neves & Nogueira, 2013). Copepoda species such as the large-sized *A. robustus* and *C. numidicus*, and Diaptomidae naupilii show a longer life cycle and were present in the reservoir throughout the year. *C. numidicus* represented the copepod with the highest density values, and has been related to less meso-eutrophic systems (Parra et al., 2008).

Spring and winter were characterized by high pH and water depth and low total phosphates. The species showing the highest association to these parameters was the large-sized cladoceran *D. longispina*, which has been previously linked to more oligotrophic conditions (Antunes et al., 2003; Tackx et al., 2004; Yagci et al., 2016). Moreover, *D. longispina*, together with *C. numidicus* and *D. mongolianum*, presented the highest relative abundance close to the dam, as shown in previous studies (Fernández-Rosado & Lucena, 2001).

Copepoda and Branchiopoda constituted the largest proportion of species during the summer. Species such as *C. quadrangular*, *A. vernalis* and Cyclopidae naupilii showed strong correlations with higher temperatures. Previous studies have linked *Ceriodaphnia* spp., *Acanthocyclops* spp. and Cyclops genera with warm meso- to eutrophic waters (Tackx et al., 2004; Pinto-Coelho et al., 2005). Dominance of small-sized zooplankton species has been generally recorded in reservoirs during summer months (Dorak et al., 2019; Muñoz-Colmenares et al., 2021a) since the increase in temperature and the drop in water level can favor the growth of species with shorter life cycles like Rotifera or small Cladocera (Pinto-Coelho et al., 2005; Obertegger et al., 2007;

Yagci et al., 2016). However, in the present study, Rotifera occurred with very low densities during summer. It should be noted that during this season we registered a drop in nutrient concentrations, specifically a decrease in carbonates and phosphates, probably due to assimilation and incorporation into biomass as well as to the alteration of the carbonate system (Armengol, 1984). This lower nutrient availability, together with limited water renewal may have determined a drop in rotifers presence, even at the tail of the reservoir.

Rotifers and small-sized cladocerans were predominant in both number and density, while large-sized zooplankton species generally occurred at lower abundances. The reduction in size of the zooplankton community is associated with eutrophic systems, as observed in lakes with a warm climate and high phosphate concentrations, often due to nutrient loading from human activities and increased evapotranspiration (Jeppesen et al., 2009). However, the coexistence of species typically associated with high trophic levels such as *Polyartha* spp., *Keratella* spp. or *B. longirostris*, with species related to more oligotrophic systems, such as *C. numidicus*, *Daphnia* spp. or *D. mongolium* (García-Chicote et al., 2019), confirms that the Zahara El-Gastor Reservoir is overall in a mesotrophic state. It should be noted that these changes in species composition were also highly dependent on season and sampling site, being the environmental conditions in winter-spring and close to the dam the most favorable for the species associated with a low tropic status. Moreover, large and actively moving cladocerans such as *Daphnia* sp. are selectively preyed by planktivorous. (Chase, 2003). In the Zahara El-Gastor Reservoir, it is documented the presence of exotic bleak (*Alburnus alburnus*). This zooplanktivorous fish may have changed the species composition of the zooplankton community by reducing the population of large-sized species (Vinni et al., 2000). In this study, Rotifera dominance was also linked to higher concentrations of chlorophyll-*a*. In other reservoirs located in the Mediterranean, the size reduction of zooplankton and the increase of chlorophyll-*a* were related to the predation pressure of exotic zooplanktivorous fish (Ordóñez et al., 2010).

CONCLUSION

The results of this study indicate that the zooplankton density and species composition of the Zahara-El Gastor Reservoir were strongly influenced by changes in environmental characteristics, potentially serving as indicators of its trophic status. Variations in the species community were mainly associated with nutrient availability, conductivity, water depth and temperature, factors highly dependent on the climatic season. Water runoff appeared to be an important factor influencing the distribution of the different zooplankton groups along the tail-dam axis of the reservoir, and spatial heterogeneity should be considered in future studies using zooplankton as a water quality indicator. Therefore, understanding how zooplankton communities are influenced by environmental characteristics is crucial for predicting the effects of water management and human activities on these ecosystems.

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