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Zooplankton assemblages in two reservoirs: one subjected to accentuated water level fluctuations, the other with more stable water levels

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Abstract The abundance, composition and dynamics of zooplankton were followed in two reservoirs of the River Douro catchment. The Serra Serrada Reservoir is subject to marked fluctuations in water levels. The highest values of total phosphorus, soluble reactive phosphorus, nitrate, water colour and chlorophyll *a* were found during the minimum level phase. Rotifera was dominant except in late summer and autumn when the cladoceran *Ceriodaphnia quadrangula* or the copepod *Tropocyclops prasinus* replaced them as the dominant zooplankton. Among the rotifers the most common taxa were *Keratella cochlearis*, *Conochilus* sp. and *Asplanchna priodonta*. Maximum rotifer density was about 80,000 ind m^{-3} in 2000, 200,000 ind m^{-3} in 2001 and 100,000 ind m^{-3} in 2002. Among the crustacean zooplankton *C. quadrangula* achieved densities of up to 45,000 ind m^{-3} and *T. prasinus*, up to 80,000 ind m^{-3}. Canonical correspondence analysis revealed a strong contribution of the variation in the stored water volume, temperature, total phosphorus, chlorophyll, nitrates, and water transparency to the observed, significant association between zooplankton assemblage and environmental variables. In the Azibo Reservoir, fluctuations in water level are smaller. Only total phosphorus, cholorophyll and conductivity varied seasonally. Cladocera and Copepoda were dominant during the whole study period. The most abundant taxa were *Ceriodaphnia pulchella*, *Daphnia longispina*, *Diaphanosoma brachyurum*, *Bosmina longirostris* and *Copidodiaptomus numidicus*. Cladocera achieved densities of up to 25,000 ind m^{-3} and Copepoda up to 15,000 ind m^{-3}. Rotifera in general reached densities of up to 6,000 ind m^{-3}. On the basis of canonical correspondence analysis only temperature and conductivity were significantly associated with zooplankton assemblage.

Keywords Reservoirs · Water level fluctuations/water stored volume · Zooplankton assemblage structure

Introduction

In regions where the rainfall is irregular and strongly seasonal and the water is used intensively by local populations, reservoirs are often subjected to marked fluctuations in water level. The

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composition, abundance and dynamics of the zooplankton populations are affected by several physical and chemical variables, which are largely influenced by the degree of these fluctuations (Wetzel 2001). An example of this is the increase in nutrient availability with greater fluctuations in water level observed by several authors (see Schmid-Araya and Zuñiga 1992; Naselli-Flores and Barone 1994; Watts 2000a, b); concomitantly, zooplankton showed a gradual shift from K-strategist towards r-strategist groups. Thus, an understanding of the mechanisms regulating these shifts may constitute an important source of information for the implementation of correct reservoir management practices. The present study was carried out on two reservoirs located in the Portuguese part of the River Douro catchment in the Trás-os-Montes region (NE Portugal). The Serra (S.) Serrada Reservoir was filled for the first time in 1995, and it has been found to be subjected to marked variations in the stored water volume. The Azibo Reservoir was created in 1982, and the observed variations in the volume of stored water are relatively much less.

The objectives of the present research were: (1) to determine zooplankton composition, abundance and dynamics during a 3-year cycle in both reservoirs; (2) to analyse whether the studied environmental variables could account for variations in zooplankton assemblages.

Study sites

The location, morphological and hydrological characteristics of both reservoirs are shown in Table 1. The climate in this region is continental, with warm, dry summers and long, cold winters. However, because of the influence of the Mediterranean climate in the Iberian Peninsula, precipitation and temperature vary greatly over the year and between years.

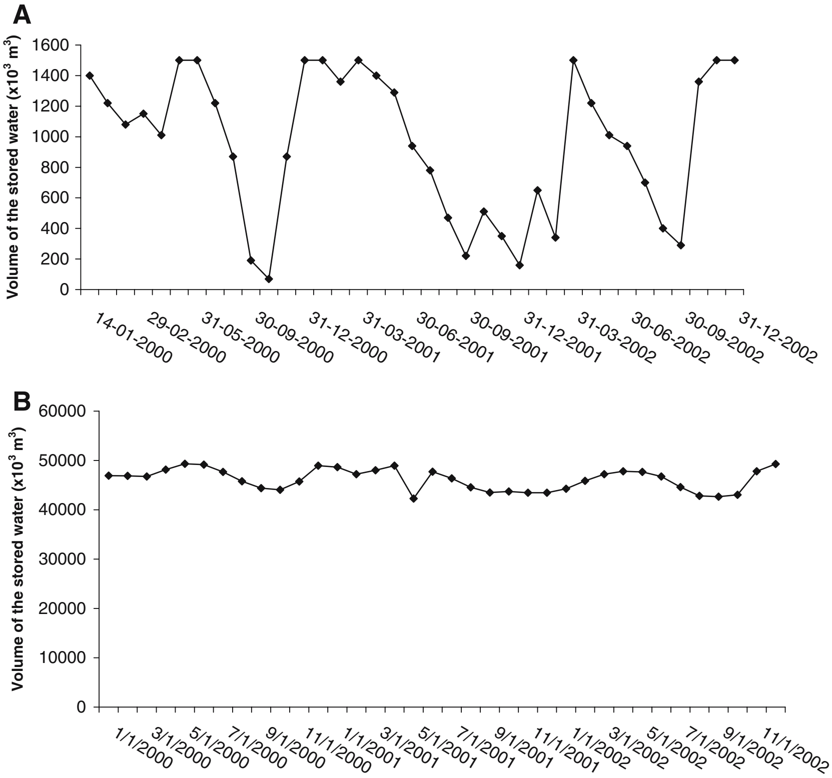
The S. Serrada Reservoir was built expressly as an urban water supply for 34,750 inhabitants (INE 2001) and to generate hydroelectric power. Consequently, the stored water volume suffers a marked reduction in the summer and late summer, inducing pronounced water level fluctuations (Fig. 1). The hydrological cycle of the reservoir is characterised by the following regime: (1) maximum level phase/maximum stored water volume, from January to the beginning of June; (2) emptying phase, from mid-June to the beginning of September; (3) minimum level phase/minimum stored water volume, from mid-September to the beginning of the first autumn/winter rainfall. During the period of study (January 2000 to December 2002), thermal stratification was observed from June to August/beginning of September, with the disruption of stratification coincidental with the lowest water level. The water outlet is located at the deepest part of the reservoir. Although human influence on the reservoir seems to be negligible, grazing (sheep and goat) can be very intense in the catchment basin during the summer months. Consequently, fires over the surrounding land are often started by shepherds to obtain better grazing for their livestock. Fire and livestock excretions are considered to be the main potential allochthonous source of nitrogen and phosphorus.

Table 1 Location and morphometric parameters of the Serra (S.) Serrada and Azibo reservoirs

	S. Serrada	Azibo
Location	Latitude: 41°57′ (N) Longitude: 6°46′ (W)	Latitude: 41°32′ (N) Longitude: 6°53′ (W)
Altitude (m)	1,300	500
Geology	Granitic bedrock	Schistic bedrock
Watershed area (km^2)	6.7	89.0
Reservoir area (km^2)	0.25	4.10
Total capacity (m^3)	$1,680 \times 10^3$	$54,470 \times 10^3$
Maximum depth (m)	18	30
Mean depth (m)	6.72	13.2
Annual water volume reduction (%)	81–95	10.0–13.6
Year of filling	1995	1982

The Azibo Reservoir was filled for the first time in 1982 and is used mainly for recreation. Although it is also used secondarily for water supply and irrigation, these factors do not significantly affect the water in the reservoir and, consequently, the seasonal reduction in the stored water volume is not very marked (Fig. 1). During the period of study, thermal stratification occurred from June to October. The direct influence of human activities on the impoundment is

Fig. 1 Variations in stored water volume (SWV) in S. Serrada (**A**) and in Azibo (**B**) during the study period [source: INAG http://www.snirh.inag.pt (2006)]



greatest during the summer when the reservoir and surroundings are used for recreational purposes, such as fishing, swimming, camping and boating. Other activities throughout the year on the surrounding land are farming and grazing (mainly sheep). Agriculture, grazing, sewage, angling and bathing can be considered to be the potential allochthonous sources of nitrogen and phosphorus in this reservoir.

Both reservoirs are considered to be meso-eutrophic, and their main source of water are small intermittent streams. For more detailed information on these reservoirs, see Geraldes and Boavida (2003).

Materials and methods

Zooplankton samples were collected at monthly intervals during the winter and at 2-week intervals during the summer, throughout three annual cycles, from January 2000 to December 2002. On each sampling date two vertical hauls (7–18 m long at S. Serrada and 20 m long at Azibo) were collected in the pelagic zone in both reservoirs using a Wisconsin-type net with a mesh size of 64 μm, which is fine enough to collect all of the rotifer species (A.M. Geraldes, personal observation). Sampling was always carried out at at the same sampling point. Animals were anaesthetised with carbonated water and preserved in sugar-saturated formaldehyde (4% v/v final concentration). Depending on the density of animals in the sample, the zooplankton were counted in subsamples of 5, 10, 20 ml or in the total sample. Because of the absence of molecular data which would have allowed us to establish their actual positioning in the ‘‘longispina’’ species complex, *Daphnia* species found in both reservoirs were identified on the basis of traditional morphological criteria.

Water samples for soluble reactive phosphorus (SRP) and total phosphorus (TP) determinations were taken from the upper 30–40 cm of the stratum, directly placed into acid-rinsed bottles and transported to the laboratory in a cold container.

During stratification, samples were also obtained from the middle water column and from the bottom. SRP concentrations were estimated by the method of Murphy and Riley (1962), and TP was assessed after acid hydrolysis with persulfate for 60 min under high temperature and pressure (APHA 1989). Water samples for chlorophyll *a* (CHL *a*) determination were obtained in the euphotic zone. Water from 500–1000 ml of sample, was filtered through a Whatman GF/A filter no more than 2 h after collection. Concentrations of CHL *a* were determined spectrophotometrically after an overnight extraction in 90% acetone. Environmental variables such as water temperature, dissolved oxygen, conductivity, pH, as well as nitrate ($N\text{-}NO_3$), ammonium ion ($N\text{-}NH_4$) and ammonia gas ($N\text{-}NH_3$) were measured in situ with a 6820 YSI Multiparameter Water Quality Monitor (Yellow Springs, Ohio). Water transparency was measured with a 20-cm black and white Secchi disk.

A Kruskal-Wallis test (Sokal and Rohlf 1981) was performed for each environmental variable to determine whether mean values, obtained at the maximum water level phase, at the emptying phase and at the minimum water level phase, were significantly different in S. Serrada. In Azibo, the same procedure was used to test whether mean values obtained at late October/early June (maximum level) and at late June/early October (minimum level) were significantly different. This test was performed using SYSTAT 8.0 (SSPS, Chicago, Ill.). The statistical association between zooplankton assemblage structure and environmental variables was quantified with the canonical correspondence analysis (CCA) using the CANOCO 4 computer programme. In this analysis, taxa were included only if they reached a relative abundance larger than 1%. Absolute zooplankton counts (numerical abundances) were transformed to $\log(x+1)$, and rare species were down-weighted. Environmental variables included in CCA were conductivity, temperature, pH, dissolved oxygen, SRP, TP, $N\text{-}NO_3$, $N\text{-}NH_4$, CHL *a*, Secchi depth and the stored water volume variation (SWV). In CCA the automatic forward selection procedure by Monte Carlo permutation tests (9999 permutations) was used to remove the redundant environmental variables, thereby allowing the selection of those contributing most to the explanation of the whole data set (Ter Braak 1995).

Results

S. Serrada Reservoir

Mean TP, $N\text{-}NO_3$, water colour, conductivity and CHL *a* concentrations were the highest during the minimum water level phase; water transparency was the lowest during the same period. SRP mean concentrations were also slightly higher during this period than during the other months of the year. TP, CHL *a* and conductivity decreased during the maximum water level phase. Mean $N\text{-}NO_3$ decreased during the emptying phase (Table 2). $N\text{-}NH_3$ concentrations were always below detection limits. During the period of highest rainfall (autumn and winter), this reservoir reached the maximum level phase in 1 or 2 weeks. Therefore, at the beginning of the maximum level phase TP, $N\text{-}NO_3$, water colour and CHL *a* values were high, gradually decreasing thereafter. The zooplankton assemblage was characteristically dominated by Rotifera, except in the summer and autumn when Cladocera [mainly *Ceriodaphnia quadrangula* (Müller)] and Copepoda [mainly *Tropocyclops prasinus* (Fisher)] became dominant (Fig. 2A) Therefore, the most abundant rotifer species were *Keratella cochlearis* (Gosse), *Conochilus* sp., *Polyarthra* sp. and *Synchaeta* sp. (Table 3). During the period of study *K. cochlearis* densities ranged between 0 and 260,536 ind m^{-3}; *Conochilus* sp. varied between 0 and 54,137 ind m^{-3}; *Polyarthra* sp. ranged from 0 to 36,606 ind m^{-3}; *Synchaeta* sp. ranged from 0 to 16,326 ind m^{-3}. *Ceriodaphnia* and *T. prasinus* maximum values were 40,107 and 71,928 ind m^{-3}, respectively (Fig. 3). The forward variable selection approach to CCA revealed a strong contribution of the SWV ($p = 0.001$), temperature (Temp.) ($p = 0.001$), TP ($p = 0.001$), Chl *a* ($p = 0.003$), $N\text{-}NO_3$ ($p = 0.018$) and water transparency ($p = 0.024$) to the observed significant association between zooplankton assemblage and environmental variables (Monte-Carlo test; $p = 0.0001$). The ordination

Table 2 Mean ± standard deviation (SD) values of the environmental variables and minimum-maximum range for pH obtained for the maximum level phase (1), emptying phase (2) and minimum level phase (3) in S. Serrada

Variables[a]	1	2	3	*p*
Water transparency (m) (Secchi)	2.9 ± 0.9	2.9 ± 1.0	1.7 ± 0.4	**
Water temperature (°C) (Temp.)	9.3 ± 5.5	19.4 ± 1.3	10.2 ± 4.1	**
Dissolved oxygen (mg l^{-1}) (DO)	8.6 ± 1.6	8.4 ± 0.9	8.6 ± 1.5	NS
Conductivity (μs cm^{-1}) (Cond.)	6.0 ± 1.5	8.3 ± 0.8	8.1 ± 1.5	**
pH (PH)	6.9–7.4	5.4–8.1	7.0–8.5	NS
N-NO_3 (mg l^{-1}) (NO_3)	5.8 ± 8.7	0.9 ± 0.8	13.3 ± 15.2	**
N-NH_4 (mg l^{-1}) (NH_4)	0.2 ± 0.5	0.1 ± 0.2	0.4 ± 0.8	NS
TP (μg l^{-1}) (TP)	59.9 ± 25.3	70.1 ± 19.2	82.0 ± 11.4	**
SRP (μg l^{-1}) (SRP)	8.7 ± 7.5	6.6 ± 4.7	9.5 ± 7.2	NS
Chlorophyll *a* (μg l^{-1}) (CHL)	1.7 ± 1.3	1.9 ± 1.6	8.0 ± 4.7	**

Kruskal–Wallis test: $*p < 0.05$, $**p < 0.01$; NS, not significant

[a] Abbreviations used in the CCA are indicated in parenthesis

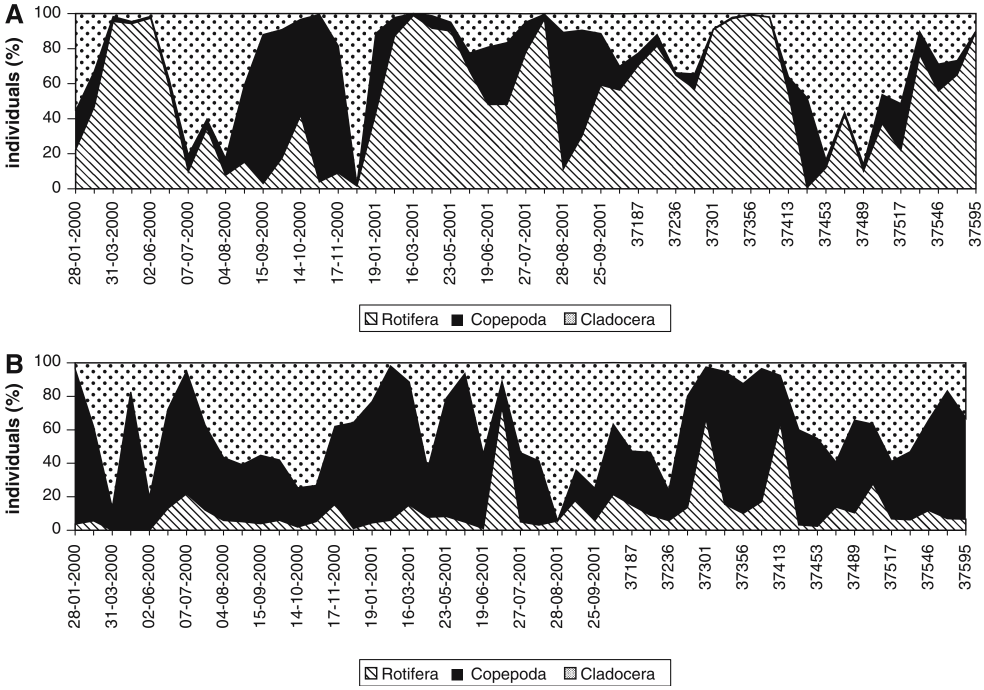


Fig. 2 Relative abundance (%) of Rotifera, Copepoda and Cladocera in the S. Serrada (**A**) and Azibo (**B**) reservoirs

space defined by the first two CCA axes (Fig. 5A) accounted for 71.4% of species environment relations and represented 29.2% of the variation in species data. *Conochilus*, *Polyarthra* and *Asplanchna* were associated with lower temperature and TP values, higher reservoir water stored volume (maximum level phase) and water transparency. *Synchaeta*, *Keratella*, *T. prasinus* and *Ceriodaphnia* abundances were related to the increase in system instability and to the highest nutrient, Chl *a* and temperature values (emptying and minimum level phases).

Azibo Reservoir

In Azibo only mean TP, water transparency, pH and CHL *a* were significantly different between the maximum and minimum levels (Table 4). N-NH_3 concentrations were always below detection limits. Zooplankton assemblage was dominated

Table 3 Mean ± SD values of the environmental variables and minimum-maximum range for pH obtained for late October/early June period (1), late June/early October (2) in Azibo

Variables[a]	1	2	*p*
Water transparency (m) (Secchi)	3.5 ± 1.3	5.0 ± 1.4	**
Water temperature (°C) (Temp.)	12.4 ± 4.4	21.5 ± 2.3	**
Dissolved oxygen (mg l^{-1}) (DO)	9.0 ± 1.4	8.6 ± 0.8	NS
Conductivity (μS cm^{-1}) (Cond.)	54.7 ± 7.9	70.8 ± 3.2	**
pH (PH)	5.4–8.2	7.1–8.4	NS
N-NO_3 (mg l^{-1}) (NO_3)	5.7 ± 6.1	3.2 ± 4.1	NS
N-NH_4 (mg l^{-1}) (NH_4)	0.5 ± 1.1	0.5 ± 1.2	NS
TP (μg l^{-1}) (TP)	56.6 ± 15.2	68.9 ± 13.6	**
SRP (μg l^{-1}) (SRP)	6.1 ± 5.3	5.9 ± 4.4	NS
Chlorophyll *a* (μg l^{-1}) (CHL)	1.8 ± 1.4	1.1 ± 1.3	*

Kruskal–Wallis test: *$p < 0.05$, **$p < 0.01$; NS, not significant

[a] Abbreviations used in the CCA are indicated in parenthesis

by Cladocera or Copepoda, except in the samplings from 13 July 2001, 14 February 2002 and 6 June 2002 when the rotifer *Polyarthra* sp. was dominant (Fig. 2B). The most abundant Cladoceran species reported in Azibo were: *Daphnia longispina* Müller, *Ceriodaphnia pulchella* Sars, *Bosmina longirostris* Müllerand *Diaphanosoma brachyurum* Liéven. Two species of Copepoda were found: The calanoid *Copidodiaptomus numidicus* Gurney, and the cyclopoid *Acanthocyclops robustus* Sars, the former dominating over the latter. Rotifera was dominated by *Polyarthra* sp., *Asplanchna priodonta*, *Keratella cochlearis* and *Conochilus* sp. (Table 3). *Daphnia* densities ranged between 0 and 9549 ind m^{-3}; *Ceriodaphnia* varied between 0 and 24,605 ind m^{-3} in 2000; *Bosmina* ranged from 0 to 1401 ind m^{-3}. *Diaphanosoma* was present only in the summer months and during this season its density varied between 64 and 1783 ind m^{-3}. *C. numidicus* densities ranged between 40 and 15,024 ind m^{-3}, whereas *A. robustus* densities varied from 0 to 860 ind m^{-3} (Fig. 4). The forward variable selection approach to CCA only revealed a strong contribution of temperature ($p = 0.0001$) and conductivity ($p = 0.0002$) to the observed significant association between zooplankton assemblage and environmental variables (Monte-Carlo test; $p = 0.006$). The ordination space defined by the first two CCA axis (Fig. 5B) accounted for 100% of species environment relations and represented 32.1% of the variation in species data. *Bosmina*, *Ceriodaphnia* and *Diaphanosoma* were associated with high temperatures and conductivity, whereas *Daphnia*, *C. numidicus*, *A. robustus*, *Asplanchna*, *Polyarthra*, *Keratella* and nauplii showed the reverse trend.

Discussion

S. Serrada Reservoir

In comparison to other reservoirs of similar dimension and located in similar geological and climatic regions (see Boavida 2000; Negro et al. 2000) S. Serrada can be considered to be a highly disturbed system. In fact, internal disturbance caused by fluctuations in the water level is intense. The increase in TP, N-NO_3 and CHL *a* concentrations during the emptying and minimum level phases could have been the result of the increment in suspended particulate material in the water column. This increment might have resulted from water turbulence generated during the emptying phase plus the disruption of stratification at the end of this phase. The existence of large amounts of suspended particulate material in the water column during the emptying phase (A.M. Geraldes, personal observation) might have been a consequence of the existing vegetation not having been removed before the filling of the reservoir area (see Kimmel et al. 1988; Robarts et al. 1992). Nutrients decreased during the maximum level phase. As this phase is a period of water level stability, the sedimentation

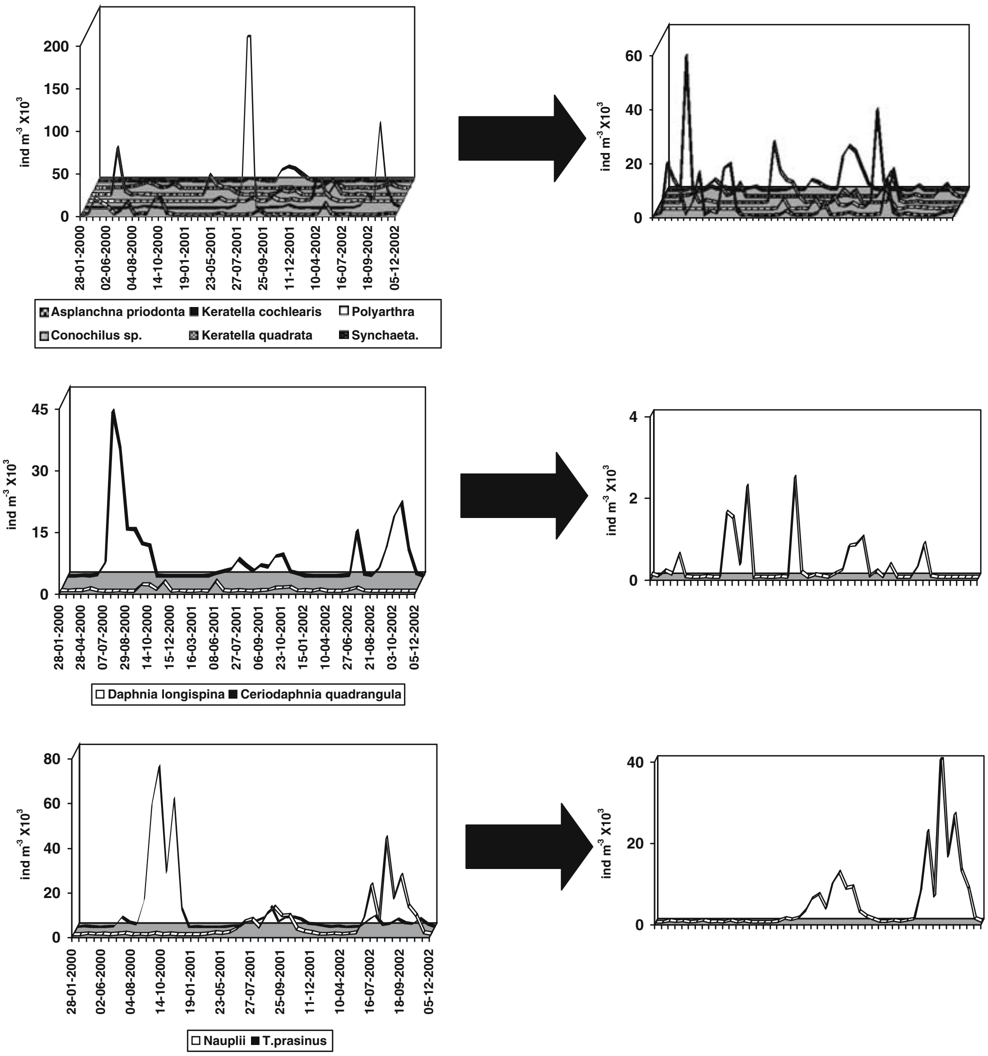


Fig. 3 Annual variation of zooplankton abundance and composition in the S. Serrada Reservoir. Graphics on the *right* are without the taxon with the largest density peaks

of particulate material could have been favoured (Boström et al. 1988; Wetzel 2001). Similar patterns of variations in the amounts of nutrient and suspended particulate material were observed by Naselli-Flores and Barone (1994) and Naselli-Flores (1999) in Sicilian reservoirs subjected to severe reductions in water volume. Another consequence of the disturbance caused by extreme water volume reduction is the exposure of littoral sediments to cycles of drying and wetting, which might have implications on nutrient cycling, namely on phosphorus availability. This assumption is supported by the results obtained by Watts (2000a, b) in reservoirs where water level fluctuations are marked and where refilling took place over a short period of time. According to this author, littoral sediments that are periodically exposed, thereby experiencing cycles of drying and wetting, have a lower capacity to adsorb nutrients than those that always remain submerged. Preliminary experiments based upon the experimental design developed by the Watts (2000a, b) and performed in S. Serrada revealed a similar pattern (A. M. Geraldes unpublished).

Specialists in small particle feeding, whose food preferences are mostly comprised of detritus-bacteria and small phytoplankton, always dominated the zooplankton assemblage in this

Table 4 Mean densities (ind m^{-3}) and percentage of occurrence of the zooplankton taxa found in both reservoirs

S. Serrada		Azibo	
Zooplankton[a]	Mean densities[b]	Zooplankton[a]	Mean densities[b]
Rotifera		Rotifera	
Keratella cochlearis (Gosse) (Kera.)	9380.5 (27.4)	*Polyarthra* sp. (Poly.)	1181.2 (8.7)
Asplanchna priodonta Gosse (Aspl.)	2689.2 (7.9)	*Asplanchna priodonta* Gosse (Aspl.)	513.9 (3.8)
Conochilus sp. Ehrb. (Cono.)	2857.9 (8.4)	*Keratella cochlearis* (Gosse) (Kera.)	226.4 (1.7)
Polyarthra sp. Ehrb. (Poly.)	1559.0 (4.6)	*Synchaeta* sp. Ehrb.	96.5 (0.7)
Synchaeta sp. Ehrb. (Sync.)	1486.5 (4.3)	*Gastropus* sp. Imhof	81.4 (0.6)
Keratella quadrata (Müller) (Kqua.)	998.0 (2.9)	*Collotheca mutabilis* (Hudson)	18.7 (0.1)
Hexarthra sp. Schmarda	144.7 (0.4)	*Conochilus* sp. Ehrb.	7.1 (0.1)
Ploesoma sp. Herrick	35.7 (0.1)	*Hexarthra* sp.	2.4 (0.02)
Gastropus sp. Imhof	31.2 (0.1)	*Keratella quadrata* (Müller)	2.0 (0.01)
Trichocerca sp. Lamark	1.6 (0.004)	*Pompholix sulcata* (Hudson)	1.7 (0.01)
Euchelanis sp. Ehrb.	1.3 (0.003)	*Filinia* sp. Bory de St. Vincent	1.0 (0.01)
Collotheca sp. Harring	1.1 (0.003)		
Cladocera		Cladocera	
Ceriodaphnia quadrangula (Müller) (Ceri.)	4108.7 (12.0)	*Ceriodaphnia pulchella* Sars (Ceri.)	4078.7 (30.0)
Daphnia longispina	279.8 (0.9)	*Daphnia longispina* (Müller) (Daph.)	1093.5 (8.1)
Chydorus sphaericus Müller	29.7 (0.1)	*Diaphanosoma brachyurum* Liéven (Diap.)	355.3 (2.6)
Alona sp.	28.2 (0.1)	*Bosmina longirostris* Müller (Bosm.)	172.8 (1.3)
Alona costata Sars		*Daphnia pulex* Leydig	30.6 (0.2)
Alona rectangula Sars		*Alona* sp.	9.9 (0.1)
Alona quadrangularis Müller		*Alona costata*	
Bosmina longirostris Müller	14.7 (0.04)	*Alona rectangula*	
Simocephalus sp. Schoedler	2.6 (0.01)	*Alona quadrangularis*	
		Chydorus sphaericus	3.2 (0.02)
Copepoda		Copepoda	
Tropocyclops prasinus (Fisher) (Tpra.)	6094.4 (17.8)	*Copidodiaptomus numidicus* Gurney (Copi.)	4457.3 (32.8)
Nauplii (Naup.)	4414.3 (12.9)	Nauplii (Naup)	1072.2 (7.9)
Eucyclops serrulatus (Fisher)	25.2 (0.1)	*Acanthocyclops robustus* Sars (Acan.)	167.0 (1.2)
Macrocyclops albidus (Jurine)	10.8 (0.03)		

[a] Abbreviations used in CCA are indicated in parenthesis

[b] Values are presented as mean densities (ind m^{-3}); the percentage of occurrence is given in parenthesis

reservoir. Most zooplanktons, *Ceriodaphnia* and *T. prasinus* included, can only consume particles smaller than 20 μm (Lampert and Sommer 1997). These assemblage patterns are typical of reservoirs subjected to periodic water level variations (see Armengol et al. 1988; Schmid-Araya and Zuñiga 1992; Błedzki and Ellinson 2000). According to those authors, the above-mentioned species have adaptive advantages in disturbed environments not only on account of their feeding behaviour, but also because they are r-strategists, thereby having shorter generation times and a greater tolerance to large amounts of organic matter in the water. An exception was *Conochilus* which, according to Sladeček (1983), is typical of environments poor in organic matter. This taxon is subsequently replaced by taxa typical of more eutrophic environments. CCA revealed that zooplankton assemblage patterns might be significantly associated with three kinds of environmental variables: (1) stored water volume; (2) those whose changes seemed to be directly

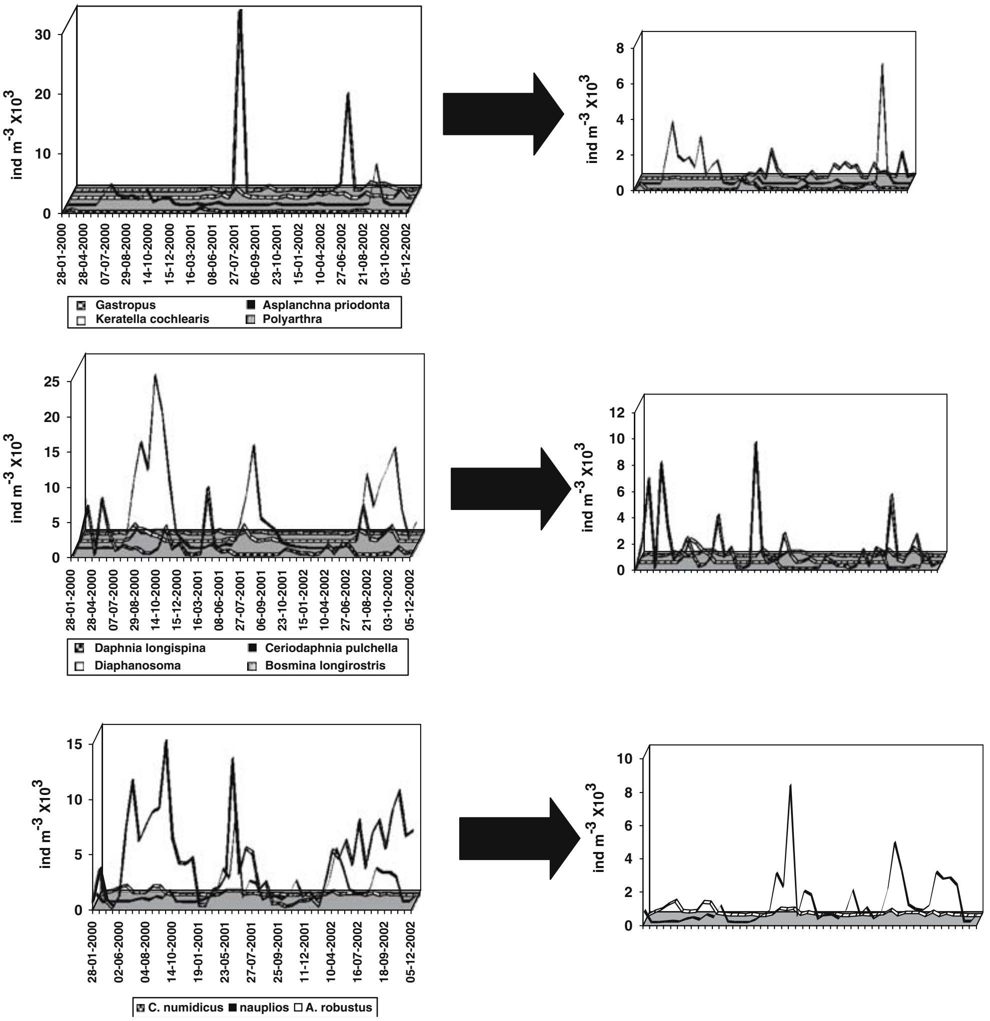


Fig. 4 Annual variation of zooplankton abundance and composition in the Azibo Reservoir. Graphics on the *right* are without the taxon with the largest density peaks

influenced by water level fluctuations (e.g. nutrient concentrations); (3) those also varying seasonally, although independently of water level fluctuations (e.g. temperature). However, zooplankton seasonal succession could have been related not only to changes in environmental variables, whether caused by water level variation or not, but also to changes in biotic parameters (e.g. in phytoplankton assemblage). In fact, according to Geraldes and Boavida (2005) *Monoraphidium*, *Cyclotella* and *Tabellaria* were dominant during the maximum water level phase, whereas *Peridinium*, *Cosmarium*, *Anabaena*, *Staurastrum*, *Crucigenia* and *Scenedesmus* were more abundant during the minimum level phase. Therefore, since a wide range of physical, chemical and biological complex interactions are likely to influence zooplankton assemblages, it is necessary to be cautious when relating the changes observed in the present study to variations in the water level/stored water volume.

In the absence of chronological data, it is difficult to relate reservoir age to zooplankton assemblage patterns. However, it is plausible to suggest that zooplankton assemblage structure could also be a consequence of reservoir age (e.g. Pinel-Alloul and Méthot 1984; Robarts et al. 1992). As this is a recently formed reservoir, a climax community had most likely not yet established at the time of this study.

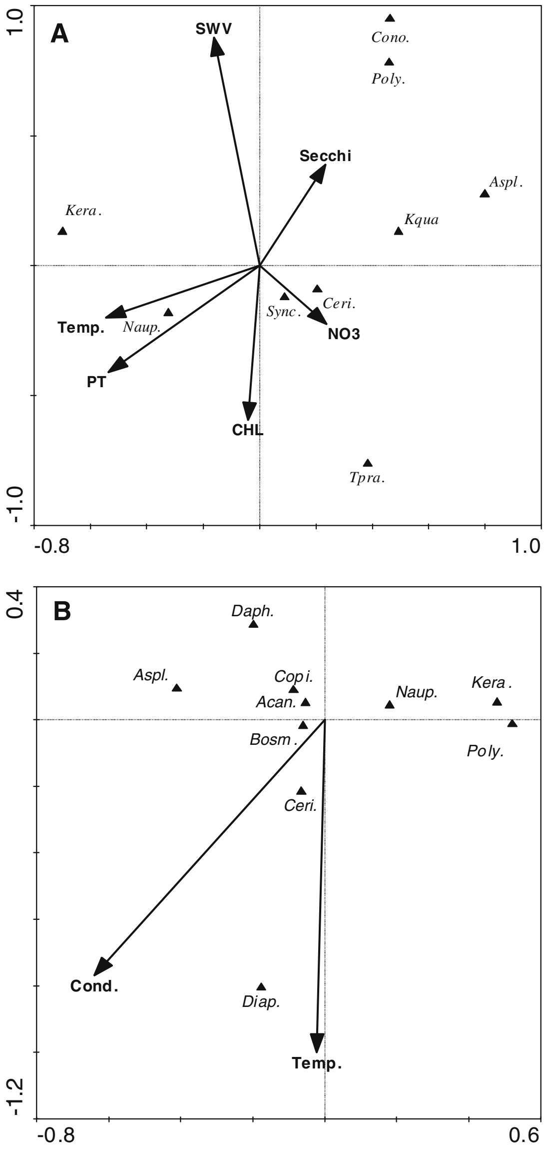


Fig. 5 Results of the CCA: S. Serrada (**A**), Azibo (**B**). Species abbreviations are shown in Table 4

Azibo Reservoir

In Azibo internal disturbance caused by water level fluctuations seems to be minimal. Consequently, changes in environmental variables (nutrient concentrations and water transparency, among others) were not very accentuated. The increase in mean TP concentrations during the late spring/summer months were probably caused by: (1) particle transportation by wind from reservoir surroundings (see Cole et al. 1990); (2) the senescence of emergent macrophytes that colonise some shallow areas of the reservoir (see James and Barko 1991). Zooplankton assemblage patterns seemed to be significantly associated only with conductivity and temperature. Geraldes and Boavida (2004a, b) observed that seasonal succession in zooplankton assemblage was strongly influenced by temperature. In support of their results, we found that during the winter and early spring months *Daphnia* was dominant and *Ceriodaphnia* was virtually absent. After this period, *Daphnia*'s population decreased to undetectable levels, while concurrently*Ceriodaphnia*'s population increased to its maximum density, becoming dominant from July to September. During this period *Daphnia* was not detected in samples, indicating that it was present at extremely low densities. Lynch (1978) also observed the replacement of *Daphnia* by *Ceriodaphnia* during the summer and attributed this phenomenon to the better efficiency of *Ceriodaphnia* to feed at temperatures above 20°C. *Diaphanosoma* was only detected during the summer, and this species is typical of warm water, being largely confined to mid- or late-summer in seasonal temperate lakes (Hart 2000). However, zooplankton assemblage features can be not only a consequence of low disturbance and temperature but also a consequence of fish assemblage shift and/or reservoir age. According to several authors, large zooplankton are especially susceptible to fish predation (Beklioglu and Moss 1996; Caramujo et al. 1997; Lampert and Sommer 1997). Siegfried and Kopache (1984) observed that the increased predation by 0+ fish and by planktivorous fish at the beginning of summer led to a decline in the *Daphnia* population. Up to the 1980s cyprinid fish were dominant in Azibo (Formigo 1990). Consequently, they could have had some impact on the cladoceran and copepod assemblages. Vasconcelos (1990a, b) reported that at this time the zooplankton assemblage was dominated by rotifers, which may be evidence of the existence of a considerable predation pressure by fish. Cyprinids are not strictly planktivorous, but they can have some impact on *Daphnia* and on other large-bodied zooplankton in some lakes and reservoirs (Winfield and Townsend 1992). However, the introduction of pike (*Esox lucius*) in the 1990s led to an accentuated decrease in the resident cyprinid fish densities. Therefore, the impact of cyprinid predation on cladoceran and copepod assemblages might have been minimised. On the other hand, pike alevins feed on *Daphnia* and copepods during the first few weeks of life, after absorbing the yolk sac and before being able to feed on macroinvertebrates and, subsequently, fish (Hunt and Carbine 1951). In this way, very young pike might have a very small temporary impact on cladoceran and copepod assemblages. However, it is difficult to assess if this shift in zooplankton assemblage was induced by changes in the fish assemblage or caused by other factors, such as the increasing age of the reservoir and the ''stabilisation'' of environmental conditions.

Conclusions

The present results suggest the following conclusion: even though conductivity, water temperature, nutrients and variations in the stored water volume (in S. Serrada) can explain some of the variability, abundance and composition of zooplankton, it is plausible to hypothesise that other factors, such as the age of the reservoirs and biotic interactions, could also play an important role in the structuring of those assemblages. However, the data obtained in this study do not provide an objective answer to these hypotheses. Therefore, complementary field work and experimental research should be carried out. There is a lack of long-term data on environmental variation patterns and their influence on biotic community dynamics. Furthermore, it is important to understand to what extent shifts in reservoir dynamics (mainly in the biotic components) are induced by water fluctuations and/or by seasonal factors acting independently of water fluctuations. Such data are fundamental to develop predictive water quality models adapted to this particular area, rendering possible the development of correct management practices with a multipurpose use perspective for the reservoir and its catchment. In addition, this data will add to the understanding of the limnology of reservoir ecosystems influenced by the Mediterranean climate.

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