Local and regional factors influencing zooplankton communities in the connected Kasseb Reservoir, Tunisia

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Abstract

Associations between zooplankton community structure and abiotic (temperature, dissolved oxygen, turbidity, nutriments) and biotic factors (chlorophyll *a* and phytoplankton community) were examined, in Kasseb Reservoir, northern Tunisia. Samples were taken bimonthly from July to December 2002 at 3 sampling stations (deepest station: Station 1, Brik River: Station 2 and M'Zaz Stama River: Station 3). From our results it is evident that zooplankton exhibit seasonally and spatially heterogeneous distribution. The highest density of zooplankton was recorded in September at a depth of 5 m (10.8×10^3 ind·ℓ$^{-1}$). At Station 1 cyclopoid copepods (65% of total abundance) were the most abundant group followed by Cladocera (21% of total abundance). At Station 2 (93% of total abundance) and Station 3 (98% of total abundance) cyclopoid copepods were numerically dominant throughout the study period. Canonical correspondence analysis (CCA) was used to estimate the influence of abiotic and biotic factors in structuring the zooplankton assemblage. Zooplankton abundance was negatively correlated with turbidity (r= -0.381, P <0.05). The results also suggest that both local (environmental parameters, competition, and predation) and regional (hydrologic connections and dispersal) factors have a significant effect on both species richness and community structure of zooplankton in Kasseb Reservoir. The presence of zooplankton species considered to be indicators of eutrophic status confirmed the high trophic levels of Kasseb Reservoir.

Keywords: Kasseb Reservoir, hydrologic connections, local and regional factors, zooplankton, heterogeneous distribution

Introduction

The Kasseb Reservoir is an important feature of Tunisia, and was built to serve a multitude of purposes, such as hydroelectric production, irrigation, and, principally, drinking water supply (30% of the population of Tunis city). The Kasseb Reservoir is directly connected to Ghdir El Goulla Reservoir (see Sellami et al., 2009).

In freshwater ecosystems the filter-feeding zooplankton play an important role in the production of the clear-water phase (Lair and Ayadi, 1989; Edmondson, 1991; Lampert and Sommer, 1997; Stella et al., 2007). These organisms are important in the structuring and dynamics of aquatic environments, as is their fundamental role in aquatic food chains (Cadjo et al., 2007) and nutrient cycling (Lansac-Tôha et al., 1997; Velho, 2000; Gillooly and Dodson, 2000). The factors affecting community composition and species diversity are often divided into 2 general categories: local processes (e.g., environmental heterogeneity and species interactions) and regional processes (e.g., dispersal, connectivity) (Ricklefs, 1987; Mouquet and Loreau, 2003; Holyoak et al., 2005). Some important local factors influencing zooplankton species richness and abundance have been identified: lake area and primary productivity (Dodson, 1991; 1992; Dodson et al., 2000), water quality (Jeppesen et al., 2000; Cottenie et al., 2001), lake depth (Keller and Conlon, 1994), latitude (Hebert and Hann, 1986), acidity (Brezonik et al., 1984; Locke, 1992), nutrients (Leibold, 1999; Jeppesen et al., 2000), toxins (Yan et al., 1996), climate (Stemberger et al., 1996), predation and competition (Brooks and Dodson, 1965; Shurin, 2000; Fernández-Rosado and Lucena, 2001; Isari et al., 2007; Larson et al., 2009). Connectivity can influence several community properties, such as local and regional diversity, and secondary productivity (e.g., Cottenie et al., 2001; Gonzalez and Chaneton, 2002; Cottenie and De Meester, 2004; Vanschoenwinkel et al., 2007). The connectivity of ecosystems is expected to influence dispersal rates and induce passive dispersal within meta-communities (Doi et al., 2010).

Abiotic and biotic processes commonly also cause lake-wide distributions of plankton to be highly variable and heterogeneous, resulting in considerable patchiness (Folt and Burns, 1999). Heterogeneous distributions of zooplankton originate from various processes, some of which can be attributed to internal factors; that is, they are related to the activity and swimming behaviour of the animals (Folt and Burns, 1999). Other causes are linked to external factors, which force organisms to be transported passively, such as by wind-driven currents (George and Edwards, 1976; George and Winfield, 2000; Rinke et al., 2006; 2009).

To our knowledge, no published research has previously addressed these issues in Mediterranean ecosystems that have been artificially connected by human alteration. We therefore conducted a study to test the hypothesis that anthropogenic influence on the connectivity of ecosystems would affect

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Received 19 February 2010; accepted in revised form 8 March 2011.

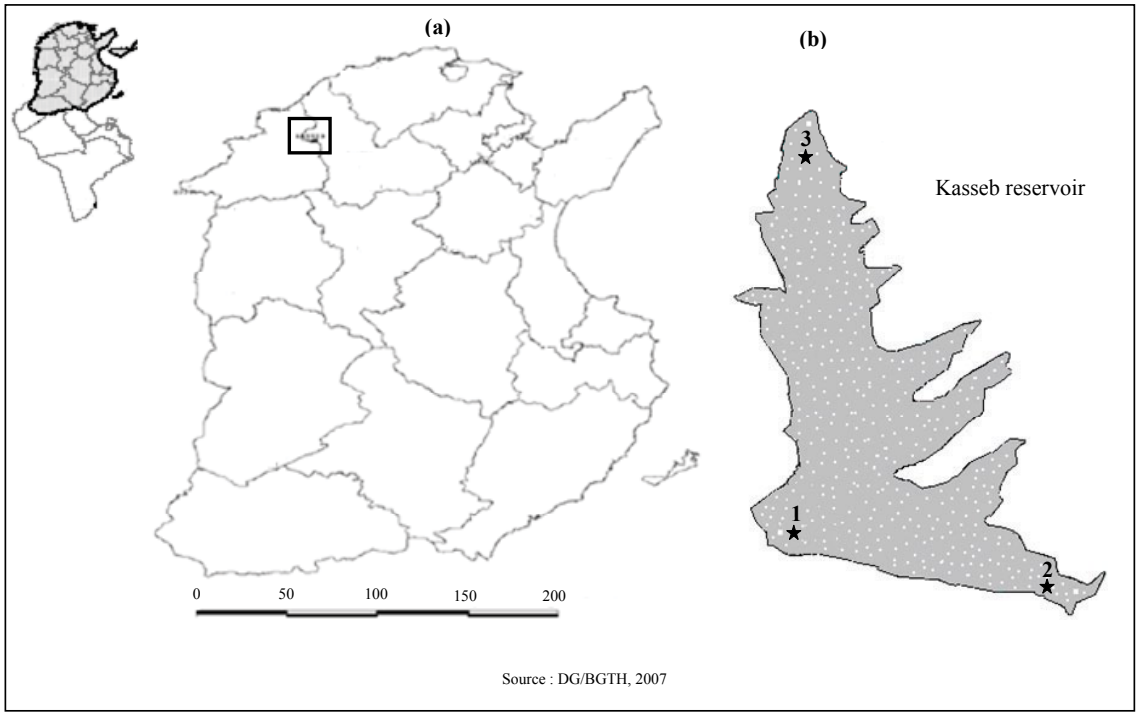

Figure 1
Location of the Kasseb Reservoir (a); sampling stations (b) Station 1: deepest area, Station 2: Brik River, Station 3: M'Zaz Stama River

zooplankton community dynamics. In Kasseb Reservoir, the artificially connected system, zooplankton communities were related to different local and regional variables, in order to determine the important structuring variables. We studied the vertical and horizontal heterogeneity of zooplankton communities in this reservoir, in order to define the principal factors responsible for zooplankton distribution.

Materials and methods

Study site

Kasseb Reservoir (K) is situated 18 km north-west of Beja city (between 36°45′30″N and 09°00′50″E) (Fig. 1). This reservoir receives water through the Brik (north- eastern part of Kasseb Reservoir, 27.9 km^2) and M'Zaz Stama Rivers (western part of Kasseb Reservoir, 73.1 km^2), the catchments of which are densely populated, with the rivers mainly used for agricultural purposes. Morphometric and other basic characteristics are shown in Table 1.

Environmental variables

In this study, samples were taken bimonthly from 3 stations in Kasseb Reservoir, between July and December 2002. Two replicates were taken at each depth/station. The 3 stations were selected as follows: Station 1 located at the deepest area, Station 2 (Brik River) and Station 3 (M'Zaz Stama River) located at nearly 25 and 35 km, respectively, from the deepest area. Water samples were collected at the surface, -5 m, -10 m, -20 m (near the bottom) at Station 1 and close to the surface at Station 2 and Station 3, with a 1 ℓ Van Dorm bottle, simultaneously for physical and chemical analyses (Fig. 1).

Water temperature was measured with a mercury glass thermometer. The dissolved oxygen concentration was measured by means of Winkler methods (Rodier, 1984). The turbidity was measured with a portable turbidimeter. Total nitrogen was assayed after oxidation to the nitrate form in an alkaline medium, using potassium persulphate. The nitrate assay was based on the formation, in a concentrated sulphuric acid medium, of a phenol disulphonic acid derivative (D'Elia et al., 1977). The total phosphorus concentrations were determined after mineralising the samples using the colorimetric protocol of Murphy and Riley (1962).

Biological variables

Phytoplankton

For phytoplankton cell counts (Fathalli, 2004), water was taken using a 1 ℓ Van Dorn bottle and fixed with Lugol solution

Table 1
Morphometric and hydrologic characteristics of the Kasseb Reservoir

Location	North-west of Beja city
Latitude	36°45′30″N
Longitude	09°00′50″E
Construction	1 969
Surface area (ha)	435
Volume (million m^3)	82
Catchments area (km^2)	101
Water temperature (°C)	18.6
Annual mean precipitation (mm)	631
Annual mean evaporation (mm)	1 678
Wind (m·s^{-1})	2.9

Available on website http://www.wrc.org.za
ISSN 0378-4738 (Print) = Water SA Vol. 37 No. 2 April 2011
ISSN 1816-7950 (On-line) = Water SA Vol. 37 No. 2 April 2011

(Schwoerbel, 1986) for counting, according to Utermöhl (1958). The taxonomic identification was done according to Bourrelly (1966; 1968; 1985), Baker (1991; 1992) and Shameel (2001). Sub-samples (0.5 ℓ) for quantification of chlorophyll *a* were filtered using Whatman GF/C filters (0.45 µm pore size filter and 25 mm- diameter) and the quantity of pigments was determined using a fluorometric method (Welschmeyer, 1994) after a methanol extraction (Herbland et al., 1985).

Zooplankton

Zooplankton samples were collected by filtering 50 ℓ (with a 1 ℓ Van Dorn bottle) through a Juday plankton net (mesh size 55 µm), preserved with 4% formalin and coloured with Bengal Pink. Two replicates were taken at each depth/station. The samples were only collected during the day – diel vertical migrations of zooplankton were not considered in this study. Therefore the abundance of the zooplankton may be underestimated. The zooplankton were identified and counted under a Leica binocular microscope, in Dolffus chambers. The taxonomic identification was carried out according to Amoros (1984), Margaritora (1985), Korovchinsky (1992), Dussart (1969) and Stella (1982). The zooplankton density was expressed as the number of individuals per sample volume (ind·ℓ$^{-1}$). The zooplankton community structure was studied by calculating the species diversity index H' (bits ind·ℓ$^{-1}$) (Shannon and Weaver, 1949); it is the most popular index (Andronikova, 1993).

This index was calculated from the density of zooplankton species:

$$H' = -\sum_{i=1}^{S} \frac{n_i}{N} \times \log_2 \frac{n_i}{N}$$

where:

*n*i is the density of i species

N is the density of the entire community, respectively.

Statistical analysis

Canonical correspondence analysis (CCA) was applied to physical (water temperature and dissolved oxygen), chemical (total nitrogen and total phosphorus) and biological parameters (chlorophyll *a*, phytoplankton and zooplankton) assessed over 12 observations. Simple log (x + 1) transformation was applied to data in order to correctly stabilise the variance (Frontier, 1973). Pearson's correlation coefficient was calculated to determine the association between the physico-chemical variables and the zooplankton community (Zar, 1999). A multiple regression was applied in order to investigate what variables may predict zooplankton abundance. A procrustes analysis was performed for the phytoplankton and zooplankton abundances. Additionally, an independent 1-way ANOVA was run to assess the effect of the temporal and spatial variation on zooplankton density.

Results

Environmental parameters

The water temperature in the Kasseb Reservoir varied from 12°C, in December along the water column, to 28°C, in September at the surface (mean ± s.d. = 19.6 ± 5.1°C) (Fig. 2a), with spatial and temporal fluctuations typical to those of a warm monomictic reservoir. The temperature of the water column increased markedly from July to September. At other stations the water temperature showed a maximum in August (Station 3; 29.5°C). The minimum values were recorded in December (12°C) for all stations (Fig. 2b). The values for dissolved oxygen concentration measured at the surface were 8.8 ± 1.5 mg·ℓ$^{-1}$ (at Station 1), 8.4 ± 0.5 mg·ℓ$^{-1}$ (at Station 2) and 7.6 ± 0.3 mg·ℓ$^{-1}$ (at Station 3). In the deepest area, turbidity ranged from 1.6 NTU, in August at a depth of 10 m, to 44.6 NTU in December at a depth of 10 m (mean ± s.d. = 10.8 ± 10.7 NTU) (Fig. 3a). However, for Station 3 the maximum value of 229 NTU was reported in December (Fig. 3b). The total nitrogen concentrations varied from 0.5 mg·ℓ$^{-1}$ in September at a depth of 10 m to 10.9 mg·ℓ$^{-1}$ in December at a depth of 5 m (mean ± s.d. = 2.5 ± 3.4 mg·ℓ$^{-1}$) (Fig. 4a). The highest total nitrogen concentration was recorded in December at Station 2 (27.4 mg·ℓ$^{-1}$) (Fig. 4b). The highest values for total nitrogen concentration were probably the result of inputs arriving at the reservoir from the surface of each catchment. At Station 1, the total phosphorus concentrations fluctuated between 0.003 mg·ℓ$^{-1}$ in September at a depth of 20 m and 0.2 mg·ℓ$^{-1}$ in August at a depth of 10 m (mean ± s.d. = 0.06 ± 0.04 mg·ℓ$^{-1}$) (Fig. 5a). For the other 2 stations, the maximum total phosphorus concentration was registered in December at Station 3 (0.1 mg l^{-1}) (Fig. 5b). Significant differences between stations were found for dissolved oxygen ($F = 3.91$, df = 35, $P = 0.05$) and turbidity ($F = 3.76$, df = 35, $P = 0.05$). Temperature ($F = 5.28$, df = 11, $P = 0.05$), total nitrogen ($F = 5.53$, df = 11, $P = 0.05$) and total phosphorus ($F = 6.04$, df = 11, $P = 0.05$) differed significantly between months (Table 2).

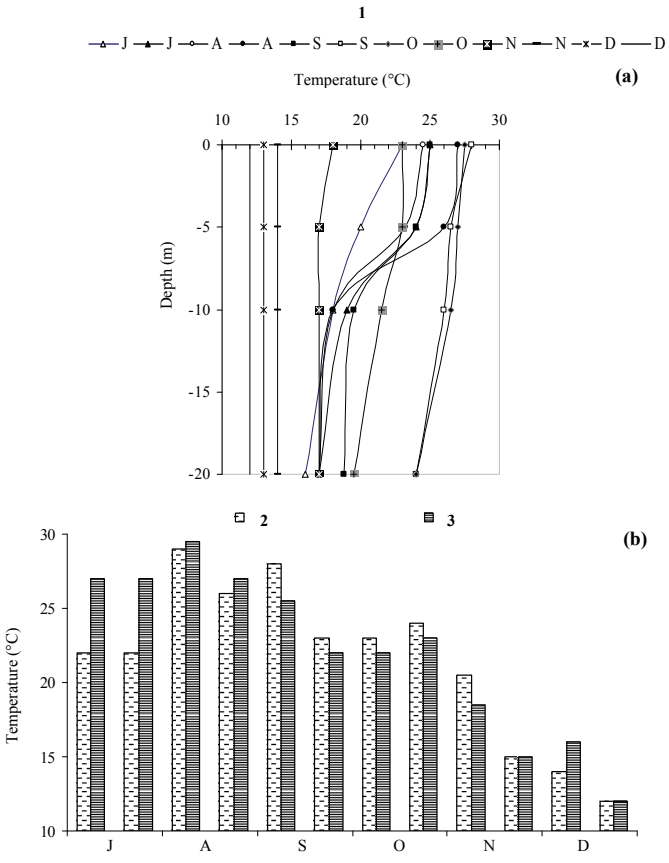

Figure 2

Spatial and temporal variation of temperature: along the water column at Station 1 (a) and at Stations 2 and 3 (Brik and M'Zaz Stama Rivers) (b) in Kasseb Reservoir

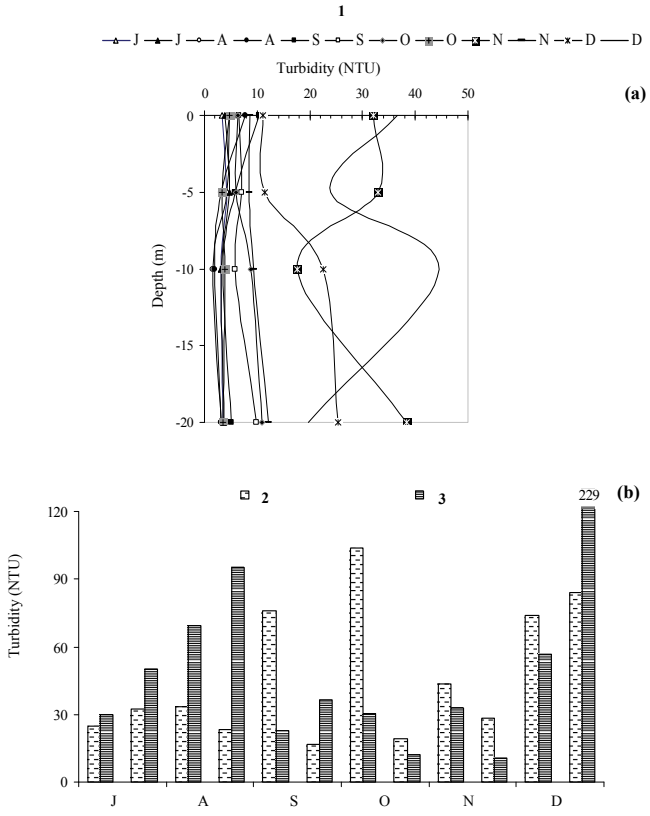

Figure 3
Spatial and temporal variation of the turbidity along the water column at Station 1 (a) and at Stations 2 and 3 (Brik and M'Zaz Stama Rivers) (b) in Kasseb Reservoir

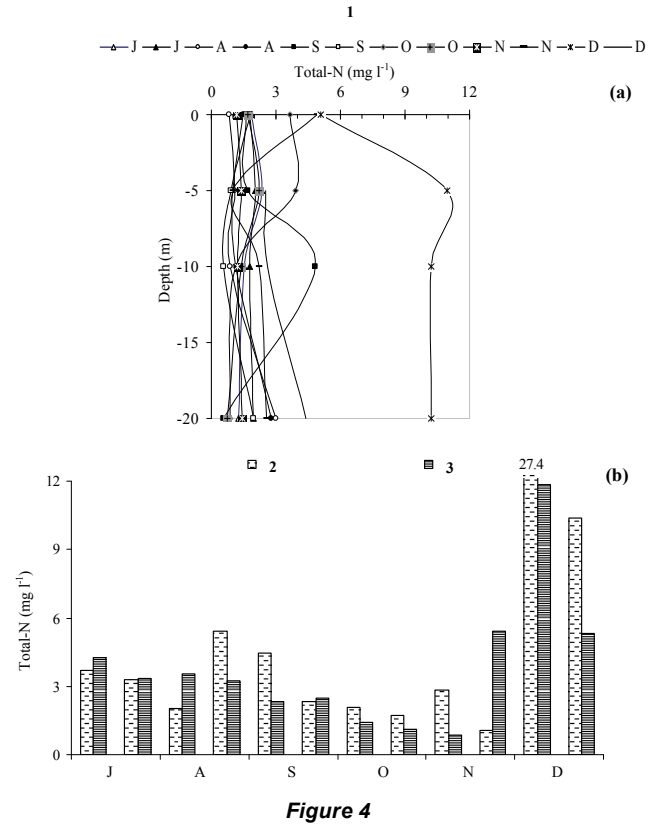

Figure 4
Spatial and temporal variation of the total nitrogen along the water column at Station 1 (a) and at Stations 2 and 3 (Brik and M'Zaz Stama Rivers) (b) in Kasseb Reservoir.

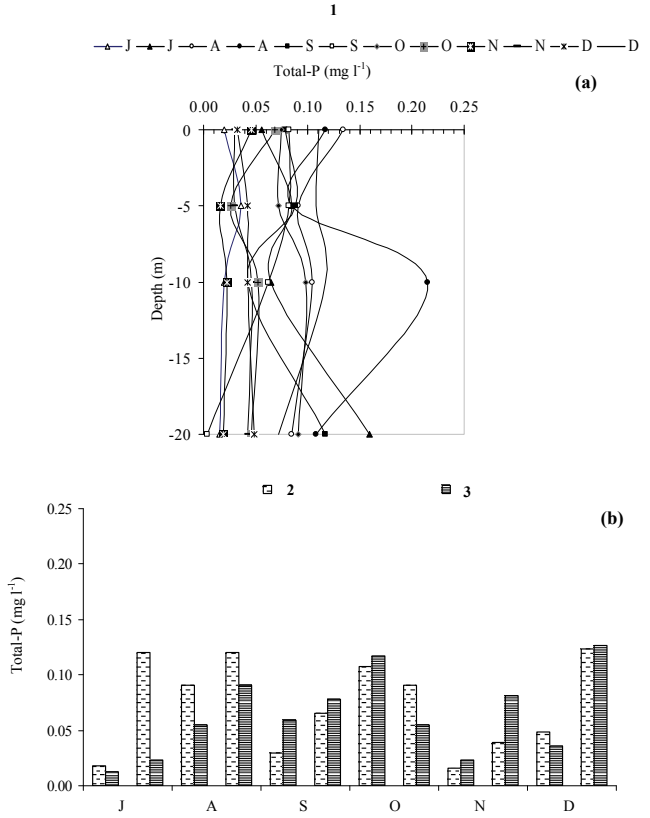

Figure 5
Spatial and temporal variation of the total phosphorus along the water column at Station 1 (a) and at Stations 2 and 3 (Brik and M'Zaz Stama Rivers) (b) in Kasseb Reservoir

Spatial and temporal distribution of phytoplankton

For the 7 groups of phytoplankton, 66 species were identified from the samples at the 3 stations (Table 3). Numerous phytoplankton species were distributed among the major taxonomic categories as follows: Chlorophyta 29, Bacillariophyceae 11, Dinophyceae 5, Chrysophytes1, Cryptohyceae 1, Cyanophyceae 15 and Euglenophyceae 4. The contribution to total cell phytoplankton density was: Bacillariophyceae 59%, Chlorophyta 22%, cyanobacteria 15% and other taxa 4% (Fathalli, 2004). The phytoplankton community was more abundant at Station 2 than at other stations. At Station 2 total density varied from 0.1×10^6 in early December to 5.9×10^6 cells·ℓ$^{-1}$ in early August (mean ± s.d. = $1.9 \times 10^6 \pm 1.8 \times 10^6$ cells·ℓ$^{-1}$) (Fig. 7a). Bacillariophyceae (75% of the total phytoplankton abundance) were numerically dominated by the species *Cyclotella ocellata* (64.6% of the total abundance).

At Station 1, the total phytoplankton abundance ranged from 0.1×10^6 cells·ℓ$^{-1}$ in July at a depth of 20 m to 5.7×10^6 cells·ℓ$^{-1}$ in early August in the surface (Fig. 6a) (mean ± s.d. = $1.3 \times 10^6 \pm 1.3 \times 10^6$ cells·ℓ$^{-1}$). Bacillariophyceae was the dominant group, accounting for 73% of the total phytoplankton abundance (Fig. 8a). The most abundant species was *Cyclotella ocellata* (79.2% of the total abundance). At Station 3, the total phytoplankton density ranged from 0.2 $\times 10^6$ at end- November to 3.0×10^6 cells l·ℓ$^{-1}$ at end- August (mean ± s.d. = $1.4 \times 10^6 \pm 1.0 \times 10^6$ cells·ℓ$^{-1}$) (Fig. 7b). Bacillariophyceae (67% of the total phytoplankton, Fig. 8c) were largely dominated by the species *Cyclotella ocellata*

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ISSN 0378-4738 (Print) = Water SA Vol. 37 No. 2 April 2011
ISSN 1816-7950 (On-line) = Water SA Vol. 37 No. 2 April 2011

Table 2
Physical and chemical parameters (mean ± sd) in the three stations of the Kasseb reservoir from July to December 2002

Parameters	Stations			F (df)	F′ (df)
	1	2	3		
Temperature (°C)	19.7 ± 4.7	19.7 ± 8.2	19.8 ± 8.2	0.001 (35)	5.28*** (11)
Dissolved oxygen (mg·ℓ$^{-1}$)	8.8 ± 1.9	6.4 ± 3.9	5.1 ± 3.8	3.91* (35)	1.28 (11)
Turbidity (NTU)	10.8 ± 10.6	44.6 ± 32.1	53.8 ± 61.4	3.76* (35)	1.49 (11)
Total nitrogen (mg·ℓ$^{-1}$)	2.7 ± 2.5	5.3 ± 7.5	3.4 ± 3.1	0.87 (35)	5.53*** (11)
Total phosphorus (mg·ℓ$^{-1}$)	0.08 ± 0.04	0.07 ± 0.04	0.06 ± 0.04	0.64 (35)	6.04*** (11)

F-value: between-groups mean square/within-groups mean square.
*Values in the same row showing the same letters are significantly different as tested with one-way ANOVA (F between stations, F′ between months) (p < 0.05 *; p < 0.01**; p < 0.001***).*

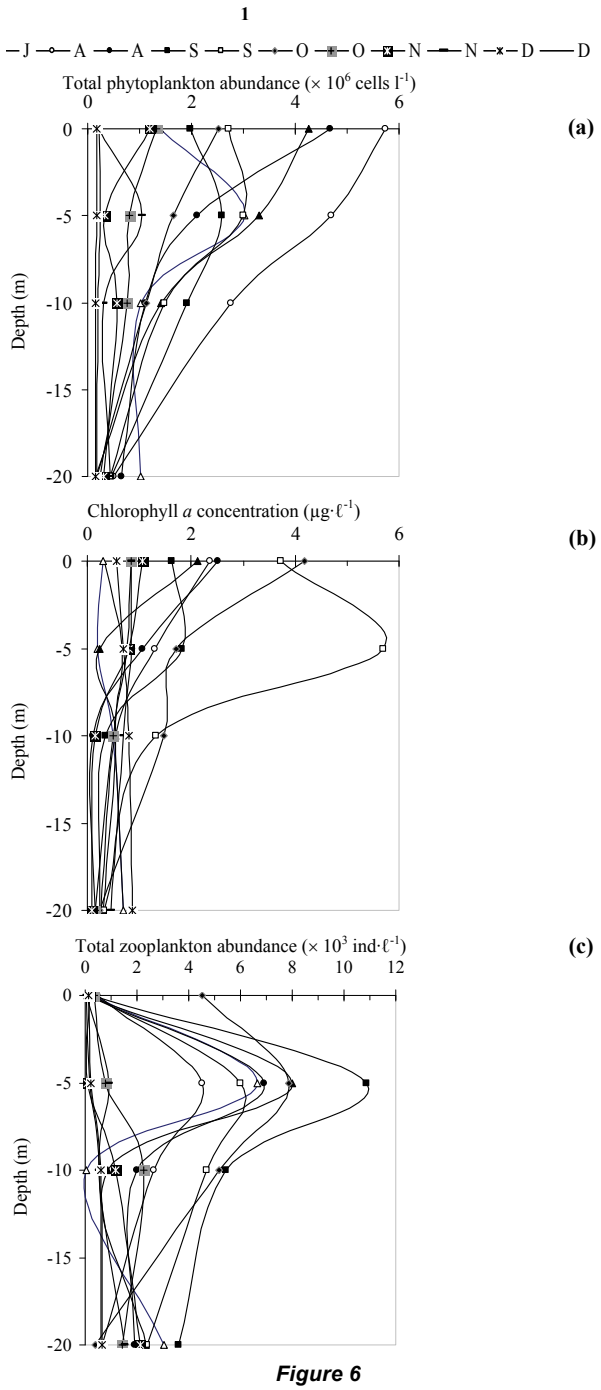

Figure 6
Spatial and temporal distribution of total phytoplankton (a), chlorophyll a (b) and zooplankton total (c) along the water column at Station 1 in Kasseb Reservoir

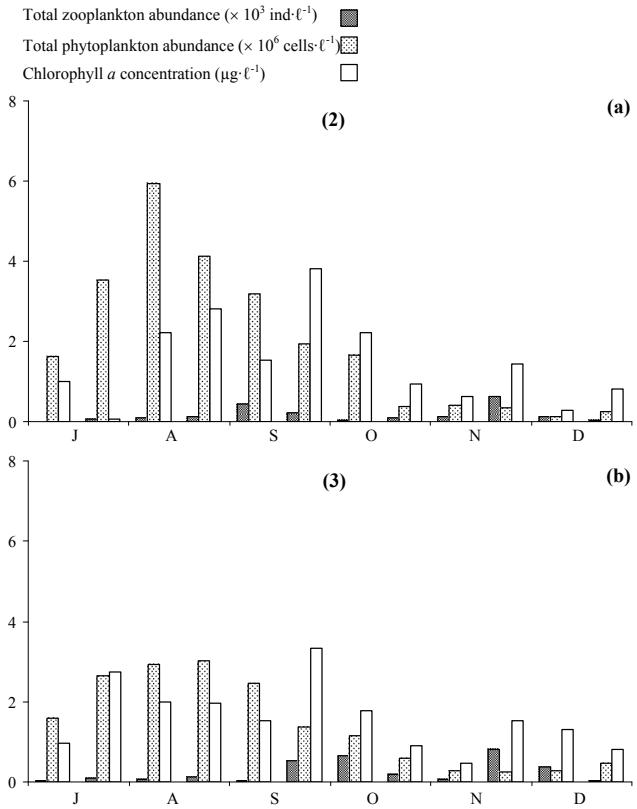

Figure 7
Spatial and temporal distribution of total zooplankton, total phytoplankton at Station 2 (Brik River) (a) and Station 3 (M'Zaz Stama River) (b) in Kasseb Reservoir

(75% of the total phytoplankton abundance). Chlorophyta were present throughout the study period reaching peaks of 1.6 × 10^6 cells·ℓ$^{-1}$ (at Station 1, Fig. 8a), 0.8 × 10^6 cells·ℓ$^{-1}$ (at Station 2, Fig. 8 b) and 0.7 × 10^6 cells·ℓ$^{-1}$ (at Station 3, Fig. 8c) at the end of September and associated with the development of *Oocystis borgei* (35% of the total phytoplankton abundance). Cyanobacteria reached a peak at the end of August (1.2 × 10^6 cells·ℓ$^{-1}$ in Station 1, Fig. 8a); due to the proliferation of the species *Hydrococcus rivularis* (90% of the total phytoplankton abundance).

Chlorophyll *a* concentrations ranged from 0.07 µg·ℓ$^{-1}$ in November at a depth of 20 m to 5.7 µg·ℓ$^{-1}$ in September at a depth of 5 m (Fig. 6b) (mean ± s.d. = 1.0 ± 1.1 µg·ℓ$^{-1}$). The highest chlorophyll *a* concentration was found at Station 2 (3.8 µg·ℓ$^{-1}$ in September) (Fig. 7a).

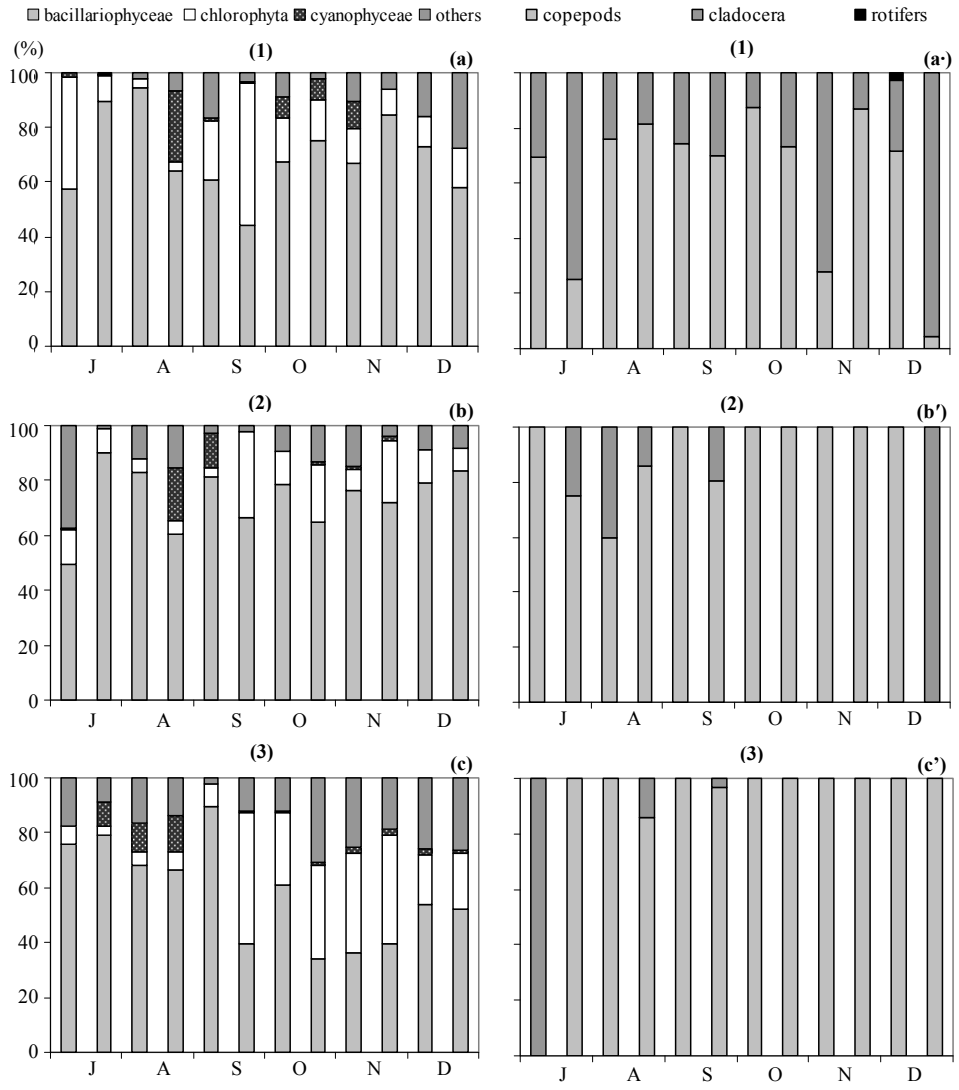

Figure 8
Spatial and temporal distribution of phytoplankton and zooplankton groups in the three stations of Kasseb reservoir (Fathalli, 2004)

Spatial and temporal distribution of zooplankton

A total of 4 cladocerans (*Bosmina longirostris*, *Diaphanosoma brachyurum, Daphnia longispina,* and *Ceriodaphnia quadrangula*), 3 copepods (*Copidodiaptomus numidicus*, *Eudiaptomus* sp., and *Acanthocyclops* sp.) and 1 rotifer (*Keratella quadrata*) were found in Kasseb Reservoir (Table 3). At Station 1, cyclopoid copepods (65% of total abundance) were the most abundant group (*Acanthocyclops* sp., 67.3% of total abundance), followed by Cladocera (21% of the total zooplankton abundance), which was represented by the species *Bosmina longirostris* (32.6% of the total zooplankton abundance). At Station 2 (93% of total abundance) and Station 3 (98% of the total zooplankton abundance) cyclopoid copepods (*Acanthocyclops* sp.) were numerically dominant throughout the study period. Calanoid copepods were absent at Station 2. The species *Eudiaptomus* sp., *Ceriodaphnia quadrangula* and *Keratella quadrata* were present only at Station 1. Significant differences between stations and months were found for the abundances of the following species: *Acanthocyclops* sp. ($F = 12.7$, df = 35, $P = 0.001$; $F = 6.57$, df = 11, $P = 0.01$), *Eudiaptomus* sp. ($F = 6.26$, df = 35, $P = 0.001$), *Bosmina longirostris* ($F = 3.25$, df = 35, $P = 0.05$), *Diaphanosoma brachyurum* ($F = 6.76$, df = 35, $P = 0.01$; = 3.01, df = 35, $P = 0.01$), *Daphnia longispina* ($F = 5.22$, df = 35, $P = 0.01$; F =3.59, df = 35, $P = 0.01$) and *Ceriodaphnia quadrangula* ($F = 11.24$, df = 35, $P = 0.001$; $F = 4.91$, df = 35, $P = 0.05$) (Table 4).

At Station 1, the total zooplankton abundance varied from 0.04×10^3 ind·ℓ$^{-1}$ in July at a depth of 10 m to 10.8×10^3 ind·ℓ$^{-1}$ in early September at a depth of 5 m (mean ± s.d. = $2.2 \times 10^3 \pm 2.6 \times 10^3$ ind·ℓ$^{-1}$) (Fig. 6c). The zooplankton abundance was significantly positively correlated with water temperature ($r = 0.779$, $P < 0.01$), and with dissolved oxygen ($r = 0.578$, $P < 0.05$) and significantly negatively correlated with turbidity ($r = -0.381$, $P < 0.05$). The zooplankton community was dominated by the cyclopoid *Acanthocyclops* sp. (58 - 83% of the total zooplankton abundance, H'= 0.57 bits ind·ℓ$^{-1}$ to 1.59 bits ind·ℓ$^{-1}$) (Fig. 8a′, Fig. 9a, Fig. 10a), with the exception of late July, early November and late December, which were dominated by Cladocera: 75% (H'= 1.28 bits ind·ℓ$^{-1}$), 72% (H'= 1.29 bits ind·ℓ$^{-1}$) and 96% (H'= 0.47 bits ind·ℓ$^{-1}$) of the total zooplankton abundance, respectively. The species *Bosmina longirostris*

Available on website http://www.wrc.org.za
ISSN 0378-4738 (Print) = Water SA Vol. 37 No. 2 April 2011
ISSN 1816-7950 (On-line) = Water SA Vol. 37 No. 2 April 2011

Table 3
List of phytoplankton species in the Kasseb Reservoir from July to December 2002 (Fathalli, 2004)

Chlorophyta	**Dinophyceae**
Ankistrodesmus cf gelifactum	*Ceratium hirundinella*
Ankistrodesmus sp.	*Gymnodinium* sp.
Botryococcus braunii	*Peridiniopsis tompsonii*
Carteria conochili	*Peridinium* sp.
Chlamydomonas sp.	*Peridinium umbonatum*
Chlorella sp.	
Coelastrum microporum	**Cryptohyceae**
Coenocystis tapasteana	*Cryptomonas ovata*
Cosmarium sp.	
Cosmarium depressum	**Chrysophytes**
Eutetramorus fottii	*Dinobryon divergens*
Lagerheimia sp.	
Lagerheimia gvensis	**Euglenophyceae**
Oocystis borgei	*Euglena acus*
Oocystis gigas	*Euglena oxyuris*
Oocystis lacustris	*Euglena* sp.
Pediastrum boryanum	*Phacus* sp.
Planctonema lauterbornii	
Scenedesmus sp.1	**Cyanophyceae**
Scenedesmus sp.2	*Borzia trilocularis*
Scenedesmus acuminatus	*Hydrococcus rivularis*
Scenedesmus acunae	*Lyngbya rubida*
Scenedesmus acutus	*Lyngbya* sp.
Scenedesmus cf hortobagyi	*Merismopedia elegans*
Scenedesmus linearis	*Oscillatoria homogenea*
Scenedesmus quadricauda	*Oscillatoria lacustris*
Selenastrum sp.	*Oscillatoria planctonica*
Staurastrum paradoxum	*Oscillatoria*
Tetraedron minimum	*pseudogeminata*
	Oscillatoria sp.
Bacillariophyceae	*Oscillatoria tenuis*
Achnanthes sp.	*Phormidium cf*
Amphora sp.	*incrustatum*
Cyclotella ocellata	*Pseudoanabaena*
Cymbella sp.	*catenata*
Gyrosigma sp.	*Pseudoanabaena*
Navicula sp.1	*constricta*
Navicula sp.2	*Synechococcus elongatus*
Nitzschia acicularis	
Nitzschia longissima	
Nitzschia sp.	
Surirella cf capronii	

was responsible for the exceptional peak that occurred in late July, accounting for 56% of the total zooplankton abundance, whereas the species *Daphnia longispina* accounted for 74% and 97% of the total zooplankton abundance in early November and late December, respectively.

The total zooplankton abundance ranged between 0.01 × 10^3 ind·ℓ$^{-1}$ in early July and 0.6 × 10^3 ind·ℓ$^{-1}$ in late November (mean ± s.d. = 0.15 × 10^3 ± 0.18 × 10^3 ind·ℓ$^{-1}$) at Station 2

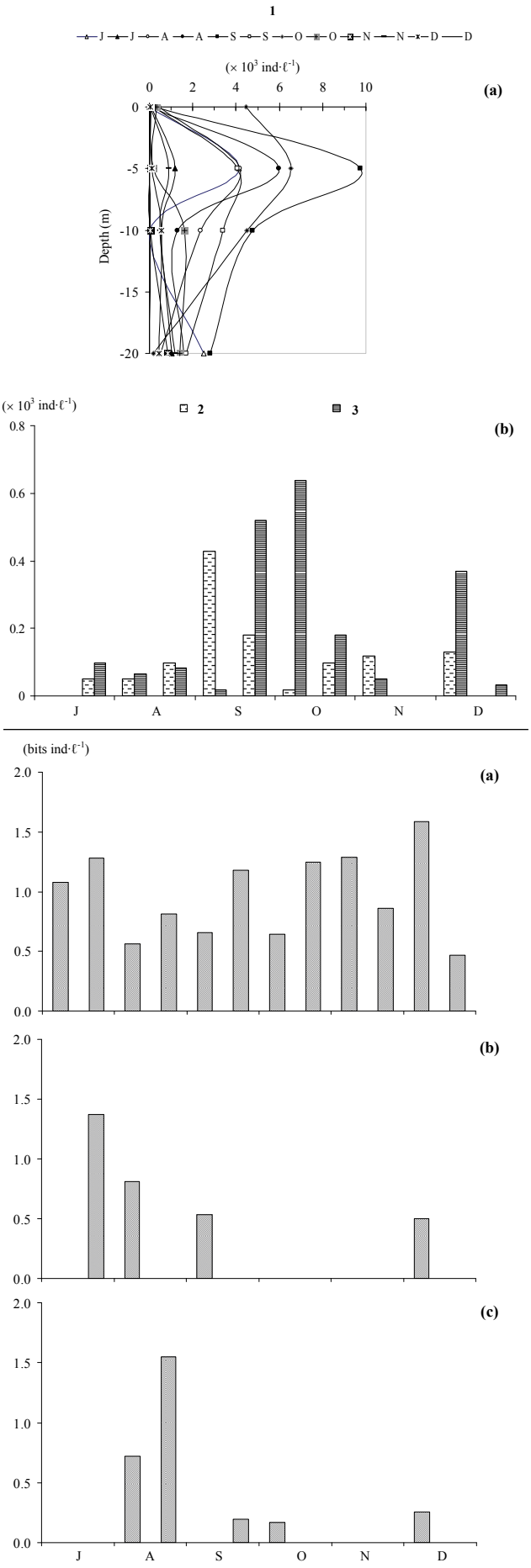

Figure 9 (top right)
Spatial and temporal distribution of Acanthocyclops sp. species along a water column at Station 1 (a) and at Stations 2 and 3 (Brik and M'Zaz Stama Rivers) (b) in Kasseb Reservoir

Figure 10 (bottom right)
Shannon and Weaver index (H') in the deepest area (a), Brik (b) and M'Zaz Stama (c) rivers

Table 4
Zooplankton species abundance (ind·ℓ$^{-1}$) in the three stations of the Kasseb reservoir from July to December 2002

Species	Stations			F (df)	F′ (df)
	1	2	3		
Copidodiaptomus numidicus	9.1 ± 30.0	0.0 ± 0.0	72.0 ± 246.8	1.00 (35)	0.92 (11)
Male	6.8 ± 23.4	0.0 ± 0.0	1.3 ± 4.6	0.83 (35)	0.98 (11)
Total female	0.8 ± 2.0	0.0 ± 0.0	2.7 ± 6.3	1.53 (35)	1.19 (11)
Female gravid	0.2 ± 1.2	0.0 ± 0.0	1.3 ± 4.6	0.71 (35)	0.84 (11)
Copepodites	0.6 ± 4.6	0.0 ± 0.0	65.4 ± 226.7	0.98 (35)	1.76 (11)
Nauplii	0.3 ±2.3	0.0 ± 0.0	1.3 ± 4.6	0.76 (35)	1.26 (11)
Eudiaptomus sp.	1.5 ± 6.4	0.0 ± 0.0	0.0 ± 0.0	1.03 (35)	6.26 (11)***
Total female	0.08 ±0.5	0.0 ± 0.0	0.0 ± 0.0	1.00 (35)	3.87 (11)***
Nauplii	1.4 ± 5.8	0.0 ± 0.0	0.0 ± 0.0	1.03 (35)	1.22 (11)***
Acanthocyclops sp.	1 489.3 ± 1 459.0	111.00 ± 261.4	181.3 ± 285.3	12.70 (35)***	6.57 (11)**
Male	143.2 ± 143.4	12.1 ± 23.1	23.0 ± 41.8	10.00 (35)***	5.23 (11)**
Total female	108.5 ± 231.6	35.6 ± 118.4	6.3 ± 11.9	1.8 (35)	1.09 (11)
Female gravid	14.0 ± 63.8	14.2 ± 47.3	4.0 ± 10.0	0.34 (35)	0.74 (11)
Copepodites	1 056.9 ± 186.54	44.2 ± 59.7	148.0 ± 221.6	12.42 (35)***	5.46 (11)**
Nauplii	166.6 ± 833.7	4.9 ± 12.9	0.0 ± 0.0	1.94 (35)	5.52 (11)***
Bosmina longirostris	720.2 ± 1 339.6	4.4 ± 7.5	2.9 ± 6.5	3.25 (35)*	0.83 (11)
Diaphanosoma brachyurum	232.8 ± 468.5	4.9 ± 9.3	4.4 ± 7.5	6.76 (35)**	3.01 (11)*
Daphnia longispina	126.2 ± 247.8	1.3 ± 4.6	0.0 ± 0.0	5.22 (35)**	3.59 (11)**
Ceriodaphnia quadrangula	8.9 ± 4.2	0.0 ± 0.0	0.0 ± 0.0	11.24 (35)***	4.91 (11)*
Keratella quadrata	0.1 ± 0.6	0.0 ± 0.0	0.0 ± 0.0	1.00 (35)	1.00 (11)

F-value: between-groups mean square/within-groups mean square.
*Values in the same row showing the same letters are significantly different as tested with one-way ANOVA (F between stations, F′ between months) (p < 0.05 *; p < 0.01**; p < 0.001***).*

(Fig. 7a) and between 0.01 × 10^3 ind·ℓ$^{-1}$ in early July and 0.8 × 10^3 ind·ℓ$^{-1}$ in late November at Station 3 (mean ± s.d. = 0.24 × 10^3 ± 0.27 × 10^3 ind·ℓ$^{-1}$) (Fig. 7b). At Station 2, the zooplankton community was largely dominated by *Acanthocyclops* sp. throughout the study period (Fig. 8b′) (60 to 100% of total zooplankton abundance, H'= 0.00 bits ind·ℓ$^{-1}$ to 1.37 bits ind·ℓ$^{-1}$, Fig. 9b, Fig. 10b), with the exception of late December which was dominated by *Daphnia longispina* (accounting for 100% of the total zooplankton abundance). At Station 3, *Acanthocyclops* sp. (71 to 100% of the total zooplankton abundance, H'= 0.00 bits ind·ℓ$^{-1}$ to 1.55 bits ind·ℓ$^{-1}$, Fig. 10c) was the dominant species throughout the study period (Fig. 8c', Fig. 9b), with the exceptions of early July, which was dominated by the cladoceran *Diaphanosoma brachyurum* (100% of the total zooplankton abundance), and late November, which was dominated by the calanoid *Copidodiaptomus numidicus* (100% of the total zooplankton abundance).

Community analysis

Canonical correspondence analysis (CCA) was performed for total zooplankton, total phytoplankton abundance and environmental variables (Fig. 11).

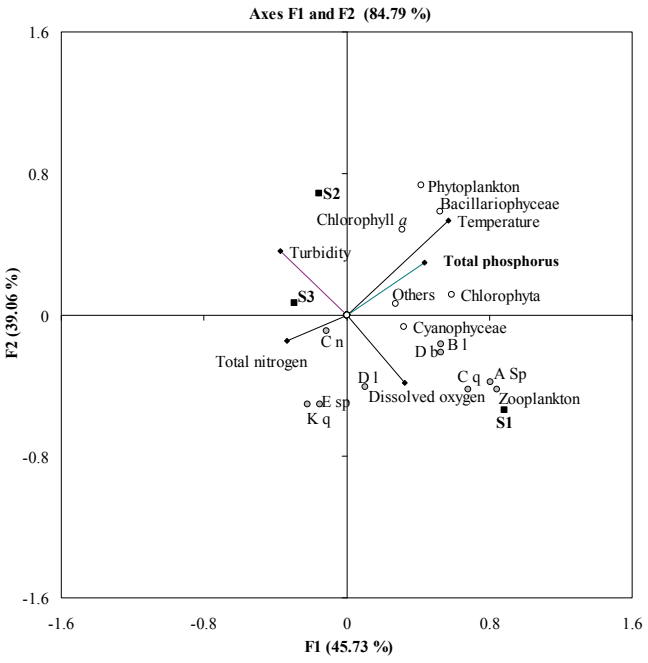

Figure 11
Canonical correspondence analysis (CCA) (Axis I and II) on mean values of environmental and biological variables in the Kasseb Reservoir (C n): Copidodiaptomus numidicus, (E sp.): Eudiaptomus sp., (A sp.): Acanthocyclops sp., (B l): Bosmina longirostris, (D b) Diaphanosoma brachyurum, (D l): Daphnia longispina, (C q): Ceriodaphnia quadrangula, (K q): Keratella quadrata. Station 1: deepest area, Station 2: Brik River, Station 3: M'Zaz Stama River.

Discussion

Our study suggests that local and regional processes interact to produce patterns of species composition and diversity of zooplankton in Kasseb Reservoir. In this system of highly connected reservoirs, Kasseb Reservoir provides the water for the Ghdir El Goulla Reservoir (Sellami et al., 2009). Connections between reservoirs can have positive and negative impacts on zooplankton communities. The Kasseb Reservoir has low

Available on website http://www.wrc.org.za
ISSN 0378-4738 (Print) = Water SA Vol. 37 No. 2 April 2011
ISSN 1816-7950 (On-line) = Water SA Vol. 37 No. 2 April 2011

diversity (8 zooplankton species). The results of this study suggest that this system is structured according to the species-sorting paradigm (Leibold et al., 2004). Connectivity can promote high community diversity by providing new species from the regional pool, but can also limit local diversity by washing out species, setting up local communities for competitive exclusion, and otherwise providing a disturbance that can offset equilibrium conditions (Cottenie and DeMeester, 2005).

The highest zooplankton densities were found in early September at a depth of 5 m (10.8×10^3 ind·ℓ$^{-1}$) for the deep southern part of the Kasseb Reservoir (Station 1), but in late November for the shallow north-eastern (Station 2) and western (Station 3) areas. A significant correlation was found between water temperature and zooplankton abundance at Station 1 (r= 0.779, P <0.01). This accords with previous studies (De Azevedo and Bonecker, 2003; Cherbi et al., 2008; Primo et al., 2009) concluding that temperature influences zooplankton distribution. By contrast, the lowest zooplankton density was found in the rainy period (December). It is likely that the rainfall washes out the zooplankton species from Kasseb to Ghdir El Goulla Reservoir. It has been reported for the floodplain of the Danube River that crustacean zooplankton species richness decreases in floodplain habitats as connection to the river increases (Baranyi et al. 2002). Many studies (Murugavel and Pandian, 2000; Guevara et al., 2009) have recognised that limnological variables associated with rainfall are of importance to the zooplankton community.

The greatest density and diversity of zooplankton was observed at Station 1, due to the relative stability of the wide reservoir body, with slower velocity of water flow relative to the 2 rivers (Stations 2 and 3). Similar results were found by Zhenbin et al. (2008). Moreover, the low density and diversity (4 species) of zooplankton observed at Stations 2 and 3 could be linked to high turbidity at these stations. Turbidity showed significant spatial differences (P <0.05). The highest values of turbidity observed for Stations 2 and 3 may be due to an increase in sediment load from surface runoff at these stations. Zooplankton abundance was negatively correlated with turbidity (r = -0.381, P <0.05). These findings confirm the results of Dejen el al (2004). Turbidity is a very important structuring variable (Scheffer, 1998) for zooplankton communities.

There was an imbalance between phytoplankton and zooplankton communities. In this reservoir, zooplanktonic organisms were probably able to feed on sources other than phytoplankton (microzooplankton and detritus). These results were in agreement with the observations of Pinto-Coelho et al. (2005) and Morgado et al. (2007), which showed detritus food chains to be a resource for zooplankton. The relationship between phytoplankton and zooplankton was illustrated by a comparison of further changes in density of both communities. Subsequently, each decrease in phytoplankton density was preceded by an increase in zooplankton density; reflecting a state of imbalance in this ecosystem. Similar results have been found in other studies (Abowei et al., 2008; Friedrich and Pohlmann, 2009; Mitra, 2009).

The highest zooplankton density was found at the upper layer (0 to 10 m) with a maximum at 5 m (10.8×10^3 ind·ℓ$^{-1}$ in the beginning of September). The vertical distribution of zooplankton was similar to that reported in other studies (Cadjo et al., 2007). Such a pattern may have been related to the food availability in the upper layer, where phytoplankton was most abundant. These findings confirm the results of Cherbi et al. (2008). Thus, zooplankton is probably an important grazer of algae during periods of high zooplankton abundance. This is supported by the findings of a study by Horn and Horn (2008).

There was no clear trophic gradient in Kasseb Reservoir; some horizontal differences in zooplankton abundance and community structure were observed. *Copidodiaptomus numidicus* was more common in the western part of Kasseb Reservoir. *Eudiaptomus* sp., *Acanthocyclops* sp., *Bosmina longirostris*, *Diaphanosoma brachyurum*, *Daphnia longispina*, *Ceriodaphnia quadrangula* and *Keratella quadrata* were dominant in the deep southern part of the reservoir. In a similar study conducted in Lake Pyhäselkä by Karjalainen et al. (1996a), *Daphnia* and *Eudiaptomus* were dominant in the southern pelagial zone.

The Cladocera community was characterised by the dominance of the smaller species in summer (*Bosmina longirostris*, *Diaphanosoma brachyurum,* and *Ceriodaphnia quadrangula*) and the larger ones in autumn (*Daphnia longispina*). *Daphnia longispina* abundance increased during autumn and winter and decreased in summer (Table 3). Similar results have been found for other freshwater systems (Primo et al., 2009).

The development of cyanobacteria in summer (the maximum was observed at the end of August: 1.2×10^6 cells·ℓ$^{-1}$ at Station 1, the deepest station, Fig. 8a) led to a decrease in *Daphnia longispina* densities. On the contrary, smaller cladocerans avoided the typically abundant cyanobacteria and fed on smaller algal particles (Paranaguá et al., 2005). These associations were confirmed by the positive relationship between the species *Bosmina longirostris*, *Diaphanosoma brachyurum,* and *Ceriodaphnia quadrangula* and cyanobacteria on the first CCA axis (G1). By contrast, *Daphnia longispina* seems to exclude itself (G3) (Fig. 10a). Frequently, the replacement of large species by small ones occurs when cyanobacteria are dominant (Leonard and Pearl, 2005; Ferráo-Filho et al., 2009). The PEG model (Plankton Ecology Group, Sommer et al., 1986) reported the replacement of smaller cladoceran species by larger ones in summer (Sommer et al., 1986; Lair and Ayadi, 1989). Many authors confirm competitive mechanisms between *Daphnia* and *Diaphanosoma* (Horn and Horn, 1990) and between *Daphnia* and *Bosmina* (Urabe, 1990). On the other hand, the low density of *Daphnia longispina* observed in summer was probably the result of grazing by *Chaoborus* larvae and planktivorous fish. Many studies have established that planktivorous fish deplete the abundance of large cladocerans such as *Daphnia* through direct grazing (Pont et al., 1991, Couture et al., 2008).

A positive relationship was shown between the species *Acanthocyclops* sp., *Bosmina longirostris* and *Diaphanosoma brachyurum* on the first CCA axis. Cyclopoids have been observed by some workers (Pinto-Coelho et al., 2005) at high trophic levels. Several studies have reported that *Bosmina longirostris* was associated with more eutrophic conditions (De Eyto, 2001; Jaramillo and Gaviria, 2003; Guevara et al., 2009). The species *Diaphanosoma brachyurum* was generally abundant at high trophic levels (Amoros, 1984).

Conclusion

The zooplankton community in Kasseb Reservoir showed spatial and temporal variations in density in relation to local and regional parameters. The phytoplankton community contributes to succession ofzooplankton community. Nevertheless, zooplankton dynamics can be affected by *Chaoborus* larvae and fish predation.

The presence of zooplankton species known to be indicators of eutrophic status reflected the high trophic condition of Kasseb Reservoir. In addition, total phosphorus concentration (25-200 $\mu g \cdot \ell^{-1}$) was within the range that is typically found in eutrophic reservoirs. It is therefore important to prevent the deterioration of Kasseb Reservoir, since it is an important drinking water supply for Tunisia.

Acknowledgements

We thank one anonymous reviewer for providing helpful suggestions for improvement. We also thank Mr Nabil Kallel, an English teacher in the Faculty of Science, for helping us in proofreading this article. The authors wish to thank A Fathalli for the phytoplankton data.

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Available on website http://www.wrc.org.za
ISSN 0378-4738 (Print) = Water SA Vol. 37 No. 2 April 2011
ISSN 1816-7950 (On-line) = Water SA Vol. 37 No. 2 April 2011