

Succession of Phytoplankton and Zooplankton Communities Coupled to Environmental Factors in the Oligo-mesotrophic Nabhana Reservoir (Semi Arid Mediterranean Area, Central Tunisia)

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Ikbel Sellami, Asma Hamza, Monia El Bour, Mohammed Alaoui Mhamdi, Bernadette Pinel-alloul, and Habib Ayadi (2016) The occurrence of plankton seasonal dynamics in Mediterranean shallow lakes is characterised by a marked interannual variability, which makes it difficult to establish reliable predictions on the dynamics and functioning of plankton in these ecosystems based on the Plankton Ecology Group (PEG) model. In the present paper we study the succession of the phytoplankton and zooplankton communities in the semi-arid Mediterranean Nabhana reservoir (Central Tunisia) and its relationships with environmental factors during the period from May 2005 to January 2006 in the deepest area of this oligo-mesotrophic reservoir. Water temperature was a keystone factors in the seasonal dynamics of zooplankton. Cyanobacteria dominated the phytoplankton community throughout the study year 2005-2006 (94-99%) and *Microcystis aeruginosa* contributed for 93% of the total cyanobacteria abundance. The zooplankton community was dominated by copepods (66%) and cladocerans (28%). The dominant species was *Copidodiaptomus numidicus* (66% of total zooplankton) followed by *Diaphanosoma brachyurum* (22% of the total zooplankton). In addition, our results showed that the peak of phytoplankton abundance (5.6×10^6 cells l⁻¹, June) coincided with that of zooplankton abundance (2.1×10^2 ind l⁻¹, June) contrary to the clear-water phase model. The cyanobacteria and copepods were responsible for these exceptional peaks that occurred in June, accounting respectively for 99% of the total phytoplankton and 82% of the total zooplankton. In the Nabhana reservoir, the trophic relationship between phytoplankton and zooplankton were implicated in the phytoplankton abundance and dynamics. The occurrence of cyanobacterial blooms is determined by biotic and abiotic factors. The dynamics between cyanobacteria and their grazers may emerge as a regulator of blooms.

Key words: Nabhana reservoir, Water temperature, Oligo-mesotrophic status, Phytoplankton, Zooplankton, PEG model.

BACKGROUND

Most research on the succession of plankton communities in lacustrine environments was performed in large lakes (George and Winfield 2000; Rinke et al. 2009). In shallow lakes,

especially in semi-arid Mediterranean regions, available information is scarce (Moreno-Ostos et al. 2007). Plankton seasonal succession has been described by the PEG model (Plankton Ecology Group, Sommer et al. 1986) for oligotrophic and eutrophic temperate lakes, and reviewed recently to

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account for complex food web trophic interactions (Sommer et al. 2012). In general terms, a rapid increase in small, fast-growing r-strategist algae, such as small centric diatoms and chlorophytes, is followed by a short period of very low algal biomass and high water transparency (the clear water phase) coupled to high abundance of large zooplankton grazers, which draws to a close at the beginning of the summer when other phytoplankton species, such as cyanobacteria, become the dominant phytoplankton group. These succession stages in the phytoplankton community occurred with marked interannual variability in Mediterranean shallow lakes making it difficult to establish reliable predictions on the seasonal dynamics and the structure of communities in these ecosystems (Beklioglu et al. 2006). We have recently shown (Sellami et al. 2010) that the phytoplankton community in the semi-arid Mediterranean Nabhana reservoir was dominated by cyanobacteria during the study year (2005-2006) with long lasting steady-states of these microorganisms. This is consistent with other studies conducted in Mediterranean freshwater ecosystems (Abrantes et al. 2006; Moustaka-Gouni et al. 2007; Hadas et al. 2015) pointing out the influence of warm climate properties on phytoplankton dynamics. Moreover, the semi-arid Mediterranean Tunisian reservoirs are stressed due to enhanced nutrient loading resulting from land runoff and sewage discharges with frequent occurrences of *Microcystis aeruginosa* blooms (Mouelhi 2000; Sellami et al. 2009). Cyanobacterial blooms are an increasing concern, worldwide, in both freshwater (Smith and Lester 2007; Hadas et al. 2015) and marine environments (Anderson et al. 2002; Ho and Michalak 2015). Numerous studies have shown that the phytoplankton abundance and species composition are governed by factors such as light, temperature, nutrients, grazers, and water movements in freshwater ecosystems (Jacoby et al. 2000; Aleya 2010). Grazing is one of the most important factors controlling the relationship between the phytoplankton and zooplankton communities (Abdel Aziz et al. 2006; Dokulil 2013), with a low grazing pressure being shown to favour algal blooms as a result of diminished top-down control (McQueen et al., 1989). Cyanobacteria blooms are the most notorious factor accounting for the decoupling in bottom-up energy transfer in eutrophic/hypertrophic systems (Sommer et al. 2012). Although laboratory studies have examined the cyanobacteria-zooplankton interactions (Gustafsson and Hansson 2004; Oberhaus et al.

2007; Ger et al. 2014), there is still few field studies examining the succession of phytoplankton and zooplankton and its coupling with environmental factors in eutrophic Mediterranean freshwater ecosystems. The objectives of this study are to describe the phytoplankton and zooplankton community structure and to discuss the main patterns of the succession of the phyto- and zooplankton species of the Nabhana reservoir, located in a semi-arid Mediterranean area, in relation to the environmental parameters. To our knowledge, the present article is the first contribution concerning the seasonal succession of phyto- and zooplankton communities in the Nabhana reservoir in relation to the steps proposed by the PEG model (Plankton Ecology Group, Sommer et al. 1986 and 2012). The main goals are to test if the cyanobacteria dominance affects the zooplankton community structure and succession, and if plankton succession in this eutrophic ecosystem misfits the Plankton Ecology Model.

MATERIALS AND METHODS

Study site

Nabhana reservoir (36°03'N and 09°54'E) is situated at about fifty kilometres South of Kairouan city (Center of Tunisia) (Fig. 1). This reservoir, constructed in 1966 on the Nabhana River, provides drinking water and irrigation to the Tunisian Sahel (1 270 360 inhabitants, 13.3% of total population of Tunisia), and has multiple uses such as the protection of the city of Kairouan against the river violent floods. Morphometric and other basic characteristics are shown in table 1.

Physical and chemical parameters

The samples were collected during the period from May 2005 to January 2006 in the deepest area of the Nabhana reservoir. At this station, a depth-integrated sample was pumped over depth intervals at surface, 5 and 10 m to represent the entire water column. Water samples for physical and chemical analyses were collected using a 1-liter Van Dorn bottle at the same depths and preserved in cold and dark conditions. Water temperature (°C), dissolved oxygen (mg.L⁻¹), salinity (g.L⁻¹), pH, and water transparency (m) were measured *in situ*. Water temperature, dissolved oxygen concentration, salinity and pH

were measured using a multiparameter probe (Multi 340i/SET). Water transparency was estimated using a Secchi disc. The concentration of the suspended matter (mg.L^{-1}) was determined by measuring the dry weight of the residue after filtration through a Whatman GF/C membrane. Nutrient concentrations were analyzed by standard colorimetric techniques with an automatic Bran and lueBBe type 3 analyzer and determined

calorimetrically using a UV-visible (6400/6405) spectrophotometer (APHA 1992) and were expressed as $\mu\text{g.L}^{-1}$.

Phytoplankton

Phytoplankton samples were taken using a 1-liter Van Dorn bottle, simultaneously with the samples for chemical analysis. Phytoplankton

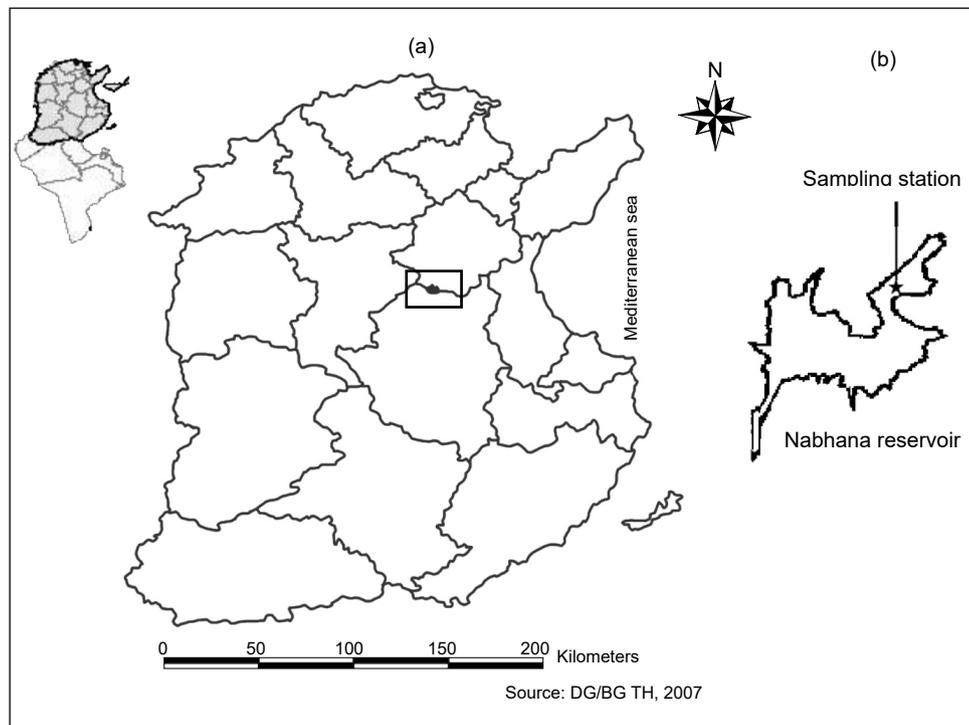


Fig. 1. Localization of the Nabhana reservoir in Tunisia (a), Map showing the sampling station in the reservoir (b).

Table 1. Morphometric and hydrological characteristics of the studied Nabhana reservoir

Location	36°03'N, 09°54'E
Construction	1966
Area (ha)	532
Catchments area (km^2)	855
Volume (10^9 m^3)	86
Mean depth (m)	16.5
Water temperature ($^{\circ}\text{C}$)	21
Annual mean precipitation (mm)	30
Annual mean evaporation (mm)	134
Nitrites (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	46 \pm 35
Nitrates (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	198 \pm 95
Ammonium (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	59 \pm 18
Total nitrogen (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	398 \pm 120
Orthophosphates (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	44 \pm 14
Total phosphorus (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	60 \pm 17
Chlorophyll-a (mean \pm s.d.) ($\mu\text{g l}^{-1}$)	5.2 \pm 2.3

enumeration was performed with an inverted microscope using the Utermöhl (1958) method after fixation with a Lugol solution (4%). The identification of algal taxa followed Bourrelly (1966, 1968, 1985), Baker (1991, 1992), and Komarek and Anagnostidis (2005). Quantification of chlorophyll-*a* was performed on water subsamples (0.5 l), and that were filtered using Whatman GF/C filters (1.2 µm pore size filter and 25 mm- diameter) and pigment extraction was performed with 90% acetone (Lorenzen 1967). The concentrations were determined by the spectrophotometry based on the absorbance at 750 and 663 nm.

Zooplankton

Samples for zooplankton (20 liters using a 5-liter Van Dorn bottle) were filtered through a 55 µm Nitex mesh and fixed *in situ* with formalin 4% solution and coloured with Bengal Pink. The zooplankton were enumerated and counted under a binocular microscope type Leica in Dolffus chambers (Paterson 1993). The taxonomic identification was carried out according to Koste (1978), Margaritora (1985) and Korovchinsky (1992). Zooplankton abundance was estimated (ind.L⁻¹). The species richness of zooplankton community structure was assessed according to the diversity index (H') as described by Shannon and Weaver (1949).

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

n_i/N . is the frequency of species *i* in the sample. *N*. number of species of the community

Statistical analyses

The data recorded in this study for physico-chemical variables (temperature, dissolved oxygen, pH, salinity, suspended matter, nitrites, nitrates, ammonium, orthophosphates, total nitrogen, total phosphorus, TN/TP and N/P ratios) and biological parameters (chlorophyll-*a*, total phytoplankton, chlorophyceae, cyanobacteria, dinophyceae, diatoms, total zooplankton, copepod, cladoceran and rotifer densities) were log(*x* + 1) transformed because of a significant deviation from a normal distribution. The data were examined with a normalized principal component analysis (PCA) (Chessel and Dolédec 1992). Pearson's product-moment correlation coefficient *r* (using

XL-stat software) was calculated to determine the association between the physico-chemical variables and the phytoplankton and zooplankton abundances. One-way ANOVA analysis was applied to identify significant differences in phytoplankton and zooplankton communities between depths and months. Cluster analysis (CA) was performed using PRIMER v5.0 for Windows XP (Clarke and Gorley 2001) and was undertaken according to the Ward-algorithmic method. The results are illustrated in a dendrogram where steps in the hierarchical clustering solution and values of the squared Euclidean distances between clusters are shown.

RESULTS

Physico-chemical parameters

Water temperature varied from 9.7 and 29°C (mean ± S.D. = 22.1 ± 6.0°C) (Fig. 2a). A seasonal variation was observed with highest values in August at a depth of 5 m and lowest values in the January at the surface and at the depth of 10 m. There are not remarkable differences of temperature with depth in this reservoir. Dissolved oxygen varied from 3.0 mg.L⁻¹ (In January at a depth of 5 m) to 8.2 mg.L⁻¹ (In June at the surface) (mean ± S.D. = 4.6 ± 1.4 mg.L⁻¹) and its vertical profiles showed that the water column was always well oxygenated in June, averaging 8 mg.L⁻¹ (Fig. 2b). The pH varied between 6.4 and 8.5 (mean ± S.D. = 8.1 ± 0.7) (Fig. 2c). Concentrations in suspended matter averaged 29.3 ± 23.8 mg.L⁻¹ (Fig. 2d), with concentrations in January being very high throughout the water column with a maximum at a depth of 5 m (104.3 mg.L⁻¹). Nutrient concentrations (nitrites, nitrates, ammonium and phosphorus) fluctuated with time and depth, but showing no clear trend. The distribution of nitrites was almost the same as that of nitrates, but their concentrations were in general much lower. Nitrites concentrations varied from 9 µg.L⁻¹ in November at a depth of 5 m to 121 µg.L⁻¹ in May at a depth of 10 m (mean ± S.D. = 46 ± 35 µg.L⁻¹) (Fig. 3a). Nitrates and ammonium concentrations displayed reverse relationships. The lowest concentrations of nitrates were recorded in July at a depth of 5 m (68 µg.L⁻¹) (Fig. 3b). The highest concentrations were observed in May at the surface (393 µg.L⁻¹) and at a depth of 5 m in November (350 µg.L⁻¹). Ammonium concentrations varied from 12 to 159 µg.L⁻¹ (mean ± S.D. = 59 ± 18 µg l⁻¹) (Fig. 3c).

The orthophosphates concentrations reached high concentrations in November-January (mean \pm S.D. = $44 \pm 14 \mu\text{g.L}^{-1}$) (Fig. 3d). Small differences in orthophosphates concentrations were shown across the water column during the period from May to August. N/P. DIN (DIN = $\text{NO}_2^- + \text{NO}_3^- + \text{NH}_4^+$) to DIP (DIP = PO_4^{3-}) ratio varied from 2.45 to 13.78 (mean \pm S.D. = 7.50 ± 3.66) in Nabhana (Fig. 3e). The averages were lower than the Redfield ratio (16), which suggested potential N limitation.

Species composition, distribution and succession of the phytoplankton and zooplankton communities

Phytoplankton and zooplankton composition

The phytoplankton community consisted of cyanobacteriae (8 taxa), diatoms (5 taxa), chlorophyceae (12 taxa) and dinophyceae (5 taxa)

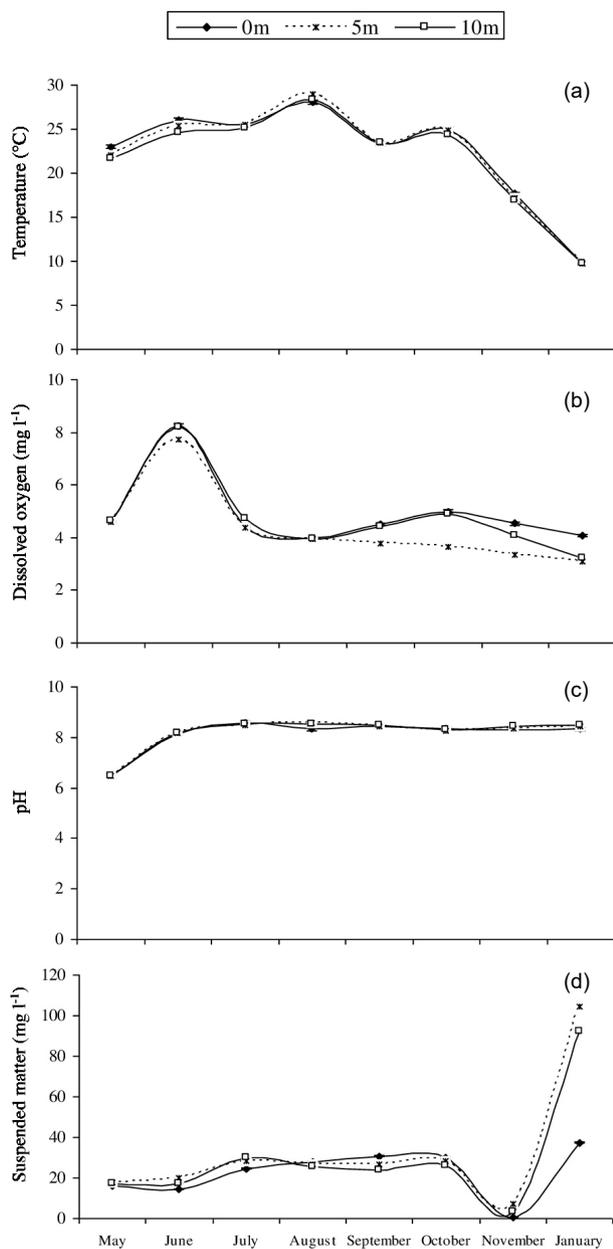


Fig. 2. Spatial and temporal variation of the temperature (a), dissolved oxygen (b), pH (c), suspended matter (d) at different depths (0, 5, 10 m) across the water column.

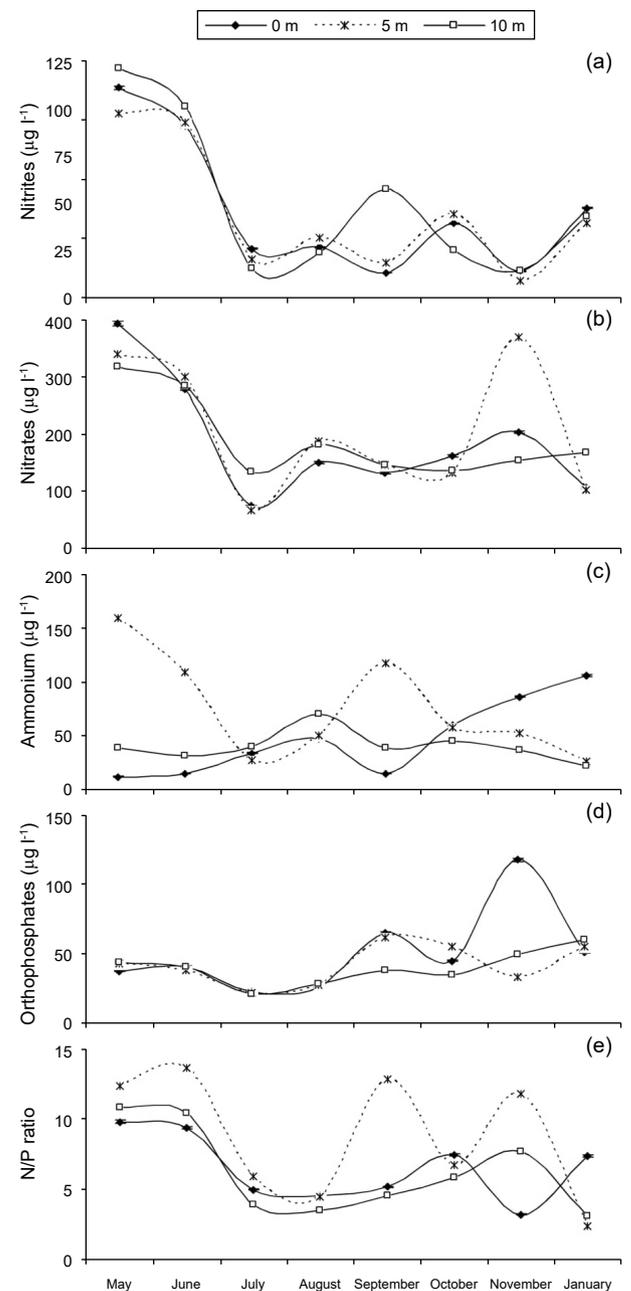


Fig. 3. Spatial and temporal variation of the nitrites (a), nitrates (b), ammonium (c) and orthophosphates (d), N/P ratio (e) at different depths (0, 5, 10 m) across the water column.

(Table 2). Cyanobacteria dominated throughout the sampling period (94-99%) and associated *Microcystis aeruginosa* which contributed 93% of the total cyanobacteria abundance. Diatoms, chlorophyceae and dinophyceae represented 0.61%, 0.3% and 0.07% of the total phytoplankton respectively.

The zooplankton community was composed of copepods (2 taxa), cladocerans (3 taxa) and rotifers (5 taxa) (Table 2). The copepods (66% of the total zooplankton) and cladocerans (28% of the total zooplankton) were the most abundant groups. The dominant species was *Copidodiaptomus numidicus* (66% of the total zooplankton) followed by *Diaphanosoma brachyurum* (22% of the total zooplankton). The rotifers were scarce

accounting for 6% of the total zooplankton. The species *Asplanchna* sp. was the most abundant, accounting for 87% of the total rotifers.

Distribution and succession

Phytoplankton abundance ranged from 0 cells l⁻¹ at a depth of 10 m (Fig. 4c) to 5.6 × 10⁶ cells l⁻¹ in June at a depth of 5 m (Fig. 4b) (mean ± S.D. = 0.6 × 10⁶ ± 1.5 × 10⁶ cells l⁻¹). The highest peaks were observed in May and June along the water column. The major groups were cyanobacteria averaging 99% of the total phytoplankton in June (Fig. 5a). The dominant species was *Microcystis aeruginosa*. This translated into a lower community diversity (H' = 0.5 bits cells l⁻¹, 12 species such

Table 2. Phytoplankton (cells l⁻¹) and zooplankton species abundance (× 10⁻³ ind l⁻¹) found in Nabhana reservoir

PHYTOPLANKTON					
		F (d.f.)		F (d.f.)	
Diatoms			Cyanobacteria		
<i>Cyclotella ocellata</i>	4859	5.39 (23)**	<i>Oscillatoria</i> sp.	5	1.32 (23)
<i>Gyrosigma</i> sp.	100	1.00 (23)	<i>Anabaena</i> sp.	4	1.00 (23)
<i>Navicula</i> sp.	56	0.96 (23)	<i>Aphanothece clathrata</i>	2133	7.40
<i>Nitzschia longissima</i>	59	0.97 (23)	<i>Gloeothece</i> sp.	17438	(23)***
<i>Nitzschia</i> sp.	3	3.00 (23)*	<i>Microcystis aeruginosa</i>	763565	2.95 (23)*
Chlorophyceae			<i>Microcystis</i> sp.	21195	3.14 (23)*
<i>Coelastrum morus</i>	6	3.00 (23)*	<i>Microcystis wesenbergii</i>	18064	2.51 (23)
<i>Oocystis borgei</i>	13	4.03 (23)**	<i>Nostoc</i> sp.	400	0.99 (23)
<i>Protochroomonas granulata</i>	877	1.43 (23)	Dinophyceae		1.34 (23)
<i>Scenedesmus crassus</i>	76	1.00 (23)	<i>Ceratium hirundinella</i>	316	
<i>Scenedesmus falcatus</i>	12	1.00 (23)	<i>Kyste de dinoflagellates</i>	72	5.23 (23)**
<i>Scenedesmus protuberens</i>	52	1.00 (23)	<i>Kyste de protoperidinium</i>	104	0.88 (23)
<i>Scenedesmus</i> sp.	159	0.90 (23)	<i>Peridinium umbonatum</i>	4	1.98 (23)
<i>Staurastrum</i> sp.	3	2.77 (23)*	<i>Polykrikos</i> sp.	150	1.0 (23)
<i>Tetraedron minimum</i>	152	1.00 (23)			9.0 (23)**
<i>Dinobryon</i> sp.	332	0.81 (23)			
<i>Cosmarium granatum</i>	7	9.62 (23)***			
<i>Cosmarium microsporum</i>	178	0.97 (23)			
ZOOPLANKTON					
		F (d.f.)		F (d.f.)	
Copepoda			Rotifera		
<i>Copidodiaptomus numidicus</i>	50020	9.50 (23)**	<i>Asplanchna</i> sp.	3664	2.45 (23)
<i>Acanthocyclops robustus</i>	326	1.18 (23)	<i>Filinia longiseta</i>	52	0.94 (23)
Cladocerans			<i>Hexarthra mira</i>	433	2.08 (23)
<i>Bosmina longirostris</i>	68	1.24 (23)	<i>Keratella cochlearis</i>	159	0.90 (23)
<i>Ceriodaphnia quadrangula</i>	4295	1.24 (23)	<i>Keratella quadrata</i>	51	1.49 (23)
<i>Diaphanosoma brachyurum</i>	16890	7.85 (23)**			

F-value. between-groups mean square/within-groups mean square. * Significant difference between the depths and months as tested with one-way ANOVA (p < 0.05 *; p < 0.01**; p < 0.001***).

as *Microcystis aeruginosa*, *Microcystis* sp.) (Fig. 6). The chlorophyll-a concentrations varied from 2.1 $\mu\text{g l}^{-1}$ in November at the surface (Fig. 4a) to 10.6 $\mu\text{g l}^{-1}$ in July at a depth of 10 m (Fig. 4c) (mean \pm S.D. = $5.3 \pm 2.4 \mu\text{g l}^{-1}$). The difference in the phytoplankton density between the depth and months was negligible (ANOVA, $F = 1.17$, $d.f. = 23$, $p < 0.05$).

Zooplankton abundance fluctuated between 0.3 in January at the surface (Fig. 4a) and 2.1×10^2 ind l^{-1} in June at a depth of 5 m (Fig. 4b) (mean \pm S.D. = $0.5 \times 10^2 \pm 0.6 \times 10^2$ ind l^{-1}) (Fig. 4b). Spatial and temporal changes in the density of zooplankton revealed significant differences between the depth and months (ANOVA, $F = 10.06$, $d.f. = 23$, $p < 0.001$).

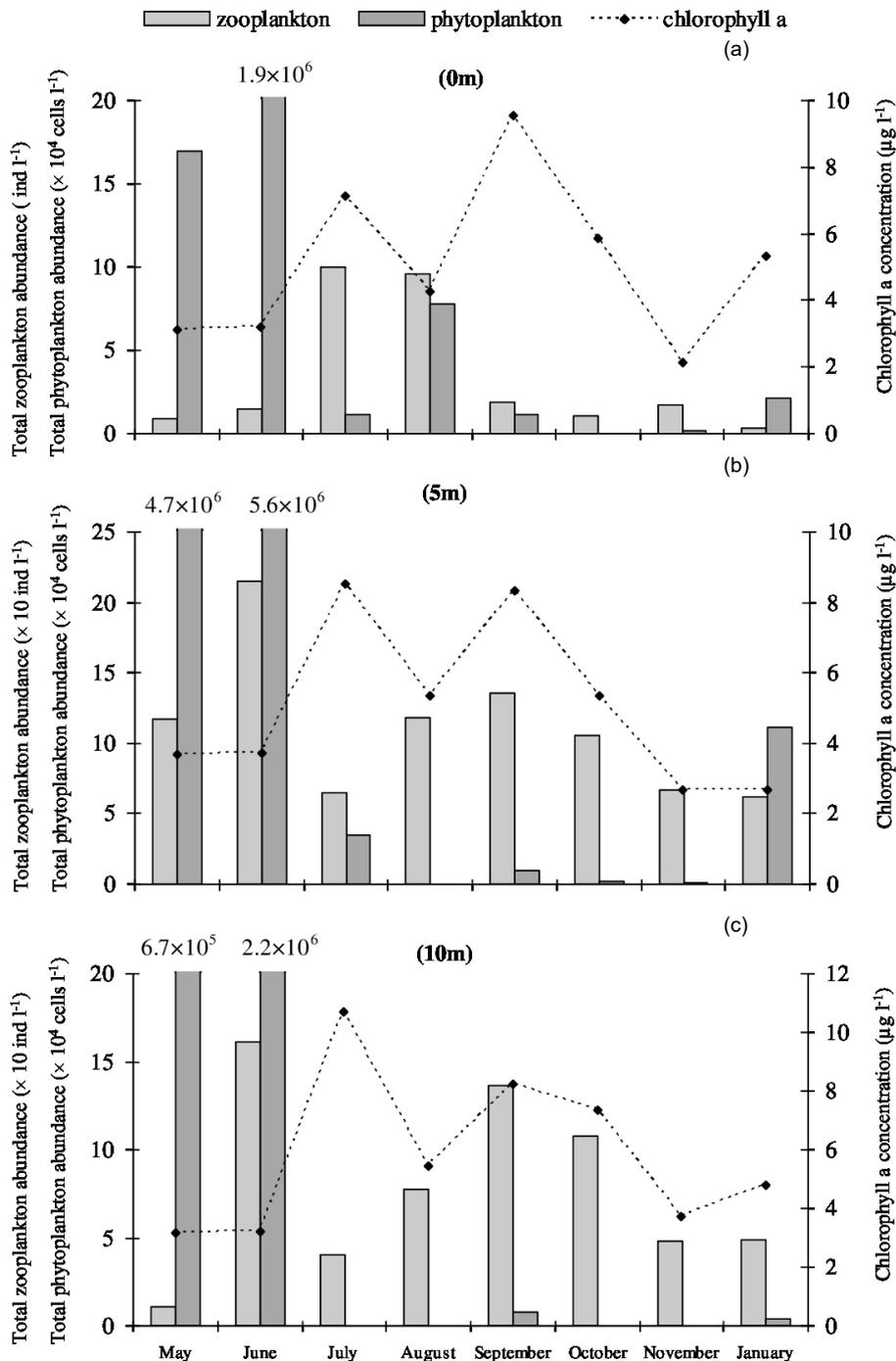


Fig. 4. Seasonal variation of total phytoplankton, zooplankton density and chlorophyll-a at 0m (a), 5m (b) and 10 m (c).

Copepods were the most abundant group averaging 82% of the total zooplankton (Fig. 5b). While copepodites of the dominant species *Copidodiaptomus numidicus* were in the greatest numbers in abundance of all copepods (1.1×10^2 ind l^{-1} in June at a depth of 5 m) and the diversity index was low ($H' = 0.98$ bits ind l^{-1} , 8 species) (Fig. 6). The significant difference was observed between the depths and months in the abundance of dominant species *Microcystis aeruginosa* ($F = 3.14$, $d.f. = 23$, $p < 0.05$), *C. numidicus* ($F = 9.50$, $d.f. = 23$, $p < 0.01$) and *Diaphanosoma brachyurum* ($F = 7.85$, $d.f. = 23$, $p < 0.01$) (Table 2).

The PCA allowed the discrimination of two groups around the F1 and F2 axes components accounting for 65.55% of the variance (Figs. 7a and 7b). The first axis component accounted for 47.73 % of the total variance and selected positively group G1 constituted by biological

parameters (total phytoplankton, cyanobacteriae) and several physico-chemical parameters (salinity, NO_2^- , NO_3^- , NH_4^+ , TN, TN/TP and N/P). F2 axis, which extracted 17.81 % of the variability, selected positively group G2 formed by total zooplankton, copepods, cladocerans, temperature and dissolved oxygen and negatively group G3 constituted by rotifers, suspended matter, total phosphorus and orthophosphates.

The total phytoplankton was significantly correlated with dissolved oxygen ($r = 0.862$, $p < 0.01$, $d.f. = 15$), with nitrites ($r = 0.913$, $p < 0.01$, $d.f. = 15$), with nitrates ($r = 0.738$, $p < 0.05$, $d.f. = 15$), with N/P ratio ($r = 0.808$, $p < 0.05$, $d.f. = 15$) and TN/TP ratio ($r = 0.784$, $p < 0.05$, $d.f. = 15$).

In addition, the different phytoplankton group depended on the nutrient availability (nitrates, nitrites, ammonium, total-N and total-P) and especially on N/P ratios which seemed to be the determining regulator of phytoplankton taxa in this

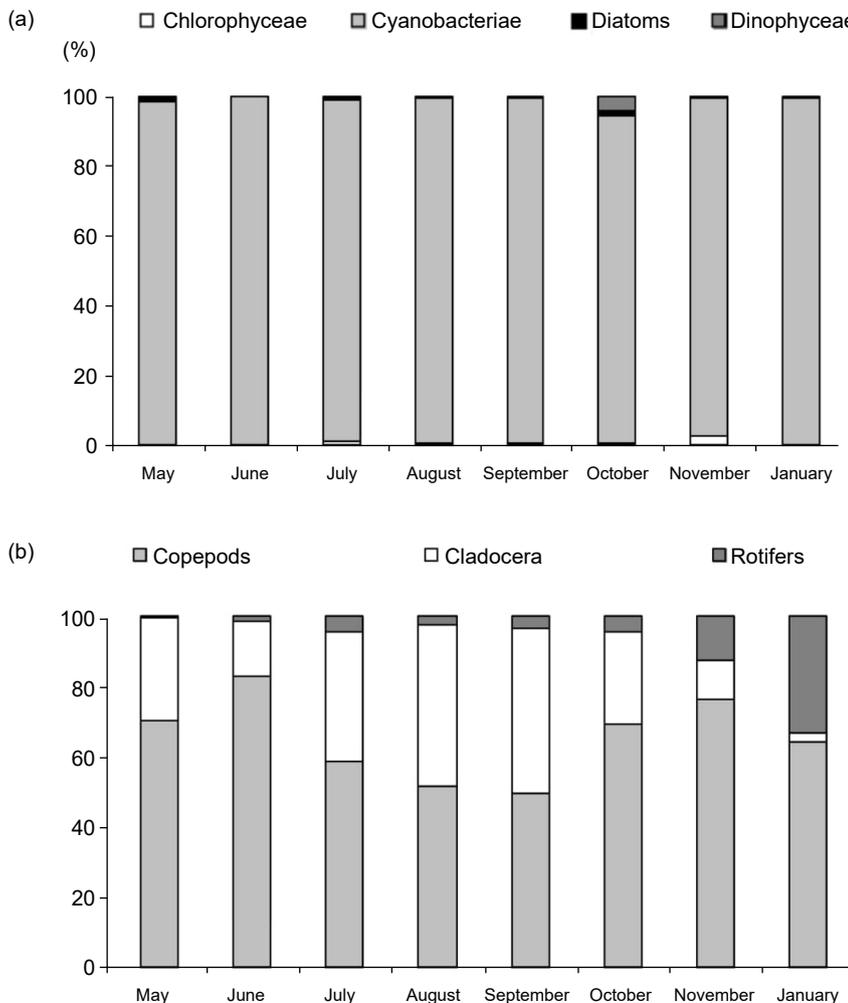


Fig. 5. Seasonal variation in the relative density of phytoplankton (a) and zooplankton (b) groups.

area. We found a significant positive correlation between cyanobacteria abundance and nitrites ($r = 0.911, p < 0.01, d.f. = 15$), nitrates ($r = 0.735, p < 0.05, d.f. = 15$), N/P ratio ($r = 0.808, p < 0.05, d.f. = 15$), TN/TP ratio ($r = 0.784, p < 0.05, d.f. = 15$); between chlorophyceae and nitrites ($r = 0.778, p < 0.05, d.f. = 15$), ammonium ($r = 0.717, p < 0.05, d.f. = 15$), N/P ratio ($r = 0.750, p < 0.05, d.f. = 15$); between dinophyceae and nitrites ($r = 0.781, p < 0.05$), ammonium ($r = 0.756, p < 0.05, d.f. = 15$), N/P ratio ($r = 0.708, p < 0.05, d.f. = 15$); between diatoms and nitrites ($r = 0.729, p < 0.05, d.f. = 15$), ammonium ($r = 0.746, p < 0.05, d.f. = 15$). The zooplankton abundance was significantly correlated with dissolved oxygen ($r = 0.939, p < 0.01, d.f. = 15$). Besides, the zooplankton groups were related to physical and chemical factors. Copepods were significantly correlated with dissolved oxygen ($r = 0.939, p < 0.001, d.f. = 15$), cladocerans with temperature ($r = 0.707, p < 0.001, d.f. = 15$), rotifers with temperature ($r = -0.892, p < 0.001, d.f. = 15$) and with suspended matter ($r = 0.827, p < 0.01, d.f. = 15$).

The distribution of the phytoplankton abundance with the chlorophyll-*a* and the zooplankton abundance is illustrated in figure 4. The abundance of phytoplankton (dominated by cyanobacteria) and copepods were significantly correlated ($r = 0.782, p < 0.05, d.f. = 15$). However, the abundance of phytoplankton did not correlate with the chlorophyll-*a* ($r = -0.465, p < 0.05, d.f. = 15$). This was also confirmed by

the (PCA) showing a linked ecological relationship between phytoplankton and copepods while other cladocerans and rotifers seemed to be independent zooplanktonic groups (Fig. 8).

DISCUSSION

In the Nabhana reservoir, the cyanobacteria steady-states was occurred and was persisted during our study year (2005-2006) with a high density recorded in June at the upper layers and associated with *Microcystis aeruginosa*. These results are in agreement with the few studies conducted in Mediterranean freshwaters (Abrantes et al. 2006; Moustaka-Gouni et al. 2007) and characterized by long lasting steady-states of cyanobacteria suggesting the existence of close relationships between climate factors and phytoplankton dynamics. The seasonal change of irradiance in lower latitudes compared to that in higher latitudes, in combination with other properties of warmer climates, are assumed to result in smoother changes in physical conditions of the lakes and reservoirs; these may allow persistence of cyanobacteria steady-states (Naselli-Florres et al. 2003).

Our results indicate that the succession of phytoplankton in Nabhana reservoir was strictly associated with the temporal variations of several environmental factors. The cyanobacteria abundance did not correlate with the temperature

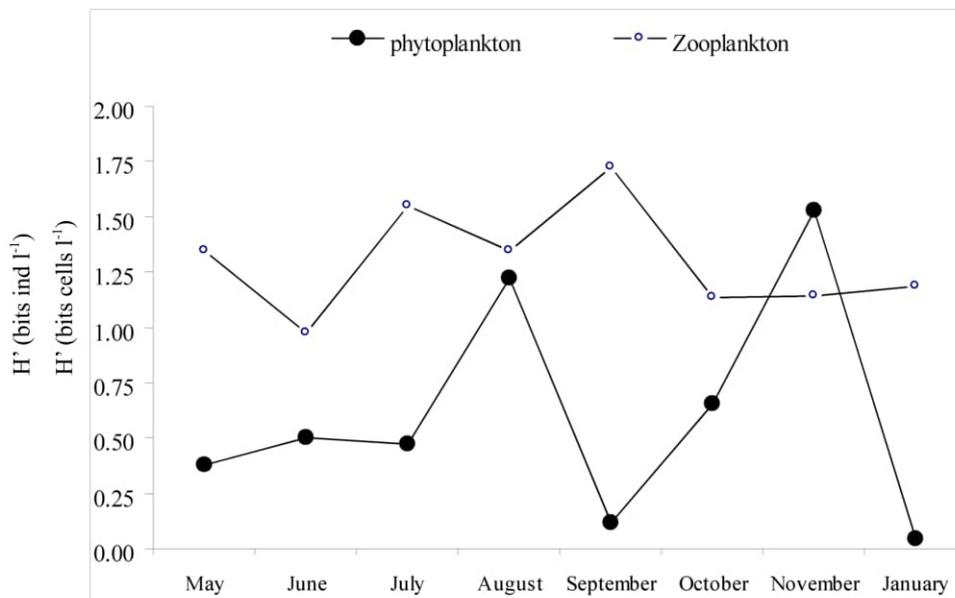


Fig. 6. Seasonal variation of diversity indices of the phytoplankton and zooplankton (H') in Nabhana reservoir.

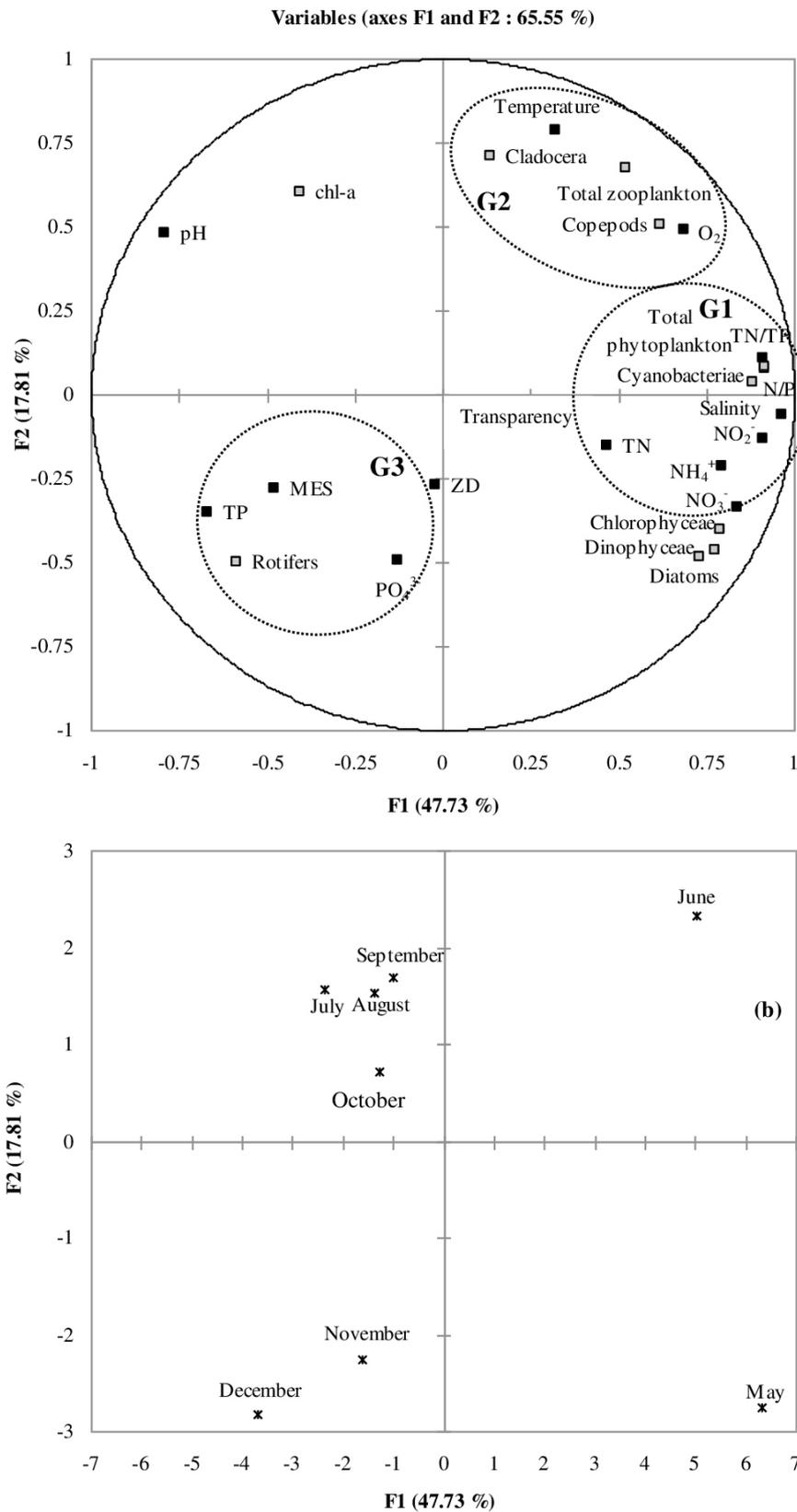


Fig. 7. Principal Component Analysis (PCA) (Axes 1 and 2) of environmental and biological variables (a) and months ordination (b) in the Nabhana reservoir. (O₂). dissolved oxygen, (SM). suspended matter, (NO₂⁻). nitrites, (NO₃⁻). nitrates, (NH₄⁺). ammonium, (TN). total nitrogen, (PO₄³⁻). orthophosphates, (TP). total phosphorus, (Chl-a). chlorophyll-a.

and with the pH. Other results showed that cyanobacteria dominance generally occurred at higher temperatures and pH values (Dokulil 2013; Strandberg et al. 2015; He et al. 2015). We found a significant positive correlation between salinity and cyanobacteria which is consistent with other findings (Domingues et al. 2007; Sinang et al. 2015). Nitrogen was found at low concentrations, while orthophosphates concentrations were high and N/P was lower than the Redfield ratio (16). This suggests that nitrogen is more likely than phosphates to be limiting to attainable growth rates of the phytoplankton as already reported by other studies (Dufour et al. 1981; Weithoff and Walz 1999). The dominance of cyanobacteria community is associated with nitrogen limitation (Quesada et al. 2004; Pilkaitytė and Razinkovas 2007). Due to their ability to fix nitrogen, cyanobacteria are known to be favoured over other phytoplankton in nitrogen-poor waters (Thomazeau 2006; Hense and Burchard 2010). Phosphorus has historically been considered to be the main factor limiting phytoplankton biomass in freshwater ecosystems, and thus the only nutrient involved in eutrophication (Guildford and Hecky 2000; Carpenter 2005). Phosphorus inputs are often associated with phytoplankton proliferation (Smith 2003, Xu et al. 2010). Simultaneous control of phytoplankton by N and P has already been shown in some other ecosystems (Dzialowski et al. 2005; North et al. 2007). Furthermore, the low chlorophyll-*a* concentration found in the Nabhana reservoir together with an N/P ratio lower than

the Redfield ratio indicates that this ecosystem is oligo-mesotrophic (OECD 1982; Vollenweider et al. 1992), confirming the observations reported in the Mediterranean reservoirs (Derraz et al. 2003; Rachiq 2003; Alaoui et al. 2007). The dominance of cyanobacteria group was explained by lower TN/TP ratio (< 29), concurring with previous results showing that cyanobacteria dominance was thought to be a function of TN/TP, with cyanobacteria more often dominant at TN/TP < 29 (Downing 1997; Downing et al. 2001). In addition, cyanobacteria abundances were correlated with nitrites, nitrates, N/P ratio, TN/TP ratio. This indicates that the cyanobacterial growth was probably induced by nitrate which occurred at the highest concentrations of all forms of nitrogen measured and resulting from land runoff and sewage discharges and linked to the intensification of agriculture (Varis and Fraboulet-Jussila 2002). Similar observations were reported in a majority of the semi-arid Moroccan reservoirs (Alaoui et al. 1994; Derraz et al. 2002; Alaoui et al. 2007) and in the Lake Guiers of Senegal in West Africa (Berger et al. 2006; Dufour et al. 2006; Quiblier et al. 2008). The availability of nutrients is the main factor that controls growth, biomass and species composition of phytoplankton (Gobler and Sañudo-Wilhelmy 2001; Komoé et al. 2009). Several hypothesised mechanisms probably contribute to the success of cyanobacteria simultaneously. This may explain why single relationships have failed to explain their dominance in various aquatic systems (Burns 1987; Hyenstrand et al. 1998).

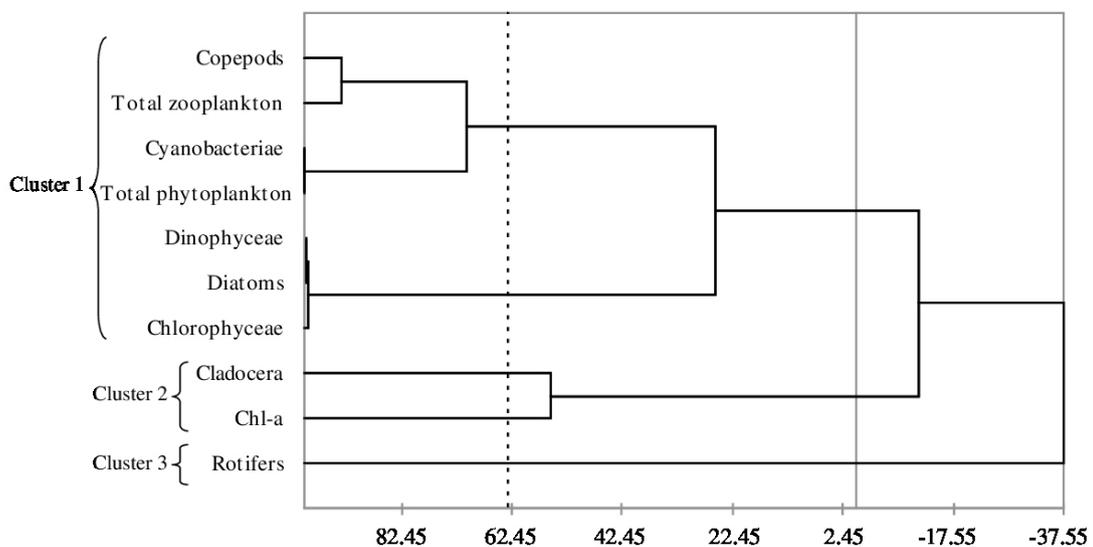


Fig. 8. Dendrogram of the Euclidean distances between the phytoplankton and zooplankton groups and chlorophyll-*a* in Nabhana reservoir.

The zooplankton community was dominated by copepods and cladocerans and associated with the development of *Copidodiaptomus numidicus* and *Diaphanosoma brachyurum* species. The total zooplankton were significantly correlated with dissolved oxygen. Our findings appear to agree with what is known about the influence of dissolved oxygen on zooplankton densities (Whitman et al. 2004). Temperature seems to have exerted a positive effect for cladocerans and negative effect for rotifers. The same result has been previously reported by Straile (2015) and Zhao et al. (2008). In contrast, others studies have showed that cladocerans declined with increasing temperature (Havens et al. 2015). Grazing by zooplankton has been shown to affect phytoplankton succession towards dominance by cyanobacteriae (Smith and Lester 2007; Alexander 2012; Lee et al. 2015). This phytoplankton group is more resistant to grazing (Sommer et al. 1986; Sommer et al. 2001; Wood 2014); unlike other finding showing that zooplankton might be an important vector of cyanobacterial toxins along the food chain (Gobler et al. 2007; Oberhaus et al. 2007; Ger et al. 2010, Hong et al. 2012).

The cyanobacteriae was positively and significantly correlated with copepods, concurring with previous results showing that copepods were less affected by cyanobacteriae, maintaining high densities throughout the bloom (Ferrão-Filho et al. 2002; Zhao et al. 2008; Wang et al. 2010). These results showed a moderate grazing by the copepod *Copidodiaptomus numidicus* on cyanobacteriae. Similar observations were reported by Meyer-Harms et al. (1999) showing the moderate grazing by the copepod *Acartia* sp. on cyanobacteriae. In addition, the concurrent increase in cyanobacteriae and copepods is probably driven by different changes of the system functioning under the nutrient enrichment conditions, *i.e.*, a relaxation of the phosphorus limitation for cyanobacteriae and an increase of the availability of the desirable food-types for copepods. The same conclusion was taken in a previous study by Zaho et al. (2008).

During two months May and June cladocerans and rotifers were at low abundance. Cladocerans and rotifers abundances were negatively correlated with cyanobacteriae. It has been reported that cyanobacterial blooms cause direct decline in numbers of large cladocerans (Trabeau et al. 2004; Ger et al. 2014) and that they can reduce the reproduction rate of rotifers (Arnold 1971) and both growth and reproduction of cladocerans (Haney 1987). The susceptibility of cladocerans

to mechanical and chemical interference from cyanobacteriae is well established (Lüring 2003; Gustafsson and Hansson 2004; Wood 2014).

CONCLUSIONS

The occurrence of cyanobacterial blooms in the Nabhana reservoir was the result of complex interactions between abiotic and biotic factors. Inorganic nutrients within this reservoir were at moderate levels with low concentrations of nitrogen which might favour nitrogen-fixing cyanobacteriae over other phytoplankton. On the other hand, the trophic relationship between phytoplankton and zooplankton were also implicated in the phytoplankton abundance and dynamics. In Nabhana reservoir, the different seasonal stages proposed by the PEG model were not observed. The phytoplankton community was dominated by cyanobacteriae that were probably beyond the grazing capacity of zooplankton dominated by copepods.

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