RESEARCH PAPER

Spatial and temporal dynamics of the steady-state phytoplankton assemblages in a temperate shallow hypertrophic lake (Lake Manyas, Turkey)

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Abstract Spatial and temporal dynamics of phytoplankton biomass and species composition in the shallow hypertrophic Lake Manyas, Turkey, were studied biweekly from January 2003 to December 2004 to determine steadystate phases in phytoplankton assemblages. Steady-state phases were defined when one, two or three coexisting species contributed to at least 80% of the standing biomass for at least 2 weeks and during that time the total biomass did not change significantly. Ten steady-state phases were identified throughout the study peiod. During those periods, Achnanthes microcephala (Kützing) Cleve twice dominated the phytoplankton biomass alone and contributed to more than 50% of the total biomass in seven phases. Microcystis aeruginosa (Kützing) Kützing, Anabaena spiroides Klebahn, Cyclotella stylorum Brightwell, Pediastrum boryanum (Turpin) Meneghini and Phacus pusillus Lemmermann were also represented once in steady-state phytoplankton assemblages. A. microcephala was dominant usually during cold periods of the year, while M. aeruginosa and A. spiroides were usually dominant in warm seasons. The total number of species showed a clear decrease during steady-state phases at all stations. All stations were significantly different in terms of the measured physical and chemical parameters (P < 0.05) and phytoplankton biomass (F = 117, P < 0.05).

Keywords Phytoplankton · Shallow temperate lake · Steady-state

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Introduction

There are more shallow lakes than deep lakes worldwide. Such lakes, used for drinking water, irrigation, fisheries and recreation, are more affected by human activities than deep lakes. The socioeconomic importance of shallow lakes calls for more scientific research on these systems (Padisak and Reynolds 2003).

In the last 2 decades, a number of studies have dealt with steady-state phytoplankton assemblages in various types of water bodies (Feuillade and Feuillade 1987; Davidson et al. 1999; Huszar et al. 2003; Naselli-Flores et al. 2003; Moustaka-Gouni et al. 2007). Such studies contributed to the understanding of the equilibrium concept in phytoplankton ecology. For identification of steady-state phases, Sommer et al. (1993) set three criteria: (1) a maximum of three species contribute more than 80% of total biomass, (2) their dominance lasts for more than 2 weeks, and (3) during the 2-week period, the total biomass does not change significantly.

Selection of dominant phytoplankton species in lakes usually depends upon unpredictable and complex combination of factors, including the physical structure of the system, the availability of nutrients, and the biotic interactions (Padisak et al. 2003; Nixdorf et al. 2003). Steadystate phases of phytoplankton aasemblages occur quite rarely in oligo- or mesotrophic lakes, but such phases dominated by cyanoprokaryotes are often seen in hypertrophic conditions in stressed shallow water bodies and usually occur in summer or late summer (Stoyneva 2003; Padisak et al. 2003; Nixdorf et al. 2003).

Although phytoplankton studies have increased since the end of the last century, the knowledge of steady-state phytoplankton ecology in temperate lakes is still far from complete. The objectives of this study were to identify the



periods of steady-state phytoplankton assemblages and to investigate the ecological conditions which promoted these assemblages during a two year study in a large temperate shallow hypertrophic lake (Lake Manyas, Turkey).

Methods

Summary of the study site

Lake Manyas is located in the province of Balıkesir, Turkey (Fig. 1). It is an important bird sanctuary and 64 ha of land at the northeastern edge of the lake has been protected as Kuşcenneti National Park since 1959. In 1998 the lake was listed in the Ramsar Convention (Turkish Ministry of Environment and Forestry 2005).

In 1976, Lake Manyas was awarded an A Class Wetland Diploma by the European Council, and the diploma has been renewed every 5 years since (Turkish Ministry of Environment and Forestry 2005). Various studies have been conducted on the lake in response to interest in this national reserve (Büyükışık and Parlak 1989; Albay and Akcaalan 2003; Karafistan and Arık-Çolakoğlu 2005; Çelik 2006; Çelik and Ongun 2006, 2007).

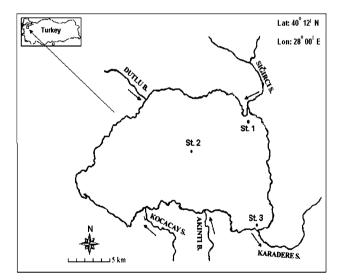


Fig. 1 The map of Lake Manyas, showing the locations of sampling stations

Lake Manyas is mainly fed by the Kocaçay and Sığırcı streams. In spring, the Dutlu and Akıntı brooks, two intermittent small streams, also enter the lake. The summary statistics for the morphometry, hydrology and wind speed of the lake is given in Table 1. The lake is threatened by excessive pollutant loading supplied by Sığırcı Stream.

Field work and laboratory analyses

Sampling started in January 2003 and ended in December 2004. Water samples were taken at three stations biweekly from about 0.3 m below the surface. First station was located near the inflow, second station was located at the midlake and the third station was located near the outflow. The measured physical and chemical environmental variables were significantly different among the stations (P < 0.05).

In the field, phytoplankton samples were placed in 250-ml dark bottles and fixed with Lugol's solution. In the laboratory, the fixed samples were first agitated, then poured into 50-ml graduated cylinders and were allowed to settle for 24 h. At the end of the settling period, 45 ml of water was aspirated from each graduated cylinder, and the remaining 5 ml of water was poured into a small glass vial for microscopic analysis.

Enumeration and identification of phytoplankton were performed using a Palmer–Maloney counting cell and a compound microscope equipped with water immersion lenses and a phase-contrast attachment according to the Utermöhl sedimentation method (Utermöhl 1958). Phytoplankton species were identified according to Geitler (1925), Hustedt (1930), Bourrelly (1970), Komárek and Fott (1983), Jensen (1985), Kelly (2000) and John et al. (2002).

Phytoplankton biomass was calculated from the biovolume data, assuming specific gravity of one (Edmondson 1971). Biovolume was calculated from cell numbers and cell size measurements (Wetzel and Likens 1991; Sun and Liu 2003).

Steady-state phases were identified according to Sommer et al. (1993). The phytoplankton species were functionally classified according to Reynolds et al. (2002) and Padisak et al. (2003).

Table 1 The summary of the morphometry, hydrology and wind speed of Lake Manyas, Turkey between 2003 and 2004

Area (km²)	Vol. (m ³)	Lat.	Lon.	Alt.	WRT (Day)	Infl. $(m^3 s^{-1})$			Outfl. $(m^3 s^{-1})$			Depth (m)			Win. Sp. (m s ⁻¹)		
				(m)		Max.	Min.	Avg.	Max.	Min.	Avg.	Max.	Min.	Avg.	Max.	Min.	Avg.
159	265×10^{6}	40°12′N	28°00′E	15	260	17500	165	6185	13350	383	6030	3.5	0.5	1.5	3.7	1.3	2.45

Vol volume, Lat latitude, Lon longitude, Alt altitude, WRT water retention time, Infl inflow, Outfl outflow, Win. Sp. wind speed



Water temperature, conductivity, pH and chlorophyll were measured using a 6600 model YSI multiprobe. Periodically, chlorophyll was measured using the conventional trichromatic method (APHA 1995) from the acetone-extracted samples to calibrate YSI multiprobe. The inorganic forms of nitrogen, ammonia–nitrogen (NH₄–N), nitrate–nitrogen (NO₃–N), and the soluble reactive phosphorus, phosphate (PO₄–P), concentrations were measured spectrophotometrically according to standard methods (APHA 1995). Water transparency was measured regularly using a Secchi disk. Wind speed data were obtained from the 25th regional branch of State Water Works.

Data were log-transformed before the statistical analysis to obtain normal distribution. Canonical correspondence analysis (CCA) (ter Braak and Verdonschot 1995) was used to investigate the relationship between the measured physical and chemical environmental variables and the monthly average biomass of dominant phytoplankton species that participated in steady-state assemblages. A one-way ANOVA test was used to test for statistical differences in the measured physical and chemical variables and the monthly average phytoplankton biomass among sampling dates and stations using SAS statistical software (SAS Institute 1990).

Results

Conductivity ranged from 0.26 to 0.99 mS m⁻¹, pH from 7.1 to 10.3, Secchi disk depth from 0.10 to 0.30 m, chlorophyll from 71 to 105 μ g l⁻¹, nitrate from 2.9 to 6.8 mg l⁻¹, phosphate from 0.11 to 0.69 mg l⁻¹ and ammonium from 0.0001 to 0.04 mg l⁻¹, respectively (Table 2). Based on the mean annual total chlorophyll concentrations (about 90 μ g l⁻¹) and Secchi disk depth (about 0.17 m), Lake Manyas was classified as hypertrophic (OECD 1982). There were significant differences in conductivity (F = 123, P < 0.05), nitrate (F = 95,

P < 0.05), ammonium (F = 131, P < 0.05), phosphate (F = 107, P < 0.05) and chlorophyll (F = 117, P < 0.05) concentrations among sampling stations.

A total of 165 phytoplankton species (145 species from the first station, 101 from the second station and 105 from the third station) were identified in Lake Manyas from 2003 to 2004. At the first station, the highest number of species (67) was observed in April 2004 and the lowest (17) was observed in January 2003. At the second station, the maximum number of species (65) was was observed in May 2004 and the minimum number (31) was observed in February 2003. At the third station, the highest number of species (69) was recorded in June 2003 and the lowest number (29) was recorded in March 2003. At all stations, chlorophytes contributed the highest number of species followed by diatoms, cyanobacteria and euglenophytes. The number of species was significantly different among sampling stations (F = 97, P < 0.05).

At the first station, the highest total phytoplankton biomass (210 mg 1^{-1}) was observed in November 2003 and the lowest (3.3 mg 1^{-1}) was observed in January 2004 (Fig. 2 a). At the second station, the highest biomass (200 mg 1^{-1}) was observed in November 2003 and the lowest (2 mg 1^{-1}) was observed in January 2003 (Fig. 2b). At the third station, the highest total biomass (129 mg 1^{-1}) was observed in September 2003 and the lowest (15 mg 1^{-1}) was observed in January 2004 (Fig. 2c).

At the first station, four steady-state phases were observed. The first phase was observed in March 2003. During that phase, *Achnanthes microcephala* (Kützing) Cleve contributed 96% of the total biomass. The second phase was observed in July 2003. During that phase, *Phacus pusillus* Lemmermann conributed 64% of the total biomass, *Anabaena spiroides* Klebahn contributed 11% and *Microcystis aeruginosa* (Kützing) Kützing contributed 10% of the total biomass. The third phase was observed in November 2003. During that phase, *A. microcephala* contributed 68% of the total biomass and *M. aeruginosa*

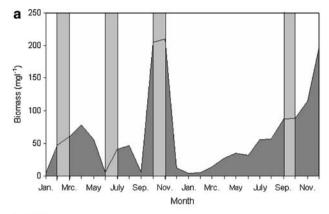
Table 2 The simple statistics for conductivity (Cond.), pH, Secchi disk depth, ammonium (NH₄-N) and chlorophyll (Chl.) of Lake Manyas from 2003 to 2004

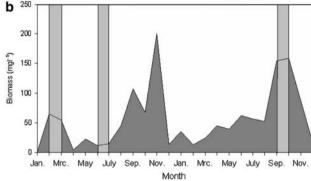
	Cond. (mS m ⁻¹)*		рН		Secchi disk depth (m)*		Chl. (μg l ⁻¹)*			NH ₄ (mg l ⁻¹)*			NO ₃ (mg l ⁻¹)*			PO ₄ (mg l ⁻¹)*					
	St.1	St.2	St.3	St.1	St.2	St.3	St.1	St.2	St.3	St.1	St.2	St.3	St.1	St.2	St.3	St.1	St.2	St.3	St.1	St.2	St.3
Max.	0.99	0.5	0.41	9.1	10.3	9.4	0.25	0.30	0.10	87	105	100	0.04	0.012	0.0015	6.8	5.4	5	0.69	0.31	0.23
Min.	0.40	0.32	0.26	7.1	8.3	8.1	0.10	0.12	0.20	71	72	81	0.01	0.001	0.0001	4	3.1	2.9	0.22	0.11	0.09
Mean	0.80	0.4	0.36	8.2	9	8.8	0.12	0.19	0.15	77	87	90	0.018	0.002	0.00023	5.17	4.37	3.56	0.46	0.19	0.15
SD	0.20	0.05	0.05	0.5	0.55	0.3	0.03	0.05	0.02	4.6	9.8	5.8	0.009	0.002	0.0003	0.81	0.62	0.65	0.11	0.06	0.04

Max. maximum, Min. minimum, SD standard deviation



^{*}P < 0.05





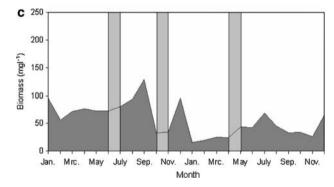
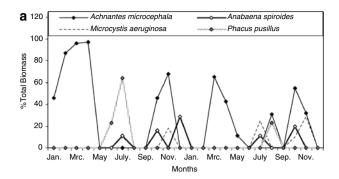
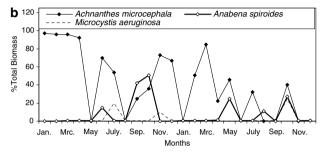


Fig. 2 Variations in the total phytoplankton biomass in Lake Manyas from January 2003 to December 2004. **a** At the first station, **b** at the second station, and **c** at the third station. *Grey* zones show the periods of steady state

contributed 25% of the total biomass. The fourth steady-state phase was observed in October 2004. During that phase, *A. microcephala* contributed 55% of the total biomass, *A. spiroides* contributed 20% and *M. aeruginosa* contributed to 19% of the total biomass (Fig. 3a).

At the second station, three steady-state phases were observed. The first phase was observed in February 2003. During that phase, *A. microcephala* contributed 96% of the total biomass. The second steady-state phase was observed in June 2003. During that phase, *A. microcephala* contributed 75% and *A. spiroides* contributed 15% of the total biomass. The third steady-state phase was observed in





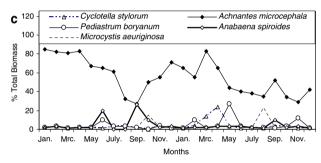


Fig. 3 The percentage contribution of dominant phytoplankton species to the total biomass. $\bf a$ At the first station, $\bf b$ at the second station, and $\bf c$ at the third station

October 2004. During that phase, *A. microcephala* contributed 40% of the total biomass, *A. spiroides* contributed 27% and *M. aeruginosa* contributed 25% of the total biomass (Fig. 3b).

At the third station, three steady-state phases were observed. The first phase was observed in June 2003. During that phase, A. microcephala contributed 65% of the total biomass, A. spiroides contributed 20% of the total biomass and Pediastrum boryanum (Turpin) Meneghini contributed 10% of the total biomass. The second phase was observed in October 2003. During that phase, A. microcephala contributed 50% of the total biomass, M. aeruginosa contributed 15% and A. spiroides contributed 10% of the total biomass. The third phase was observed in April 2004. During that period, A. microcephala contributed 72% and Cyclotella stylorum Brightwell contributed 24% of the total biomass (Fig. 3c).

Besides the non-significant change in the total biomass and the number of dominant phytoplankton species, stable



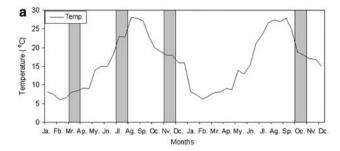
periods of the surface water temperature was taken into consideration when defining steady state phases in Lake Manyas. Water temperature did not change significantly during March, July and November 2003 at the first station (Fig. 4a). At the second station, temperature was stable from July to September 2003 and from August to October 2004 (Fig. 4b). At the third station, temperature did not change significantly from June to July, from October to November 2003 and from March to May 2004 (Fig. 4c). Steady state phytoplankton assemlages were observed during the above mentioned stable periods of the surface water temperature.

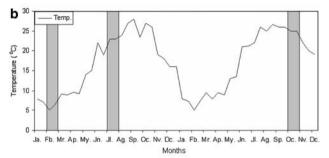
Only 6 out of the 165 species (A. microcephala, A. spiroides, M. aeruginosa, P. pusillus, C. stylorum and P. boryanum) participated in steady-state assemblages during the study period. A. microcephala (functional group D) persisted throughout the year, making it the majority of the total biomass usually during the cold periods of the year. A. spiroides (functional group H1) and M. aeruginosa (functional group M) were dominant during summer and fall. Besides the above common dominant species, P. pusillus (functional group W1) was dominant at the first station in July 2003. C. stylorum (functional group A) was dominant in March 2003 and P. boryanum (functional group J) was dominant in June 2003 at the third station.

At the first station, the first axis of CCA had an eigenvalue of 0.49 and explained 70% of the variance in dominant species and in the measured environmental parameters. The second axis had an eigenvalue of 0.17 and explained 25% of the variance in dominant species and in the measured environmental parameters (Table 3). The first axis was associated with chlorophyll, phosphate, ammonium and pH. The second axis was associated with nitrate and conductivity. At this station, *A. microcephala* was positioned near the center of the ordination diagram. *A. spiroides* took an intermediate position between the first and second axis. *M. aeruginosa* was positioned on the positive side of the first axis and *P. pusillus* was positioned on the positive side of the second axis (Fig. 5a).

At the second station, the first axis of CCA had an eigenvalue of 0.27 and explained 86% of the total variance in dominant species and in the measured environmental parameters. The second axis had an eigenvalue of 0.003 and explained 9% of the total variance in dominant species and the measured environmental parameters (Table 3). The first axis was associated with nitrate, phosphate, pH and chlorophyll. The second axis was associated with water temperature. At this station, A. microcephala was positioned near the center of the ordination diagram. M. aeruginosa and A. spiroides were positioned on the positve side of the second axis (Fig. 5b).

At the third station, the first axis of CCA had an eigenvalue of 0.17 and explained 57% of the total variance





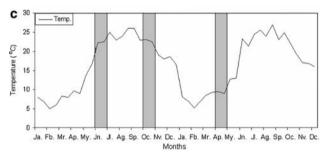


Fig. 4 Spatial and temporal variations in the surface water temperature of Lake Manyas from January 2003 to December 2004. *Grey* zones show the periods of steady state

in dominant species and in the measured environmental parameters. The second axis had an eigenvalue of 0.08 and explained 18% of the total variance in dominant species and in the measured environmental parameters (Table 3). The first axis was associated with pH and chlorophyll. The second axis was associated with temperature, phosphate and nitrate. At this station, *A. microcephala* and *P. boryanum* were positioned near the center of the ordination diagram. *M. aeruginosa* and *A. spiroides* were positioned on the positive side of the second axis (Fig. 5c).

Discussion

In total, 165 phytoplankton species were identified in Lake Manyas throughout the study period. The highest number (69) was observed in June 2003 at the third station and the lowest number (17) was observed in January 2003 at the first station. The number of species decreased during the steady-state phases at all stations. This decrease is an expected result, because during the equilibrium conditions



Table 3 Summary statistics for canonical correspondence analysis (CCA)

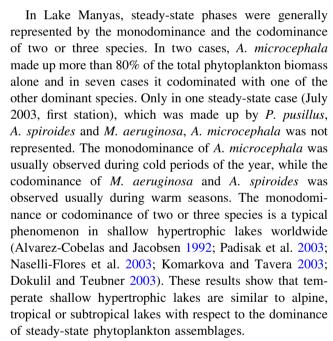
Axes	1			2			3			4			
Stations	St.1	St.2	St.3										
Eigenvalues	0.489	0.269	0.166	0.169	0.029	0.082	0.038	0.015	0.032	0.466	0.129	0.013	
Spenv. correlations	0.825	0.896	0.847	0.764	0.546	0.762	0.360	0.412	0.484	0.000	0.000	0.340	
Cum. Per. var. of sp.	37.6	51.8	26.6	50.6	57.3	39.8	53.5	60.2	44.9	89.3	85.1	47.0	
Cum. per. var. spenv.	70.2	86.0	56.7	94.6	95.2	84.6	100.0	100.0	95.5	0.0	0.0	100.0	
Total inertia	St.1	1.302											
	St.2	0.519											
	St.3	0.624											
Sum of all eigenvalues	St.1	1.302											
	St.2	0.519											
	St.3	0.624											
Sum of all canonical eigenvalues	St.1	0.696											
	St.2	0.312											
	St.3	0.293											

Sp.-env. correlations species-environment correlations, Cum. Per. var. of sp. cumulative percentage variance of species data, Cum. per. var. sp.-env. cumulative percentage variance of species-environment relation

either dominant species outcompete other species or the environmental conditions may not be suitable for the growth of other species (Reynolds 1993). The surface water temperature in Lake Manyas was usually stable when steady-state phytoplankton assemblages were observed. During equilibrium phases, the environment is sufficiently persistent to allow the competitive exclusion to occur, resulting in lower diversity (Hardin 1960).

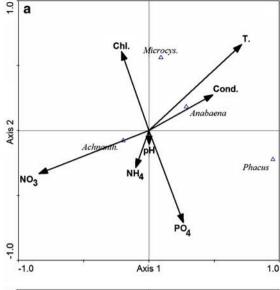
Padisak et al. (2003) found that the total number of species clearly increased in ten Hungarian lakes when they were not in equilibrium state. Studies on European lakes show that the composition of equilibrium assemblage is forced by the physical and chemical structure of the water column towards the dominance of species physiologically adapted to grow under such conditions (Elliott et al. 2000). The results of this study show that, in temperate shallow hypertropic lakes, equilibrium conditions lead to a decrease in the number of species.

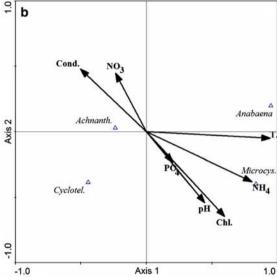
Abrupt variations in phytoplankton biomass with contribution from different taxonomic groups have been observed throughout the study period. Nevertheless, periods with constant biomass have been identified (Fig. 2). In 10 of 144 sampling periods, the additive dominance of the three most abundant species reached or exceeded 80% of the total biomass. In 134 of the sampling periods, the additive dominance of the 3 most abundant species did not exceed 70% of the total phytoplankton biomass, indicating that in Lake Manyas phytoplankton assemblages are usually far from equilibrium. Our results corroborate findings of earlier studies conducted on shallow eutrophic lakes in this region (Stoyneva 2003; Moustaka-Gouni et al. 2007).

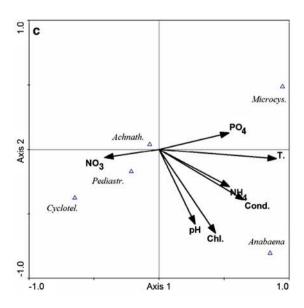


A. microcephala contributed more than 80% of the total phytoplankton biomass in 24 sampling periods (usually in cold periods), but only in four cases (in March 2003 at the first station and in February 2003 at the second station) the total biomass did not change significantly between two sampling periods (P > 0.05). The periods of the steady-state phases made by A. microcephala were characterized by low water temperature and higher nutrient concentrations. The monodominance (contribution of a single species to 80% or more of the total biomass) by cyanobacteria is usually detected during summer in hypertrophic conditions (Stoyneva 1998, 2003; Moustaka-Gouni et al.









◄ Fig. 5 Species—environmental variables biplot of canonical correspondence analysis (CCA). a At the first station, b at the second station, and c at the third station. The angles represent dominant species and the arrows represent environmental variables. Symbols: T. temperature; Cond. conductivity, NO₃ nitrate, PO₄ phosphate, NH₄ ammonium, Chl. chlorophyll; Achnanth. Achnanthes microcephala; Microcys. Microcystis aeruginosa; Anabaena, Anabaena spiroides; Cyclotel. Cyclotella stylorum; Pediastr. Pediastrum boryanum; Phacus, Phacus pusillus

2007), but in Lake Manyas the monodominance by *A. microcephala* was observed in cold periods. This difference is probably due to the inherent characteristics of *A. microcephala*.

The functional classification approach (Reynolds et al. 2002) is commonly used for describing conditions that promote or impede the dominance of certain types of phytoplankton species in water bodies (Naselli-Flores et al. 2003; Dokulil and Teubner 2003; Padisak et al. 2003). *A. microcephala* is classified in D assemblages, which inhabit shallow, nutrient rich and turbid waters. *A. microcephala*, the most dominant species in Lake Manyas, fitted well into this classification. High turbidity (Secchi depth less than 0.2 m) and high nutrient concentrations in Lake Manyas have contributed to its dominance throughout the year. Johnson et al. (1997) state that *Achnanthes* species can tolerate low light intensities.

Canonical correspondence analysis (ter Braak and Verdonschot 1995) is often used to visualize the seasonal patterns of phytoplankton species and the conditions accounted for such patterns in aquatic systems. In this context, the biomass of dominant phytoplankton species that made the steady-state assemblages and the measured physical and chemical parameters were analyzed using CCA. CCA showed that cyanobacteria species that made steady-state assemblages were closely related to water temperature. A. spiroides (functional group H1) and M. aeruginosa (functional group M) were always positioned close to the water temperature in the ordination diagram. These two species are commonly found in shallow eutrophic waters and usually cause blooms during warm seasons worldwide (Zohary et al. 1995; Via-Ordorika et al. 2004; El-Bestawy et al. 2007). It seems that high temperature and nutrient concentrations and low underwater light promote the steady-state dominance of M. aeruginosa and A. spiroides in the temperate shallow hypertropic lakes. The position of A. microcephala near the center of the CCA ordination diagram indicates its yearlong abundance.

Specific abilities of *M. aeruginosa* and *A. spiroides*, such as photoadaptation and buoyancy regulation, to effectively exploit resources contribute to the development of the steady-states made by these species (Reynolds et al. 2002). *M. aeruginosa* has the capability of diel migration that allows it to accumulate at the surface layer. In this



way, *M. aeruginosa* avoids direct competitition with the other species and thus increases its number. *M. aeruginosa* has often been found dominant in summer steady-state phytoplankton assemblages of hypertrophic shallow lakes in southeastern Europe (Stoyneva 2003; Moustaka-Gouni et al. 2007). Alvarez-Cobelas and Jacobsen (1992) state that *A. spiroides* is a stress-tolerant colony forming specialist and is widely collected from hypetrophic water bodies.

C. stylorum (functional group A), P. boryanum (functional group J), and P. pusillus (functional group W1) were represented in steady-state phytoplankton assemblages only once througout the study period. In the CCA diagram, C. stylorum could not be identified with any measured environmental variable, but P. boryanum showed a close relationship to nitrate. Although C. stylorum is known to grow best in oligotrophic lakes, this species is commonly collected from the eutrophic lakes across Turkey (Aykulu et al. 1983; Akbay et al. 1999). Reynolds et al. (1982) state that some centric diatoms such as species of Cyclotella are able to increase under almost any given environmental condition. Studies show that P. boryanum has always been a common member of phytoplankton assemblages in the lakes of this region (Albay and Akcaalan 2003; Miola et al. 2006).

During summer, *P. pusillus* grew excessively at the first station. Borics et al. (2003) state that environments with extremely high levels of organic matter favor the development of euglenoids. Shipin et al. (1999) found that species of *Phacus* were among the most versatile heterotrophic feeders and grew extremely well under high organic content and low light conditions. The first station receives direct waste from Sığırci Stream with higher organic matter and therefore it has lower transparency. These conditions probably promoted the development of *P. pusillus* at this station.

In conclusion, steady-state phases are rare in temperate shallow hypetrophic lakes. *M. aeruginosa* and *A. spiroides* represented in steady-state phytoplankton assemblages of Lake Manyas are common members of the steady-state phytoplankton in nutrient rich lakes worldwide (Naselli-Flores et al. 2003), but *A. microcephala*, the most dominant species in Lake Manyas, is not a common member of steady-state assemblages in hypertrophic shallow lakes. These patterns of steady-state phytoplankton assemblages are specific to temperate shallow hypertrophic lakes.

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