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Phytoplankton equilibrium phases during thermal stratification in a deep subtropical reservoir

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SUMMARY

1. Equilibrium and non-equilibrium hypotheses have often been used to explain observations in community ecology. Published case studies have demonstrated that steady state phytoplankton assemblages are more likely to occur in deep lakes than in shallow mixed ones.
2. Phytoplankton seasonal succession was studied by weekly sampling in Faxinal Reservoir (S Brazil), a subtropical deep, clear, warm monomictic and slightly eutrophic reservoir. This study demonstrated an alternation of steady and non-steady state phases of phytoplankton assemblages with different dominant species during the steady states.
3. During the studied period, three steady states were identified with different dominant algal species: *Anabaena crassa* (Cyanobacteria), *Nephrocytium* sp. (green algae) and *Asterionella* (diatoms).
4. Each steady state in Faxinal Reservoir developed under stratified conditions of the water column according to the predictions of the disturbance concepts. Apparently, the major forces driving the development and persistence of these steady-state phases were closely related to thermal stratification and its consequences.
5. This study is the first report on development of more than one steady state within a year in a stratified water body. The development of three steady states might be the result of the relatively long stratification period in the Faxinal Reservoir and to its unique geochemical features.

Keywords: Brazil, equilibrium phase, monomictic reservoir, steady state

Introduction

Equilibrium and non-equilibrium viewpoints may simply be considered as two ends of an ecological spectrum (Harris, 1986). In unstable environments, growth rates may be reduced and populations are limited by environmental factors (non-equilibrium). In more stable environments, population size may rise as a result of higher growth rates and competition between species becomes important (equilibrium).

Equilibrium and non-equilibrium hypotheses have often been used to explain community ecology. Steady state conditions are expected to be more likely to occur in deep lakes than in shallow mixed ones (Mischke & Nixdorf, 2003). Most reported phytoplankton steady-states have been related to stratified conditions (Dokulil & Teubner, 2003; Leitão *et al.*, 2003; Morabito, Oggioni & Panzani, 2003).

In natural phytoplankton communities, it is often difficult to determine whether a given ‘phase’ in a seasonal sequence can be considered to be in

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equilibrium or not, due to a lack of chemical data and/or to insufficient sampling frequency (Sommer *et al.*, 1993). Constancy of biomass is needed as a measure of functional persistence of the ecosystem (top-down and bottom-up controls are probably equilibrated or bottom-up dominates; Padisák *et al.*, 2003a). A maximum of three species contributing to at least 80% of total biomass for more than 2 weeks, without considerable variation in total biomass, has been proposed as a criterion to identify an equilibrium phase (Sommer *et al.*, 1993).

Ecologists have quite different opinions about the importance of competition in shaping diversity. For example, Harris (1986) assumes that competition contributes to the generation of diversity over evolutionary time scales but it may not be necessary to invoke competition as a mechanism to explain the maintenance of diversity over ecological time scales. In Connell's (1978), intermediate disturbance hypotheses competitive exclusion is the major mechanism that results in low diversity and the latter has been supported by theoretical models (Tilman, 1977), laboratory experiments (Sommer, 1985) and field studies (see a selection of papers in Padisák, Reynolds & Sommer, 1993).

Nevertheless, equilibrium theory takes one extreme viewpoint: competition was acting, is acting, and will always be acting (Harris, 1986). Steady state is a dynamic equilibrium as losses and gains are acting through time, and result in a relative invariance of the assemblage. Moreover, the mechanisms controlling steady-state phytoplankton assemblages would be competition, and/or trophic relationships and/or biogeochemical processes, and so on. Many other selective forces (grazing, allelopathy, bloom from a bank of resting stages, invasions, parasitism, etc.) in a complex aquatic system could be acting simultaneously, or alternately, and this may lead to the establishment of a steady state (Rojo & Álvarez-Cobelas, 2003). Each species in non-equilibrium community occupies a different niche that results from and reduces direct competition and thus species composition is more or less stable depending on environmental predictability (Whittaker, 1975).

In temperate-climate phytoplankton, a steady state is hard to find (Naselli-Flores *et al.*, 2003). Temperate zones are moderately stable in terms of physical and biological conditions in comparison to other geographical regions. Steady state conditions are more probable and longer lasting in tropical (Ganf, 1974; Rott, 2002) and polar region (Allende & Izaguirre, 2003) because seasonal changes vary over a narrower range and at least one season is considerably longer than the others.

In this paper, we analyse the weekly changes of phytoplankton composition and biomass in a subtropical, eutrophic, monomictic reservoir in order to identify equilibrium phases, according to the definition given by Sommer *et al.* (1993). These phases are generally expected during thermal stratification when disturbance is weaker and progression towards equilibrium is likely to occur.

Methods

Study site

Faxinal Reservoir (29°05′00″S; 51°03′30″W) is the main water supply system of Caxias do Sul City (400 000 inhabitants), in the south of Brazil (Fig. 1). It has a surface area of 3.1 km^2 at 700 m a.s.l. The Reservoir is deep (z_{max} = 30 m), warm monomictic and eutrophic (TP 29.4 $\mu g\ L^{-1}$ and chlorophyll *a* 15 $\mu g\ L^{-1}$ – epilimnion annual mean). The regional climate is temperate without a dry season (Cfa type; Köppen, 1936) with an average annual temperature of 16 °C and precipitation between 1800 and 2200 mm.

Sampling

The criteria for sampling were based on those set by the Water Company sampling protocol: weekly algal monitoring (at the surface) and monthly nutrient analyses in the Faxinal Reservoir, in the water intake sampling station (Fig. 1) since 2002. Although this sampling frequency was set to be sufficient for management needs, it is adequate to follow changes in phytoplankton composition (Sommer *et al.* 2003) and its adequacy was supported recently by Monte-Carlo simulations (Honti, Istvanovics & Osztoics, 2007).

Profiles of temperature, dissolved oxygen, pH and conductivity were measured with a multiparameter probe Horiba (model U-10), at 1 m intervals from the surface to the bottom. Transparence of the water was estimated with a Secchi disk; turbidity (NTU) was measured with a turbidimeter HACH 2100P. Phytoplankton samples were taken weekly (January 2004–January 2005) from the surface layer (between 0

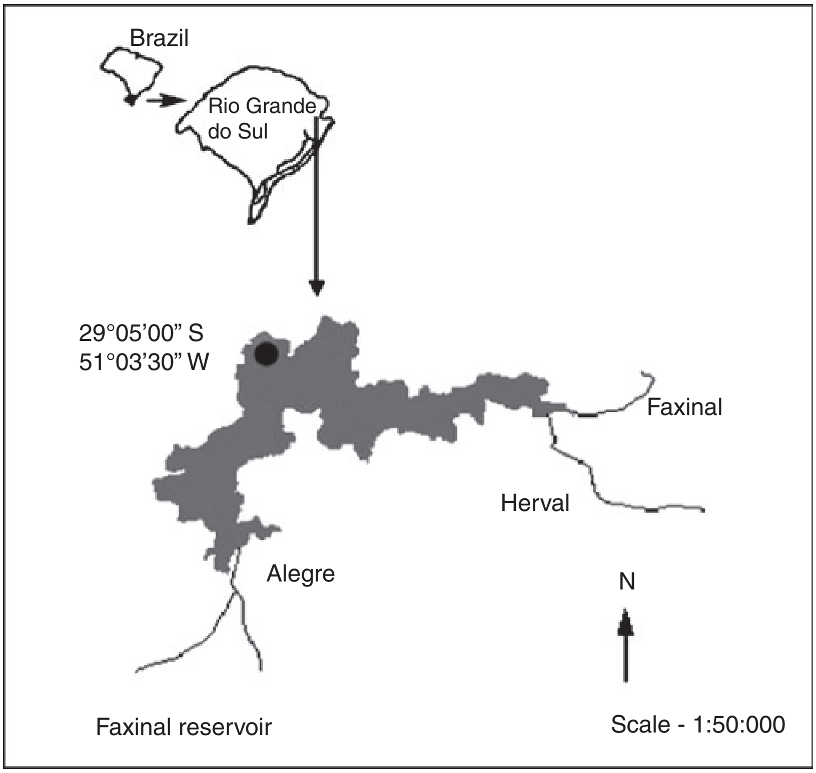

Fig. 1 Faxinal Reservoir showing the sampling station.

and 0.5 m) at the deepest part of the reservoir with a Van Dorn bottle (2 L), and they were preserved with neutral Lugol's iodine solution.

Monthly samples for analyses of inorganic nutrients were collected at the surface, with a Van Dorn Bottle (2 L), at a fixed time (09:00 am).

Sample analysis

Dissolved inorganic nutrients – soluble reactive phosphorus (SRP), nitrite (NO_2-N), nitrate (NO_3-N), ammonium (NH_4-N) and soluble reactive silicate (SRSi) – were analysed in filtered samples (Sartorius membrane cellulose acetate filters; 0.45 μm). SRP and NO_2-N were measured spectrophotometrically (Murphy & Riley, 1962; Aminot & Chaussepied, 1983). NO_3-N was measured by flow injection analysis using the cadmium reduction method (Wood, Armstrong & Richards, 1967; modified by Aminot & Chaussepied, 1983), NH_4-N by the indophenol spectrophotometric method (Solorzano, 1969; modified by Strickland & Parsons, 1972) and SRSi by the molybdate method (Mullin & Riley, 1955).

Phytoplankton was quantitatively analysed with a Leica - DMIL inverted microscope (Utermöhl, 1958) at 400×. Settling units (cells, colonies and filaments) were enumerated in random fields (Uhelinger, 1964) and at least 100 specimens of the most frequent species were counted (Lund, Kipling & Lecren, 1958).

Data analysis

Euphotic zone (z_{eu}) was calculated as 2.7 times the Secchi depth (Cole, 1994) and mixing zone (z_{mix}) was estimated from temperature and dissolved oxygen profiles. The ratio between euphotic and mixing depths ($z_{\mathrm{eu}} : z_{\mathrm{mix}}$) was used as a measure of light availability (Jensen *et al.*, 1994).

The dimensionless parameter relative water column stability (RWCS) was calculated according to Padisák *et al.* (2003b) by comparing the density difference between bottom (D_{b}) and surface (D_{s}) water to the density difference between 4 °C (D_4) and 5 °C (D_5) of pure water, using the formula:

$$\mathrm{RWCS} = \frac{D_{\mathrm{b}} - D_{\mathrm{s}}}{D_4 - D_5}$$

Phytoplankton biomass was estimated volumetrically (Edler, 1979; Hillebrand *et al.*, 1999) assuming a specific gravity of 1 mg mm^{-3} (Wetzel & Likens, 2000).

Steady-state phases were identified according to Sommer *et al.* (1993): no more than three coexisting species, contributing more than 80% to the total biomass, for at least 2 weeks. The Shannon and Wiener function was used to measure compositional diversity (Shannon & Weaver, 1949) from biomass data; evenness was calculated according to Pielou (1966).

Nonparametric correlation (Spearman) analyses were used to determine relationships among the biomasses of dominant species and the environmental factors (mixing regime, light and nutrients).

Results

Physicochemistry scenario

Temperature profiles allowed us to identify only one period of total vertical mixing, which occurred in winter (June–August 2004; Fig. 2). Consistently, the relative stability of the water column (RWCS) reached its maximum of 296 in January 2004 (Fig. 3). The mixing zone was euphotic during summer and autumn, and the euphotic depth decreased to only 60% of the epilimnion during spring (Fig. 4). Turbidity

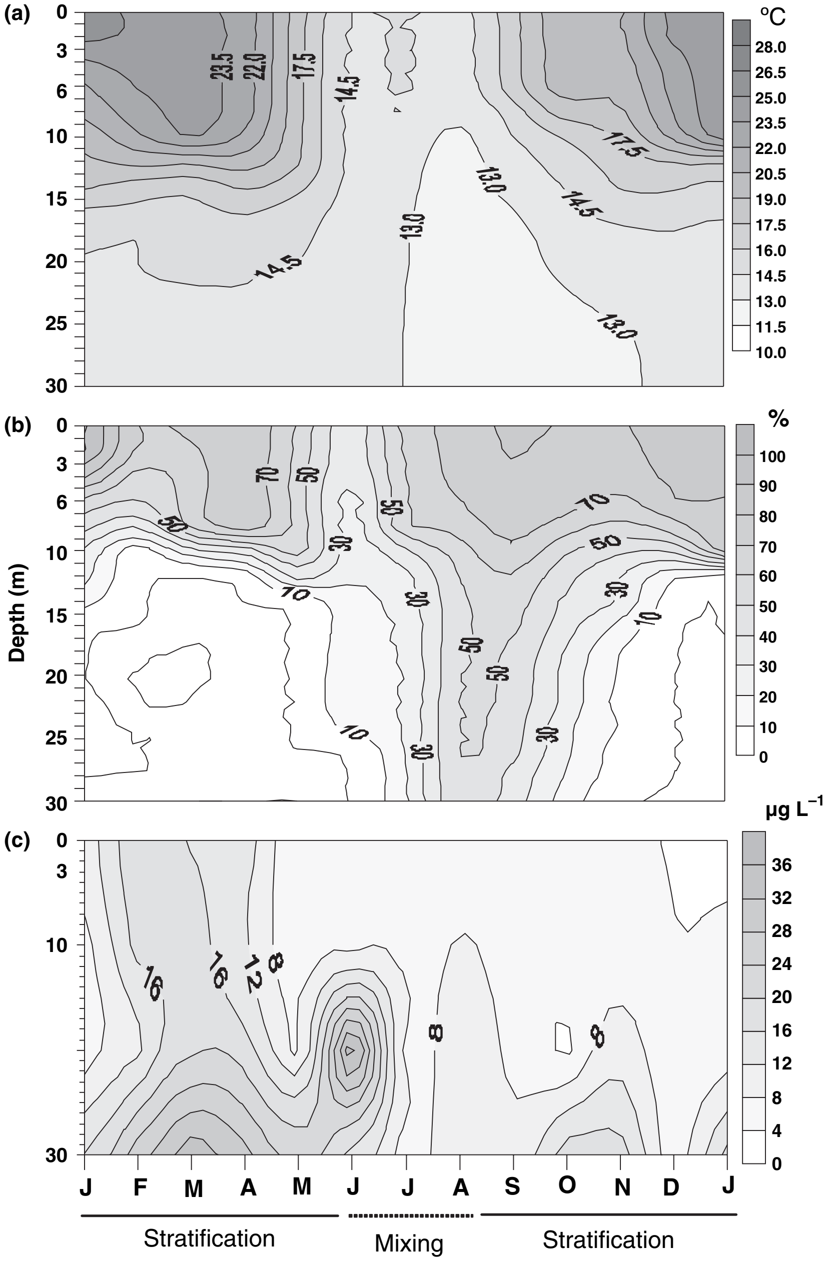

Fig. 2 Depth-time isopleths of (a) temperature (ºC); (b) dissolved oxygen (%); (c) soluble reactive P (μg L^{-1}) in Faxinal Reservoir in 2004.

was closely related to the mixing regime with high values during the mixing period (Fig. 4).

Anoxic conditions were observed from 14 m to the bottom of the reservoir only during the first stratification period. Orthograde oxygen profiles were recorded only during the mixing period (Fig. 2). Slightly alkaline conditions characterized the epilimnion during the entire period, with an annual average pH of 7.58 (Fig. 4).

Nutrient dynamics (Table 1) were driven by the stratification pattern. In particular, SRP showed its highest values in the first stratification period (Fig. 2c), probably due to the strong hypolimnetic anoxia. At the same time, dissolved inorganic nitrogen (DIN) and SRSi concentrations were low. After the vernal overturn, SRP decreased and ammonium increased sharply, followed by a similar increase in nitrate concentrations that indicated a gradual

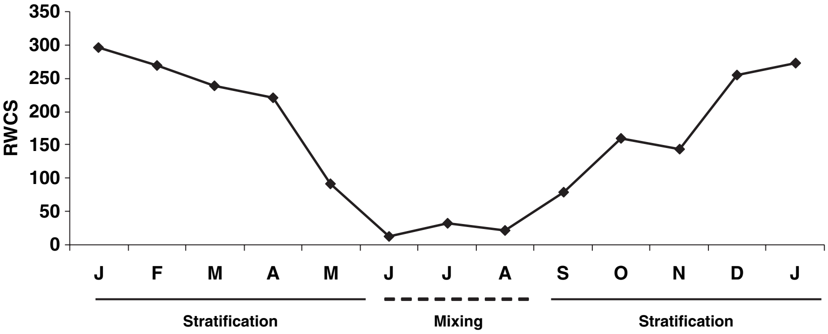

Fig. 3 Seasonal variation of relative water column stability (RWCS) in Faxinal Reservoir in 2004.

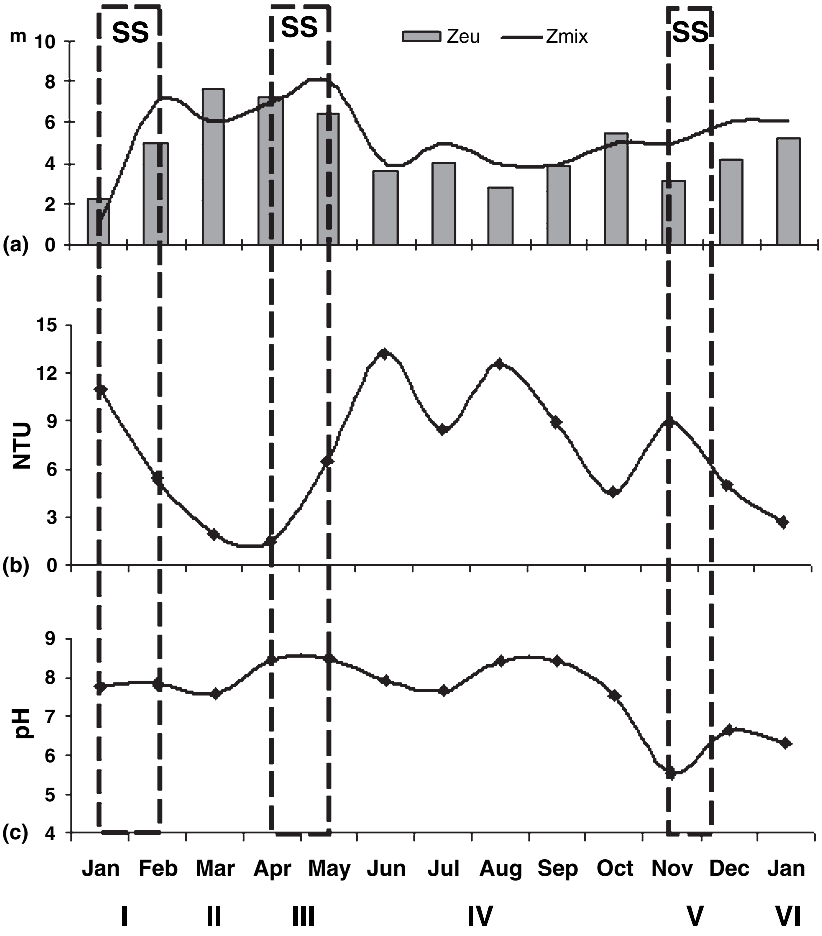

Fig. 4 Seasonal variation of: (a) euphotic zone (shade bar) and mixing zone (black line), (b) turbidity (NTU) and (c) pH in Faxinal Reservoir in 2004. Shaded areas (SS) indicating steady states identified by the phytoplankton composition.

Table 1 Mean and ranges of limnological variables and compositional features of phytoplankton, in the epilimnion of Faxinal Reservoir in 2004

	I (SS)	II	III (SS)	IV	V (SS)	VI
Temperature (°C)	25.7 (25.0–26.2)	24.5 (23.8–25.1)	23.5 (23.1–24.1)	16.7 (13.7–21.6)	20.7 (19.9–21.2)	24.5 (23.9–24.7)
Conductivity (µS cm^{-1})	27.0 (26.0–28.0)	26.6 (26.0–27.0)	27.0	38.0 (27.0–55.0)	37.5 (37.0–38.0)	38.9 (37.0–41.0)
PH	7.9 (7.8–8.0)	7.7 (7.5–7.9)	7.4 (7.0–7.6)	7.2 (6.5–8.0)	6.4 (5.8–6.8)	6.9 (6.3–7.4)
DO (mg L^{-1})	9.4 (9.1–9.9)	6.6 (7.2–7.6)	7.4 (7.2–7.6)	7.1 (3.4–8.8)	8.4 (7.9–8.7)	7.6 (7.1–7.8)
% DO	105.5 (101.8–111.6)	72.5 (78.3–81.3)	79.9 (78.3–81.3)	67.4 (30.1–86.1)	85.9 (79.1–89.9)	83.7 (79.1–89.9)
SRSi (µg L^{-1})	2463 (1112–4920)	2223 (1122–2833)	2190 (2078–2423)	4133 (1101–9542)	2173 (944–2724)	1603 (449–3249)
N-NH$_4^+$(µg L^{-1})	75.1 (53.2–93.8)	119.7 (44.8–221.2)	38.6 (23.8–53.2)	249.2 (26.6–1113.0)	58.0 (50.4–63.0)	70.1 (49.0–88.2)
N-N0$_3^-$ (µg L^{-1})	84.7 (15.4–201.6)	48.8 (7.0–78.4)	87.6 (15.4–219.8)	219.9 (21.0–387.8)	192.8 (172.2–215.6)	77.9 (22.4–105.0)
N-N0$_2^-$ (µg L^{-1})	2.2 (1.5–2.9)	4.0 (2.0–6.7)	1.7 (0.8–2.2)	2.4 (0.3–6.7)	2.3 (2.0–2.9)	2.1 (1.0–2.9)
SRP (µg L^{-1})	39.9 (2.8–111.0)	25.4 (13.0–61.1)	12.8 (11.5–14.3)	4.8 (1 .9–9.6)	4.4 (2.5–6.2)	3.0 (1.6–4.3)
DIN (µg L^{-1})	164.4 (89.6–294.0)	173.7 (40.6–264.6)	126.2 (40.6–264.6)	460.8 (65.8–1215.2)	253.1 (226.8 281.4)	149.5 (95.2–190.4)
Richness (no. taxa)	6 (5–8)	15 (5–24)	20 (13–24)	15 (10–25)	14 (5–25)	12 (12–13)
Diversity (bits mg^{-1})	0.28 (0.07–0.69)	1.67 (1.10–2.08)	0.71 (0.48–1.05)	1.23 (0.02–2.43)	1.06 (0.72–1.48)	1.58 (1.14–1.82)
Eveness (%)	6.1 (3.9–12.3)	33.2 (6.2–66.3)	51.3 (42.9–63.7)	46.7 (9.0–76.7)	41.7 (26.4–75.6)	49.2 (28.8–73.2)
Biomass (mg L^{-1})	48.3 (11.8–73.9)	18.0 (5.6–39.7)	66.6 (16.9–92.1)	25.8 (0.5–357.4)	26.4 (16.8–43.9)	6.8 (3.3–10.3)

SS, steady state phase.

nitrification. The re-establishment of thermal stratification in autumn resulted in a decrease in SRSi concentrations but no marked changes in the other nutrients.

Phytoplankton dynamics

Seasonal composition of phytoplankton allowed six different periods to be distinguished (Fig. 5). Three steady state phases were identified, with different dominant algal groups: period I was dominated by *Anabaena crassa* (Lemmermann) Komárková-Legnerová; period III by *Nephrocytium* sp. and period V by *Asterionella Formosa* Hass. Table 1 shows the main limnological variables of Faxinal Reservoir and the diversity-related compositional characteristics of its phytoplankton recorded in the epilimnion during the six periods.

Period I (January 8–February 10) This period was characterized by a 6-week long steady state with dominance of *A. crassa* making up to 90–99% of total biomass (Fig. 5). Strong stratification prevailed and the euphotic zone extended to the entire mixing zone (Fig. 4). The lowest DIN and the highest SRP concentrations were registered in this period. The highest stable phytoplankton biomass values (mean value = 48.3 mg L^{-1}) were found in this period, and species richness was low (Table 1, Fig. 6).

Period II (February 17–April 6) In late summer an abrupt shift in phytoplankton composition took place. Cyanobacteria were replaced by several chlorophyte species without clear dominance patterns (Fig. 5). This period lasted for 5 weeks during which the number of taxa and diversity were high (Fig. 6) and no significant differences in nutrient concentrations occurred compared to period I.

Period III (April 14–May 5) A second steady state phase was identified in autumn in parallel with the erosion of the thermocline. The colonial green alga *Nephrocytium* sp. dominated the assemblage, making up to 66–90% of total phytoplankton biomass (Fig. 5). Phytoplankton diversity was consistently low; however, species richness was somewhat higher than in the previous period (Fig. 6). Inorganic nutrient concentrations changed inversely: SRP decreased and DIN significantly increased (Table 1).

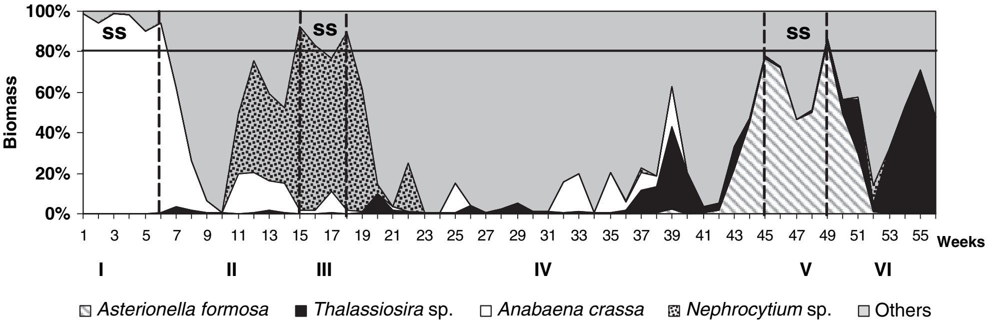

Fig. 5 Seasonal variation of dominant phytoplankton species biomass (%) in Faxinal Reservoir in 2004. SS, steady state phase.

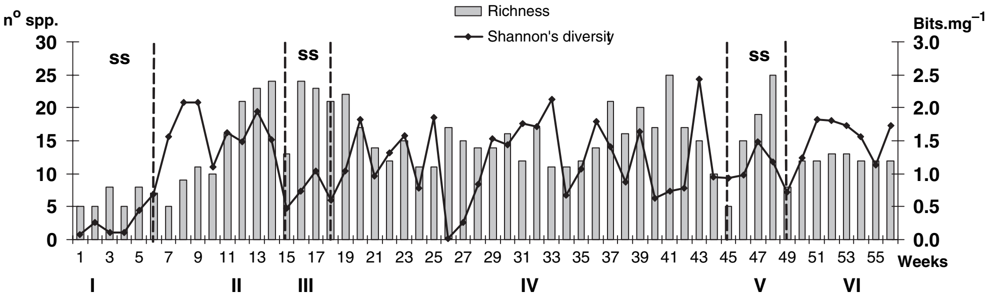

Fig. 6 Seasonal variation of species richness (grey bars) and Shannon's diversity (black line) in Faxinal Reservoir, in 2004. SS, steady state phase.

Period IV (June–August 2004) Mixing occurred in this period. Phytoplankton biomass was low without evident dominants but with highly variable diversity (Figs 5 & 6). High concentrations of DIN and SRSi were recorded (Table 1).

Period V (November 3–December 15) After the onset of thermal stratification, high amounts of SRSi allowed growth of diatoms. First *Thalassiosira* sp. started growing but it was rapidly replaced by a fast growing population of *A. formosa.* The latter dominated the phytoplankton assemblage for more than 2 weeks (Fig. 5) and this period can be taken as a third equilibrium phase with low diversity values (Fig. 6) and decreasing SRSi and DIN (especially nitrate) concentrations (Table 1).

Period VI (December 15–January 26) After the decline of *A. formosa*, *Thalassiosira* sp. started growing again (Fig. 5). Due to the small size of this diatom, phytoplankton biomass was low (average = 6.8 mg L^{-1}). SRP dropped below the detection level and might have been limiting phytoplankton growth as well as SRSi (Table 1).

The identified steady-state species were significantly correlated with most of the expected environmental factors, such as mixing regime, light and nutrients (Table 2). A strong correlation was seen between *A. crassa* biomass and temperature ($P < 0.001$). This species was also positively correlated with turbidity, water stability and SRP (all $P < 0.05$), and negatively correlated with NO_3-N ($P < 0.05$). In addition, significant positive correlations were observed between *Nephrocytium* sp. biomass and both euphotic and mixing zones; conversely negative relationships were found with turbidity and NO_3-N (all $P < 0.001$). *Asterionella formosa* biomass was significantly positively correlated with NO_3-N ($P < 0.05$), and negatively correlated with SRSi, SRP (both $P < 0.001$) and NH_4-N ($P < 0.05$).

Discussion

Dating, at least, back to Hutchinson's (1961) famous paradox, equilibrium and non-equilibrium concepts have been a focus of ecological research, both terrestrial (see for example Wilson, 1994) and aquatic (Padisák, 1994). In fact, contemporary ecology

Table 2 Results from Spearman's correlation between dominant species biomass and environmental variables (only significant values $P < 0.05$ are shown)

	Biomass		
Abiotic variable	*Anabaena crassa*	*Nephrocytium* sp.	*Asterionella formosa*
Temperature	0.44*		
z_{eu}		0.54*	
z_{mix}		0.47*	
Turbidity		−0.45*	
pH	0.37		
Conductivity		−0.28	
NH_4-N			−0.28
NO_3-N	−0.63	−0.48*	0.40
SRSi			−0.35*
SRP	0.68		−0.53*
RWCS	0.50		

SRSi, soluble reactive silicon; SRP, soluble reactive phosphorus; RWCS, relative water column stability.
*$P < 0.001$.

(whether terrestrial or aquatic) relies heavily on these concepts, either directly or indirectly. It is not unusual in such thoroughly discussed topics for different researchers to have contrasting opinions. Thus, Harris's (1986) early concepts were principally based on physiological ecology of phytoplankton and on dynamic features of population changes in lakes. Here, however, we base our discussion on the more community-ecology oriented concepts originating in Sommer's (1983, 1984, 1985, 1989, 1991a,b), and their later expansion to temporal changes of phytoplantkon in natural environments.

According to the criteria set by Sommer *et al.* (1993), our study has demonstrated the alternation of steady and non-steady state phases of phytoplankton assemblages dominated by different species. Each steady state in Faxinal Reservoir developed under stratified conditions of the water column. The major forces driving the development and persistence of these steady-state phases seem to have been closely related to thermal stratification and its consequences.

The overwhelming dominance of *A. crassa*, during summer, constituted the clearest and most obvious steady state phase, strongly related to water column stratification parameters, RWCS and temperature. Low nitrogen concentrations and high SRP favours the growth of this nitrogen-fixing cyanobacterium. The dominance of bloom-forming cyanobacteria has been linked to physical and chemical features of waterbodies the mechanistic explanation comprises: (i) water column stability and algal buoyancy control (Reynolds, 2006); (ii) high water temperature (Shapiro, 1990); (iii) nutrient content, particularly low N : P ratios (Smith, 1983), high P (Trimbee & Prepas, 1987; Watson, Mc Cauley & Downing, 1997), (iv) low CO_2/high pH (Shapiro, 1990); (v) low underwater light (Smith, 1986; Havens *et al.*, 1998). Cyanobacterial steady states are always accompanied by low diversity and have been described in many eutrophic lakes in the North temperate zones (Elliott, Reynolds & Irish, 2000; Mischke & Nixdorf, 2003; Morabito *et al.*, 2003). These cyanobacterial steady states have been attributed to strong vertical segregation of the water column and the consequent increased selectivity set by a reduced mixing depth.

During the autumn, the water column was still stratified, but the RWCS was declining. The mixed epilimnion and low availability of nutrients contributed to dominance by *Nephrocytium* sp., forming the second steady state in Faxinal Reservoir. The stronger positive correlations with z_{eu} and z_{mix}, and negative correlations with turbidity and nitrate support this hypothesis. Non-motile Chlorococcales embedded in mucilage are able to grow under thermal stratification and in a relatively deep optical depth; they are dependent on water turbulence in the epilimnion for resuspension (Happey-Wood, 1988). Green algal steady states occur less frequently as compared to cyanobacteria. There are few described cases from deeply stratifying water bodies; the filamentous *Planctonema lauterbornii* Schmidle was observed in a reservoir in France (Leitão *et al.*, 2003) and other filamentous green algae may also form a steady state as indicated, for example, by the recurrent dominance of *Mougeotia* sp. in Lake Garda, Italy (Salmaso & Padisák, 2007). In two North American lakes, *Botryococcus braunii* Kützing has been reported twice in an equilibrium phase formed by three species (Huszar, Kruk & Caraco, 2003) of which in one case the co-dominants were chlorococcalean green algae [*Willea wilhelmii* (Fott) Komárek and *Eutetramorus planctonicus* (Korsikov) Bourrelly]. *Nephrocytium* sp., which formed the second steady state in Faxinal Reservoir, is morphologically similar to *Eutetramorus* since both are chlorococcalean, colonial green algal species and their colonies are embedded in thick mucilage. Clear epilimnia might contribute to the success of these species since colonial green algae generally have a substantially higher light demand than most planktonic cyanobacteria or diatoms (Padisák, 2003).

After the winter overturn, with low biomass values and no clear species dominance, the stability of the water column again started increasing. The more stable conditions in dominance, the water column stability again started increasing. This more stable environmental condition, in spring favoured the development of the third steady-state (period V), due to the rapid increase of the diatom *A. formosa*. This species has already been observed in steady state in lakes and reservoirs of different trophic status (Albay & Akcaalan, 2003; Morabito *et al.*, 2003). In Faxinal Reservoir, the dominance of this species was significantly correlated with the decrease of dissolved nutrients. The dominance of *A. formosa* might be related to its fast growth rates coupled to the fact that the diatoms are good competitors for nutrients, especially phosphorus (Sommer, 1988). The deficiency in SRP in this period was probably caused by its unavailability in the epilimnion due to stratification and little redistribution of nutrients through mixing (Miller *et al.*, 2005). The observed fluctuations in *A. formosa* dominance are probably due to the occurrence of a calm period when most of the population might have sunk to the bottom of the mixed layer, so that its contribution to total biomass was underestimated due to the depth of sampling. The sinking may be halted when cells reach the thermocline, where they may accumulate in the metalimnetic layer and eventually be resuspended after a wind event (Willén, 1991).

Phytoplankton assemblages are sensitive to periodic, largely weather-driven disturbances that prevent succession from proceeding towards an ecological equilibrium (Reynolds, Padisák & Sommer, 1993). This is the major reason why equilibrium phases rarely establish in standing waters. Most previous case studies have reported either a lack of such phases or the establishment of only one in a seasonal cycle (Naselli-Flores *et al.*, 2003). These singular equilibria typically establish either under stressed conditions or in late summer (Padisák *et al.*, 2006; Hajnal & Padisák, 2008). In this sense, as far as we know, Faxinal Reservoir represents a unique case with three phytoplankton steady states, involving different major taxonomic groups during 1 year of study. In terms of nutrient availability, size and morphometry, Faxinal Reservoir does not differ from other reservoirs where steady state phases have already been recorded (Albay & Akcaalan, 2003; Leitão *et al.*, 2003). However, some remarkable features can be emphasized. The first is linked to a longer duration of stratification as compared to most of the lakes where steady states have been previously investigated; the longer period may allow the establishment of more than one such phase. A second reason concerns the geochemical features of Faxinal Reservoir. It was built on an old geological formation with low release of ions and this is combined with high precipitation. These limnological peculiarities result in very low conductivity values, and consequently in low buffering capacity. The latter, along with the anoxic hypolimnetic conditions, allows nutrient concentrations to vary over a wide range. However, these changes are not rapid or frequent enough to be classified as disturbance events that would prevent the establishment of equilibrium phases.

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