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Phytoplankton and Equilibrium Concept: The Ecology of Steady-State Assemblages.

Steady state of phytoplankton assemblage in the tropical Lake Catemaco (Mexico)

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Abstract

Phytoplankton of the tropical lake Catemaco (Veracruz, Mexico) showed similar species composition during samplings from 1993 to 1995. There were two small dominant cyanobacterial species *Cylindrospermopsis catemaco* Kom.-Legn. et Tavera and *Cylindrospermopsis philippinensis* (Taylor) Kom., and a group of larger algae and cyanobacteria that were always present, however in smaller numbers: *Aulacoseira granulata* (Ehr.) Simons morphotype *curvata*, *A.* cf. *italica* (Ehr.) Simons mf. *curvata*, *Fragilaria construens* (Her.) Grun., *Achnanthes minutissima* Kütz., *Planktolyngbya circumcreta* (G.S.West) Anagn. et Kom., *Chroococcus microscopicus* Kom.-Legn. et Cronberg. Moreover we found several other scarcely present species. The percentage of total biomass of the two dominant species of *Cylindrospermopsis* varied between 34 and 81%, but they accounted for 80 to 95% of abundance. Apart from geomorphological features and climate conditions, biological variables played an important role. Fish-stock was formed by filter-feeding native herbivorous species of fish *Dorosoma petenense* (Günther), *Bramocharax caballeroi* (Contreras et Rivera), *Astyanax mexicanus* (Filippi), and an introduced, also herbivore *Oreochromis niloticus* (L.). Feeding activity of fish removed large species of algae and cyanobacteria as well as detrital remnants and zooplankton from the water. Smaller, inedible cyanobacteria remained in the water and formed the stable portion of the phytoplankton, dominant both in biomass and abundance. CANOCO analysis of samples and species variability demonstrated results of competition between two species of *Cylindrospermopsis*: steady state during the dominance of *C. catemaco* lasting probably for the whole year 1993 (one dry and one wet season) and steady state during the dominance of *C. philippinensis* in 1994 and 1995. According to the functional classification of phytoplankton suggested by Reynolds et al. (2002), Catemaco dominant assemblage would belong to the functional group $\mathbf{S_N}$.

Introduction

According to Reynolds et al. (2002) and Rojo & Álvarez-Cobelas (2003), "a steady-state assemblage means the invariance of its species composition over some time period". Thus, the dominant species should represent at least 50–80% of total abundance and the steady state period should last at least 2 weeks.

The definition of a steady state must also account for the stability of biomass concentration of the assemblage. Rojo & Álvarez-Cobelas (2003) suggested not insisting on its invariability in case the percent share of main dominant species remains the same. However a recommendation was accepted by attendants of the 13th IAP symposium (Naselli-Flores et al., 2003) to look for steady state situations maintained by competition between the potential dominants and not by biomanipulation or random events. The steady state is understood as the result of a dynamic equilibrium.

A phytoplankton steady state in temperate regions under completely natural conditions, i.e. without biomanipulation, is not easy to find. Disturbance of the system due to seasonal changes and weather variability is too great and variable. Shallow, polymictic lakes or ponds in summer are more promising biotopes (Nixdorf et al., 2003, Mischke & Nixdorf, 2003). Among deep water-bodies situated in temperate zones, lakes with a long retention time have a greater chance to have a steady state in warm, quiet summers (Salmaso, 2003), especially when the conditions are favourable for filamentous cyanobacteria (Reynolds, 1994). A permanent limitation by some of the important nutrients and a stable temperature course can reduce the assemblage to one or two competing dominants. Not only physical factors but also biotic events (spring outburst of calanoids, increasing abundance of filtering herbivorous *Daphnia* species etc.) influence exchange of the phytoplankton species and interrupt a potential steady state soon after its occurrence. Temperate zones are moderately stable in terms of physical and biological conditions in comparison with other geographical zones. Steady state conditions would be more probable and longer lasting in tropical (Ganf, 1974; Rott, 2002) and polar regions (Allende & Izaguirre, 2003) because of the smaller ranges in physical changes.

The geomorphology of water-bodies and their water discharge are other important arguments for the appearance of the steady state of phytoplankton. Shallow polymictic lakes are promising localities for the establishment of a phytoplankton steady state. Their everyday overturn (atelomixis, Barbosa & Padisák, 2002) provides a 'dynamic equilibrium' state for the phytoplankton by its regularity. Based on the preconditions for a steady state, shallow tropical lakes with long retention times and regular mixing due to wind appear to be the most convenient biotope for the emergence and susceptibility of the steady state (Ganf, 1974; Reynolds, 1989; Rott, 2002).

Considering the complex of biota that influence the phytoplankton of any of water bodies, top down control plays a more and more decisive role with increasing eutrophy. However, highly eutrophic and hypertrophic water bodies are exceptions to this point of view. The high bulk of inedible algal biomass in the water results in this potential pool of organic matter and nutrients starts to have a driving role for the water body (Reynolds, 1984). Especially when composed of cyanobacteria, such assemblages can remain for a long time in the lake even if they may not be photosynthetically active. In temperate zones such populations may disappear only with autumnal cold weather and mixing of the water column (Reynolds et al., 1991; Komárková & Hejzlar, 1998). Maintenance of such a steady state situation can be predicted from the previous behavior of the epilimnion, and should be carefully followed especially by water work authorities in reservoirs used for drinking water production. Production of toxic substances by the dominant cyanobacterial assemblage is very probable (Chorus & Bartram, 1999). In our opinion, a situation where the remnants of summer populations survive during the autumnal months cannot be considered as a steady state.

The aim of this paper is to describe the steady state conditions in a shallow tropical lake with small physical and chemical disturbances during the dry and rainy seasons and with a long retention time. This steady state is the result of a cycling food web and the existence of a special composition of phytoplankton due to competition between the two dominant cyanobacteria.

Lake Catemaco

The lake is situated between 18° 27′–18° 21′ N and 95° 01′–95° 07′ W in Los Tuxtlas region, State Veracruz, in an extensive volcanic area, at 332 m above sea level (Fig. 1). Climate is humid and hot (air temperatures between 12 and 38 °C), with a long lasting rainy season in the summer. The region is regarded as one of the most humid in Mexico (Fig. 2).

The primary vegetation is evergreen tropical forest (Miranda & Hernandez, 1963). However, a great portion of the land around the lake has been deforested recently and used for agriculture and livestock purposes. The small town of Catemaco (about 60 000 inhabitants, Tavera & Castillo, 2000) is situated on the west shore and more than about 10 000 people, mainly fishermen with families, live around the lake. The town releases waste water into the lake.

The lake is a rich source of fish-stock, composed of native Poecilidae and Characidae (*Dorosoma petenense, Bramocharax caballeroi, Astyanax mexicanus*), and an introduced cichlid *Oreochromis niloticus* (tilapia). An adequate portion of fishstock is netted every day by fishermen living in the surroundings. Catemaco lake is catalogued as one of the most productive in Mexico.

Water in lake has a permanently slightly blue-green color and transparency is low. The species composition of phytoplankton and appearance of specific spe-

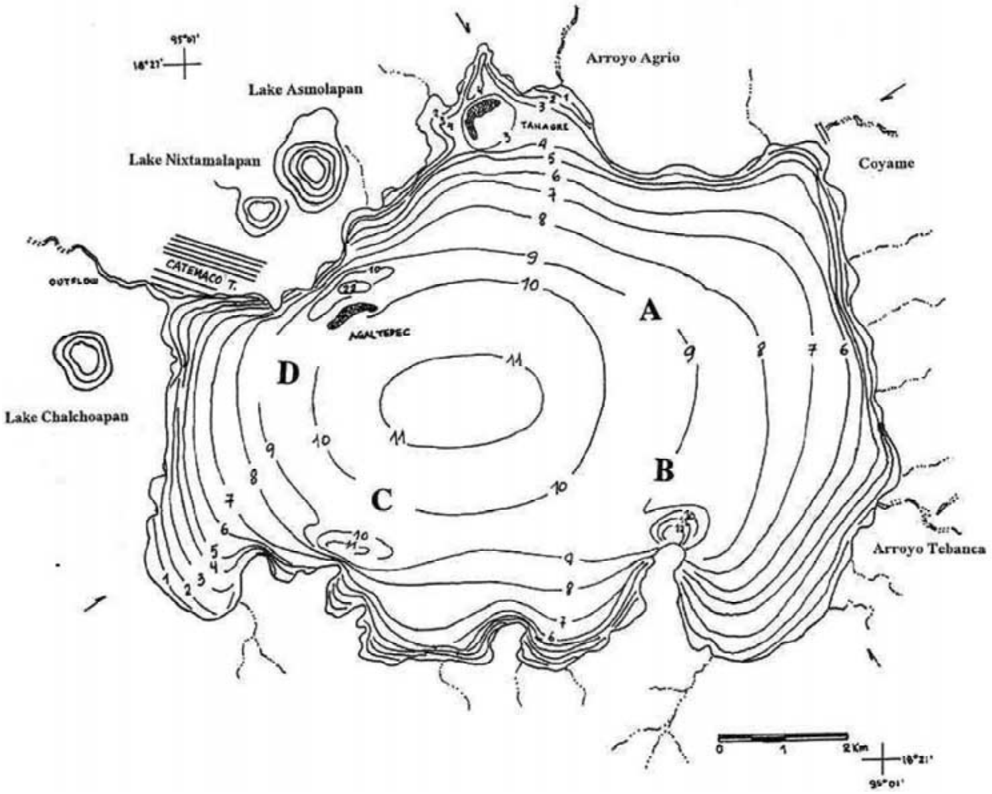

Figure 1. Lake Catemaco, Veracruz State, Mexico. Morphometry and bathymetry from Pérez-Rojas & Torres-Orozco (1992). Sampling sites are marked with capitals.

cies of Cyanobacteria were studied in detail in 1993 (Komárková & Tavera, 1996).

Morphometrically the bed is a rounded shallow bowl without deep bays (Fig. 1). The surface of the lake is 72.5 km^2 and the area of the watershed is 244 km^2. Maximum depth is 11 m and mean depth 7.6 m. Relative depth (z_R, Hutchinson, 1957) is 0.229%, so that there exist conditions for a permanent mixture of the water column. Average retention time is 0.9 year. The bottom is formed of clays and silt clays and covered with voluminous layer of organic matter. There is a transition to coarse sand with pebbles and gravel toward the littoral.

The region is rather windy, with a mean wind speed of 3–4.2 m.s^{-1} (Atlas Nacional de México 1990). Maximal wind speed is reached either during the winter winds ('nortes') from November to February, or during cyclones in the Gulf of Mexico which can occur from July to September.

Methods

Sampling of phytoplankton, zooplankton and measuring of the main chemical and physical variables (pH, alkalinity, oxygen concentration, conductivity, temperature, transparency) were performed at four pelagic sites (A–D, see Fig. 1). We chose six sampling periods from the total sampling set (Table 1), representing dry and rainy periods in the three consecutive years: May and August 1993 (DRYMay3, RAIAug3), May and September 1994 (DRYMay4, RAISep4), and May and August 1995 (DRYMay5, RAIAug5). Each of them is a mean of samples taken at four sites in the lake (A–D, Fig. 1).

Samples for more detailed chemistry were taken only in May and August in 1993 and were analyzed in the Chemical Laboratory of the IMTA, Juitepec, Morelos. As the other analyses from 1995 were fewer and were processed in another laboratory, we decided to use only the data from 1993 to determine the ranges of nutrient concentrations in the lake.

Table 1. Frequency of phytoplankton sampling during three successional years. Rain season is marked in black

	J	F	M	A	M	**J**	**J**	**A**	**S**	**O**	**N**	**D**
1993		x	x	x	x	x		x				
1994	x				x				x	x	x	
1995	x	x	x	x	x	x		x				

Samples from all four sites were taken at the surface, 3m, and the horizon above the bottom (mostly 7 or 9 m) using a Van Dorn sampler. Qualitative samples for zooplankton were taken by hauling an Epstein plankton net (70 and 200 μm mesh) from the bottom to the surface at each site. A chlorophyll concentration was estimated according to Lorenzen (1967) and corrected for pheopigments. Phytoplankton was estimated by counting the cells after sedimentation in Utermöhl chambers (Lund, 1951; Sournia, 1978). The abundance of each species is presented as the number of organisms (or units) per milliliter; filamentous and coenobial algae were considered as a unit. Cell volumes were calculated from measures of their shapes and applied to the relevant geometrical solids. Biovolume was converted to biomass and expressed as mg l^{-1} fresh mass (FM). The samples were preserved in Lugol solution. Other biological samples were preserved in 1.5–3% formalin. Analyses were conducted on the biomass data (fresh mass, – FM), as they are better comparable than the numbers of cells and coenobia or colonies (filament biovolumes of dominant *C. catemaco* and *C. philippinensis* differed 7 times, coenobia of *Pediastrum* can be several thousand times more voluminous than a filament of *Cylindrospermopsis*).

Phytoplankton composition was evaluated from two points of view using detrended correspondence analysis (DCA, Ter Braak & Šmilauer, 2000). Each sample and species biomass were taken separately and submitted to analysis for similarity between the assemblages.

Zooplankton samples taken using the 200 μm mesh Epstein plankton net were determined only informally to species.

Samples of adult fish specimens were obtained in August 1993 and October 1994 from fishermen from their catch in the morning at the shore of the lake. In October 1994 the fish were immediately killed and kept on ice before the examination, in August 1993 they were preserved by formalin. Their guts were examined for their contents.

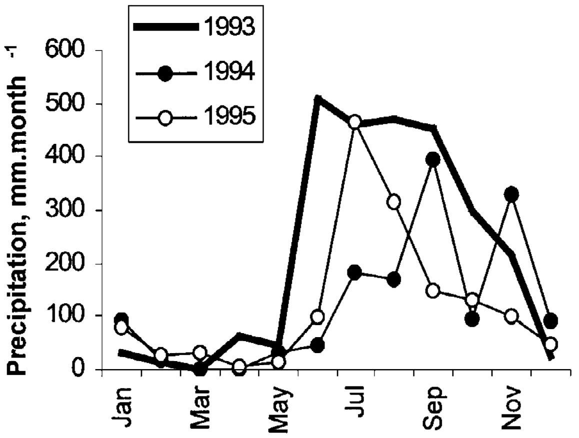

Figure 2. Yearly courses of precipitation in the years studied (Observatorio Nacional de México, Tavera & Castillo, 2000). Extremely heavy rains were in June and July 1993.

Results

Concentrations of the main nutrients and elements in samples from the dry and wet periods in 1993 are given in Table 2. Concentrations of the forms of nitrogen, sulfates and silica were higher in the rainy season. Even if the water column during the dry season should have been more stable, the daily stratification was better developed in August. The discrepancy is a consequence of only one sampling in the period. However, we checked all of the available data in 1993 and found that the character of the chemical environment did not change substantially over the periods. Temperature and chlorophyll *a* levels were similar between the wet and dry seasons (Table 2).

Yearly courses of precipitation are shown in Figure 2. Rather short dry periods from January to May were followed by longer lasting warm rains that culminated in September. In 1993, high precipitation started already in June and continued until November. That year, the June to November precipitation was almost twice as high as the long-term average. Therefore, the chemical data in Table 2 represent a maximal concentrations of nutrients, as the nutrient load was much higher than the average values (Tavera & Castillo, 2000).

Species composition in units of FM is given in Figure 3a, b. Diatoms, Chlorophyceae, and the group of 'other cyanobacteria' were not abundant. In the

Table 2. Average data on the concentration of nutrients and other chemical and physical variables in May and August 1993. Each number is a mean for 4 sampling sites (A–D). Differences between dry and rainy seasons are marked in black. No difference was found in temperature

		May (dry season)			August (rainy season)		
		surface	3 m	9 m	surface	3 m	9 m
Alkalinity	meq l^{-1}	0.97	1.00	1.00	0.85	0.80	0.85
P-PO_4	$\mu g\ l^{-1}$	10	10	10	10	10	10
N_{org}	$\mu g\ l^{-1}$	77	93	93	140	290	380
N-NO_3	$\mu g\ l^{-1}$	35	30	31	50	45	52
N-NH_4	$\mu g\ l^{-1}$	154	154	158	140	142	140
$N_{tot.}$	$\mu g\ l^{-1}$	268	280	291	330	430	580
$SO_4{}^{2-}$	mg l^{-1}	2.6	2.3	2.2	4.3	4.1	5.6
COD	mg l^{-1}	20.4	51.2	30.7	45.0	40.5	63.0
Mg^{2+}	mg l^{-1}	6.9	6.9	6.9	7.2	6.7	7.4
K^{+}	mg l^{-1}	2.3	2.3	2.4	2.6	2.9	2.9
Na^{+}	mg l^{-1}	15	14	18	20	21	20
Si^{3+}	mg l^{-1}	1.0	1.1	1.1	1.3	1.2	1.7
Ca^{2+}	mg l^{-1}	6.2	6.4	6.4	6.6	6.3	6.9
pH		8.9	8.6	7.8	8.6	8.9	8.8
Temperat.	° C	28.9	27.3	27.0	28.0	28.0	28.0
Transp.	m	0.6			0.55		
Chlor. *a*	$\mu g\ l^{-1}$	46.7	48.3	43.0	69.0	51.2	29.7

first sample, *Cylindrospermopsis catemaco* was dominant. The same composition was found roughly in other samples from this period (Tavera, unpublished results). The second sample from the rainy season of 1993 still maintained this pattern, even if the numbers of *C. philippinensis* were increasing. The dominance of *C. philippinensis* increased beginning with the dry period of 1994, and remained so up to the last sampling in summer 1995. The same pattern is seen when given as percentage of total fresh mass (Fig. 3b). Tavera (1996) studied the number of heterocytes in the filaments of both *Cylindrospermopsis* species. She found much more heterocytes in the population of *C. philippinensis* than in *C. catemaco*. *C. philippinensis* responded successfully to low nitrogen concentration, which decreased greatly due to low precipitation levels in the following quiet and drier years of 1994 and 1995 (NO_3-N dropped from 30–52 to 5.4 $\mu g\ l^{-1}$, NH_4-N from 140–158 to 14 $\mu g\ l^{-1}$, P-PO_4 remained almost unchanged, Tavera, 1996). This pattern of phytoplankton composition lasted for the following two years, with small variations in the occurrence of additional species.

Species biomass data were also analyzed by DCA (Fig. 4). Together with analysis of the species, individual samples were plotted. Even if the number of the samples is very low for this type of analysis, the distribution corroborated our results. The samples were distributed into two groups, situated in the same place as the dominant and attendant species. While *C. catemaco* was related to the 1993 samples, the other four samples were joined to *C. philippinensis* (see white arrows and the indication).

It is interesting that there was no difference between the samples from the rainy and dry periods. The main reason for the shift of dominance and the appearance of new species in the lake was evidently the change in the summer precipitation levels between 1993 and 1994, as mentioned above. Heavy flooding rains in 1993 enabled *C. catemaco* to dominate (vegetation cells have no aerotopes) along with the appearance of heavy planktonic diatoms (*Aulacoseira granulata, A. italica)* and coenobia of *Pediastrum boryanum* (Turp.) Menegh., *P. simplex* Meyen, *P. duplex* Meyen, and *P. simplex* var. *biwaense* Fukush. The rains helped in mixing the whole water column and probably lifted up a lot of sedimented nutrients. Runoff from the surrounding agricultural lands also introduced high concentrations of nutrients to the lake. In the next two years, precipitation returned to mean

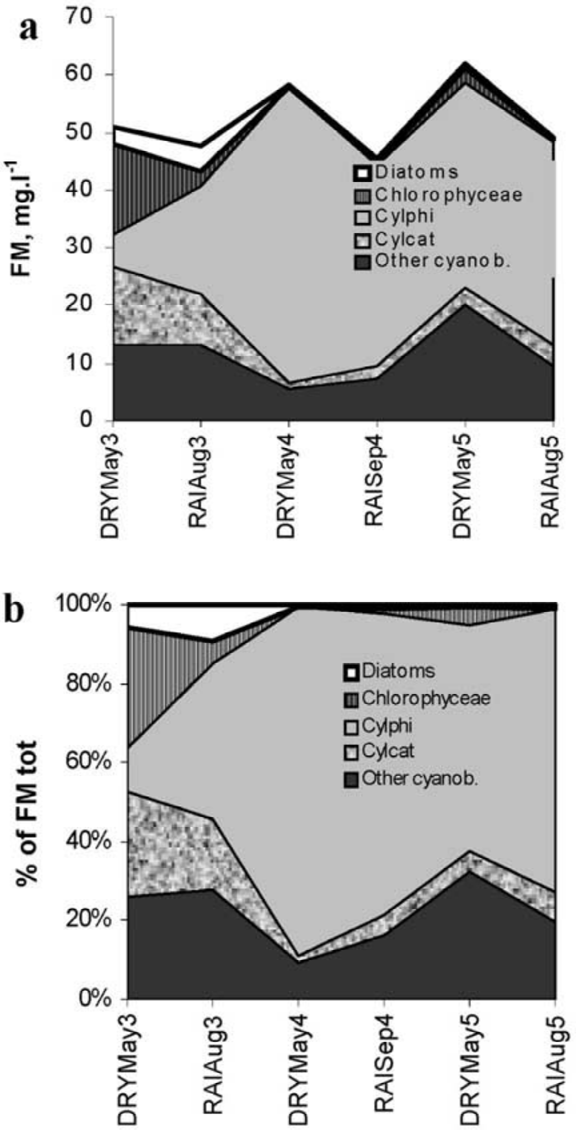

Figure 3. Fresh mass (FM, biovolume, 3a) and share of individual dominants on the total FM (3b) during six samplings in dry and rainy seasons in three subsequent years.

values and the phytoplankton used up most of the nutrient load in primary production.

Stomach and gut contents of different herbivorous fish were studied in summer 1993 and 1994 from the fish yield of the Catemaco fishermen. A high percentage of the contents consisted of the rests of large diatoms and green algae, while small sized *Cylindrospermopsis* filaments were relatively few. There was a large difference between the composition of the phytoplankton assemblage and the gut content of the native and dominant clupeid *Dorosoma petenense* (Fig. 5a,

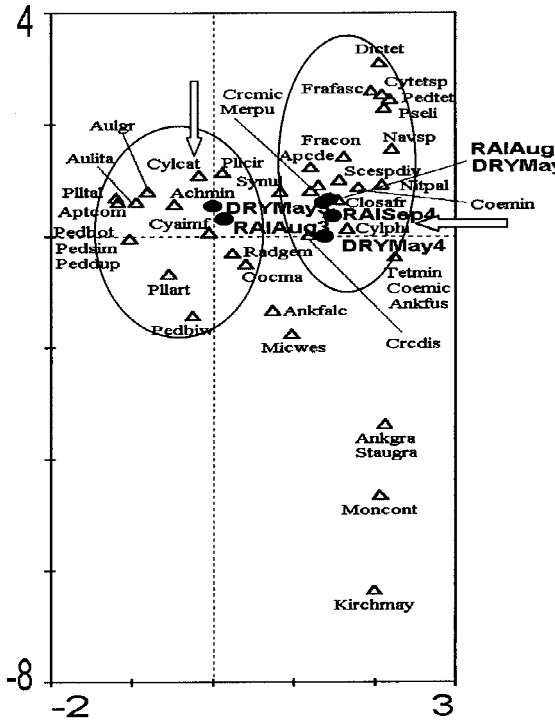

Figure 4. Detrended correspondence analysis (DCA) of FM of individual species and their distribution over first and second DCA axes. Comparison is done for whole samples taken in 6 seasons in three subsequent years. Abbreviations: Achmin – *Achnanthes minutissima* Kütz.; Ankfalc – *Ankistrodesmus falcatus* (Corda) Ralfs; Ankfus – *A.fusiformis* Corda; Ankgra – *A. gracilis* (Reinsch) Korš; Apcde – *Aphanocapsa delicatissima* W. et G.S. West; Aptcom – *Aphanothece comasii* Kom.-Legn. et Tavera; Aulgr – *Aulacoseira granulata* (Ehr.) Simonsen mf. *curvata*; Aulita – *Aulacoseira italica* (Ehr.) Simonsen; Closafr – *Closteriopsis acicularis* (G.M. Smith) Belcher et Swale var. *africanum*; Coemic – *Coelastrum microporum* Näg. in A.Br.; Coemin – *Coelomoron minimum* (Bernard) Kom.-Legn. et Tavera; Crcdis – *Chroococcus distans* (G.M. Smith) Kom.-Legn. et Cronb.; Crcmic – *Ch. microscopicus* Kom.-Legn. et Cronb.; Cyaimf – *Cyanodictyon imperfectum* Cronb. et Weibull; Cylcat – *Cylindrospermopsis catemaco* Kom.-Legn. et Tavera; Cylphi – *C. philippinensis* (Taylor) Kom.; Cytetsp – *Cyanotetras* sp.; Dictet – *Dictyosphaerium tetrachotomum* Printz; Fracon – *Fragilaria construens* var. *construens* (Ehr.) Grunow; Frafasc – *F. fasciculata* (Agardh) Lange-Berth.; Kirchmay – *Kirchneriella mayori* (G.S.West) Kom.-Legn.; Merpu – *Merismopedia punctata* Meyen; Micwes – *Microcystis wesenbergii* (Kom.) Kom. in Kondr.; Moncont – *Monoraphidium contortum* (Thur.) Kom.-Legn.; Navsp – *Navicula* sp.; Nitpal – *Nitzschia palea* (Kütz.) W.Smith; Oocma – *Oocystis marssonii* Lemm.; Pedbiw – *Pediastrum simplex* var. *biwaense* Fukush.; Pedbor – *P. boryanum* (Turp.) Menegh.; Peddup – *P. duplex* Meyen; Pedsim – *P. simplex* Meyen; Pedtet – *P. tetras* (Ehrenb.) Ralfs; Pllart – *Planktolyngbya arthrospiroides* Kom.-Legn. et Tavera; Pllcir – *P. circumcreta* (G.S.West) Anagn.et Kom.; Plltal – *P. tallingii* Kom. et Kling; Pseli – *Pseudanabaena limnetica* (Lemm.) Kom.; Radgem –*Radiocystis geminata* Skuja; Scespdiv – *Scenedesmus* sp.div.; Staugra – *Staurastrum gracile* Ralfs; Synul – *Synedra ulna* (Nitzsch) Ehr.; Tetmin – *Tetraedron minimum* (A.Br.) Hansg.

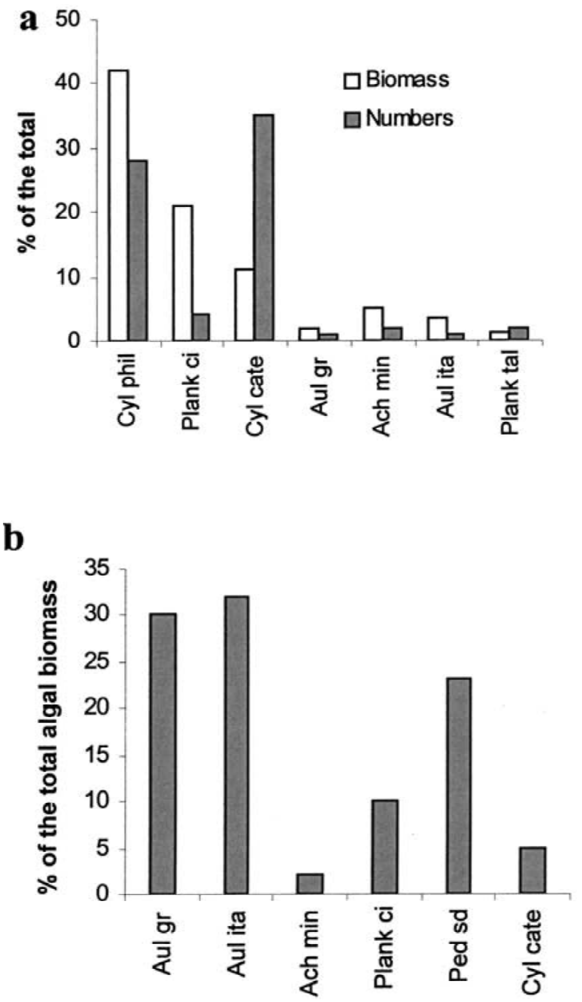

Figure 5. Percentual composition of the planktonic algae and cyanobacteria in the Catemaco lake in August 1993 (5a) and corresponding shares in the guts of 12 cm long specimens of *Dorosoma petenense* (5b).

b). While the gut content consisted mostly of debris from algae larger than 40–50 μm, *Cylindrospermopsis* occupied the largest percentage in the phytoplankton.

Discussion

A simplified food web model of Lake Catemaco is presented in Figure 6. The main predators (white shad, *Bramocharax caballeroi* and tilapia, *Oreochromis niloticus*) of the phytoplankton were mostly dependent on the large fraction of the phytoplankton (>20 μm). Large zooplankton such as *Daphnia* sp., *Macrocyclops albidus* (Jurine), *Mastigodiaptomus albuquerquensis* (Herrick), and *Diaphanosoma* sp. were not taken into account, as they have much lower concentrations compared with the fishstock (Tavera & Castillo, 2000). However, in case large daphnias are present, they filter off their portion of the phytoplankton.

Zooplankton and all larger particles of organic detritus and plant debris were greatly consumed by herbivorous fish (Drenner et al., 1982). Drenner et al. (1982) studied prey escape concerning the gizzard shad in experiments. They found that large daphnias had a small chance to sustain their populations under high predation pressure of fish, while *Diaphanosoma* and *Diaptomus* were better able to avoid swallowing. Larvae and juvenile fish were probably dependent on zooplankton very much, as was found for closely related gizzard shad from North America (*Dorosoma cepedianum*, Pierce et al., 1981; Dettmers & Stein, 1992). Small zooplankton as *Bosmina longirostris* (O.F.Müller), *Brachionus havanaensis* (Rousselet), and *Keratella americana* (Carlin) were more frequent. These can consume small particles and bacteria and can remove partly also *Cylindrospermopsis* and small algae. Except for *Diaphanosoma*, all of the species were found in Lake Catemaco already in 1985 by Suárez et al. (1986). They also found a 90% dominance of cyanobacteria.

Drenner et al. (1984) measured the distances between the rake gills of the related species *Dorosoma cepedianum*. They found distances between 1 and 85 μm in five studied specimens of the same size as was a majority of *Dorosoma petenense* specimens from Lake Catemaco (body length 136–163 mm). Also other species of fish present in the lake were consumers of phytoplankton: *Bramocharax caballeroi*, *Astyanax mexicanus* and the introduced species *Oreochromis niloticus* (tilapia). The steady state based on competition between the dominant species (see Fig. 6 right bottom) concerns here the assemblage already modified by long lasting and permanent predation pressure of the fish, or fish and zooplankton. Even if many other algae of such small size existed in the lake, none of them was able to grow under such poor nitrogen concentration and low light conditions. In comparison with cyanobacteria, green algae were well digested.

Bodola (1966) observed that *Dorosoma cepedianum* consumed large amounts of *Microcystis aeruginosa* colonies and filaments of *Anabaena spiroides*; however, the cells remained viable after passing through the guts. The vitality of blue-greens and algae isolated from the fish guts can be tested also by

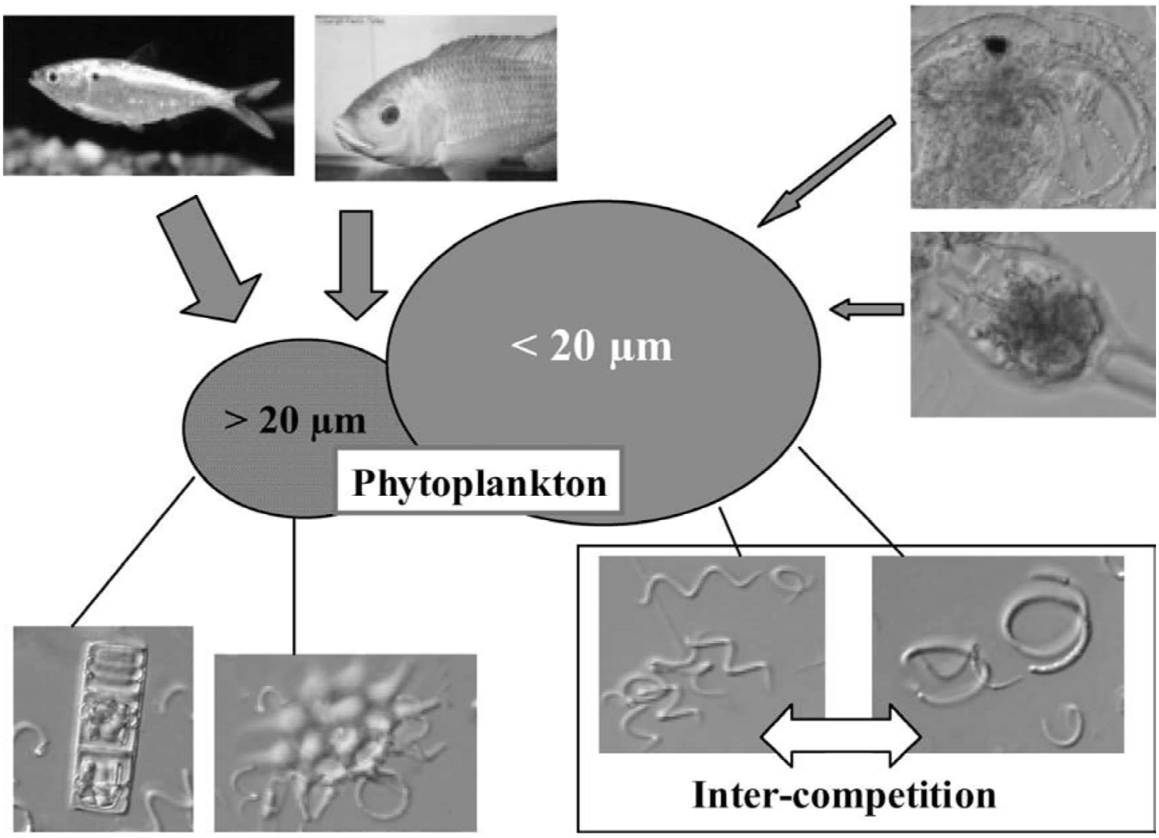

Figure 6. Simplified food net in the lake Catemaco. Dark arrows: predation on the phytoplankton. Large (>20 μm) and small (<20 μm) phytoplankton: while small phytoplankton is supported by predation activity of herbivorous fish, large particles are removed. Predation pressure on small phytoplankton is negligible. Inter-competition can exist between the inedible species, *Cylindrospermopsis catemaco* and *C. philippinensis* (see white double-arrow to the right bottom).

cultivation (Dokulil, 1983, on *Sarotherodon mosambicus*). However, adult specimens of tilapia have a pH of about 1.4 in their digestive organs (Moriarty, 1973; Payne, 1978; Northcott et al., 1991; Tavera, 1996), so cyanobacteria could be digested by tilapia.

The lake probably has enough nutrients for growth of diatoms only in rainy and windy summers, when the concentration of nutrients increases and heavy filaments are able to counter sedimentation (Tavera & Castillo, 2000). Everyday fishing of herbivorous fish on the lake provides a regulation of the fish-stock which keeps the food web functioning. Small sized cyanobacteria were probably dominant in the lake already for many years (analysis of the sample collected by E. Rott in 1970 detected dominance of *C. catemaco* and *C. philippinensis*). Such a long lasting steady state of the phytoplankton composition is mostly conditioned by a sort of biomanipulation, as other potential competitors (large buoyant colonies, flagellates, filamentous buoyant species) are removed mechanically from the environment (equivalent of pasture). Drenner et al. (1984) found a similar modification of the phytoplankton assemblage due to the presence of herbivorous fish as we did. Larger species (there *Ceratium*) were suppressed while the smallest algae and bacteria were enhanced. A convenient niche for the development of cyanobacteria was supported by high and stable temperature and low transparency, as the cyanobacteria irradiance demand is low (Oliver & Ganf, 2000). Also the Redfield ratio (Reynolds, 1984) was appropriate for nostocalean cyanobacteria which can supply the missing concentration of N by nitrogen fixation activity of heterocytes.

Tavera & Castillo (2000) explained the further eutrophication of the lake by an increase in the percentage of total cyanobacteria forming the phytoplankton (from 64–83% in 1993 to 94–99% in 1994 and 1995). However, phytoplankton biomass did not increase substantially. The important change was diminution of the portion of large phytoplankton, which was probably a consequence of increasing predation pressure by herbivorous fish and increased sedimentation processes during the quiet 1994 and 1995 years.

Stable physical conditions and certain morphometrical features of the lake are necessary characteristics of the lakes occupied by a phytoplankton assemblage enrolled to the S_N group. Such lakes should be warm (tropical) and shallow enough as to be polymictic, mostly mixed every day. Tavera (1996) calculated the relative depth (Z_R) that indicated the instability of the water column (Hutchinson, 1957). The value for Catemaco is very low (0.228), which indicated a high instability and daily mixing. Diurnal measurement in the lake during one day proved also the establishment of short lasting stratifications of oxygen concentration and temperature; however, pH values remained unchanged. Climatic conditions in the region ensured small seasonal variations in water temperature (22–26 °C). The retention time of the lake was computed to be about one year (except for the extremely rainy year 1993), which is also one of the preconditions for development of a stable equilibrium system.

Maximum biomass of phytoplankton in a shallow polymictic eutrophic lake (4–5 m deep) with available nutrients was assumed to be about 200 μg l^{-1} chlorophyll *a* (Reynolds, 1984). Tavera (1996) recorded concentrations between 17 and 60 μg l^{-1} of chlorophyll *a*, which also proved that the phytoplankton grew under permanent limitation of nutrients. The main factors for maintenance of a stable steady state, including permanent limitation by physical factors and nutrients (Reynolds, 1997), were therefore present in Catemaco Lake during all of the study.

Conclusions

Phytoplankton biomass in Lake Catemaco consisted from 36 to 81% of two very small cyanobacterial species, *Cylindrospermopsis catemaco* and *C. philippinensis* during all three years studied.

Algae larger than 20 μm (in GALD) and zooplankton were scarce but always present. They were mainly filtered by phytophagous species of fish: *Dorosoma petenense, Bramocharax caballeroi, Astyanax mexicanus* and *Oreochromis niloticus.*

Everyday fishing forced the fish-stock to rejuvenate, even if the food supply for fish (large particles) was kept low.

Strong predation pressure by filter-feeding herbivorous fish, permanent mixing and low transparency and limitation by lack of nitrogen manifested in small differences in biomass of total phytoplankton during the yearly cycles and in permanent dominance of two species of the genus *Cylindrospermopsis.* Exchange of the two dominant species, *Cylindrospermopsis catemaco* Kom.-Legn. et Tavera and *C. philippinensis* (Taylor) Kom., took part after extremely high precipitation in the rainy period of 1993. Before and after the change, a probably long lasting steady state of the phytoplankton assemblage existed in the lake as a result of inter-species competition.

The eutrophic character of the lake, its shallowness and permanent mixing of the water column well fit the characteristic dominance of *Cylindrospermopsis* belonging to the functional group $\mathbf{S_N}$ (Reynolds et al., 2002).

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