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Seasonal and spatial dynamics of a ciliate assemblage in a warm-monomictic Lake Alchichica (Puebla, Mexico)

Dinámica temporal y espacial de la comunidad de ciliados en un lago monomíctico-cálido Alchichica (Puebla, México)

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ABSTRACT

The distribution of the ciliate assemblage was surveyed along a depth gradient in the maar crater, athalassohaline, warm monomictic Lake Alchichica (Puebla, Mexico) from June 2003 to October 2006 (monthly). DAPI staining was employed to count ciliates while the Quantitative Protargol Staining was used for their identification. Peritrichs often numerically dominated the ciliate assemblage; a maximum of 54 cells ml⁻¹ (*Rhabdostyla* sp.) was observed in the surface layer at the end of the mixing period, during the development of diatoms (*Cyclotella alchichicana*), cyanobacterial (*Nodularia* sp.) bloom and its decay. Minute spirotrichs (particularly *Halteria grandinella*) and a haptorid, *Belonophrya pelagica* occasionally dominated the epilimnion while mixotrophic *Euplotes* cf. *daidaleos* and *Pelagothrix* sp. were important round the oxycline along with haptorids, particularly *Phialina* sp. Scuticociliates *Cyclidium glaucoma*, *Uronema nigricans*, and anaerobic ciliates *Isocyclidium globosum* and *Caenomorpha* sp. dominated within the hypolimnetic assemblages.

Key words: Ciliates, athalassohaline lake, anoxic.

RESUMEN

De junio de 2003 a diciembre de 2006 se estudió mensualmente la distribución de la comunidad de ciliados en el gradiente de profundidades del Lago Alchichica (Puebla, México), un lago cráter, tipo maar, atalasalino de comportamiento monomíctico-cálido. La tinción de DAPI fue empleada para el recuento de los ciliados y la tinción de protargol cuantitativa para su identificación. Frecuentemente los ciliados peritricos dominaron numéricamente la comunidad. Al final del periodo de estratificación y durante el desarrollo de las diatomeas (*Cyclotella alchichicana*) y el florecimiento y posterior decaimiento de las cianobacterias filamentosas (*Nodularia* sp.), se observó un máximo de 54 cél. ml⁻¹ de *Rhabdostyla* sp. en la superficie del lago. Los espirotricos pequeños (particularmente *Halteria grandinella*) y los haptóridos como *Belonophrya pelagica*, dominaron ocasionalmente en el epilimnion, mientras que los ciliados mixotróficos: *Euplotes* cf. *daidaleos* y *Pelagothrix* sp. estuvieron asociados a los haptóridos grandes, particularmente a *Phialina* sp. y fueron importantes alrededor de la oxiclina. Los escuticociliados: *Cyclidium glaucoma*, *Uronema nigricans* y los ciliados anaerobios: *Isocyclidium globosum* y *Caenomorpha* sp. dominaron en el hipolimnion.

Palabras clave: Ciliados, lago atalasalino, anoxia.

INTRODUCTION

The importance of ciliates in the pelagic marine microbial loop (*sensu* Azam *et al.*, 1983) as well as in freshwater environments of a moderate trophic status has been demonstrated (Pace, 1982; Gates, 1984; Müller, 1989; Šimek *et al.*, 1990; Müller *et al.*, 1991). Many authors have shown that an effective feeding and rapid growth of ciliates were detected when they could explore rich food-patches such as phase borders where food particles are accumulated (the thermocline or oxycline). It has been repeatedly documented that a peak in protozoa distribution temporarily coincided also with the decomposition of primary production (Taylor & Heynen, 1987; Weisse *et al.*, 1990; Macek *et al.*, 1994; Šimek *et al.*, 1995; James *et al.*, 1995). Generally, a maximum of the ciliate distribution was found in the metalimnion or below it (reviewed in Beaver & Crisman 1989; Fenchel *et al.*, 1990; Sherr *et al.*, 1991; Macek *et al.*, 1994; Šimek *et al.*, 1995), apparently related to microaerobic processes. If an oxycline did not occupy the same position as a thermocline, additional ciliate maxima could be found there and/or in the layer above the water body floor.

More information is available from shallow water bodies with light conditions, which are sufficient to provide both oxygenic and anoxygenic photosynthesis (Berninger *et al.*, 1986; Finlay *et al.*, 1996; Macek *et al.*, 2001). Species of genera *Loxodes* and *Spirostomum* were related to nitrate and/or sulphate microbial reduction (Finlay *et al.*, 1983; Guhl & Finlay 1993; Foissner *et al.*, 1995) while others of *Metopus* and *Caenomorpha*, were found to be strictly anaerobic (Foissner *et al.*, 1992; Decamp & Warren 1997).

However, Foissner *et al.* (1999) doubted the existence of typical anaerobic-pelagic (hypolimnion) species. Apart from peaks of the above mentioned ciliates, the presence of anaerobic ciliates was accepted as a result of migration of benthic species. The typical anaerobes (genus *Caenomorpha* but also scuticociliates) possess hydrogenosomes instead of mitochondria; moreover, their metabolic pathways need co-metabolism with symbiotic microbes (Esteban *et al.*, 1993; Fenchel & Finlay, 1995). On the other hand, there is evidence that the "symbiont" acquisition could be provided via ingestion (van Hoek *et al.*, 2000).

In the present study we have tried to provide more comprehensive information on the seasonal ciliate assemblage development throughout the water column including an anoxic layer of crater Lake Alchichica (Puebla, Mexico), from June 2003 to December 2006.

MATERIAL AND METHODS

Study site and sampling. We conducted the study in the large and deep maar-crater Lake Alchichica (Puebla, Mexico) with extended hypolimnetic anoxia classified as tropical, warm and monomictic (Filonov *et al.*, 2006). Alchichica is located at 19°

24' N; 97° 24' W at an altitude of 2340 m.a.s.l. Mean and maximum depths are 40.9 and 62 m, respectively, surface area being 2.3 km²; salinity averaged 8.5 g L⁻¹. The climate of the region is dry-temperate, with a mean annual temperature of 12.9 °C and annual precipitation less than 400 mm.

The only sampling station was located above the maximum depth; samples from 5 to 12 depths were taken monthly (within 12:00 to 15:00) using a Niskin (USA) or IHE (Czech Republic) sampler. The sampling depths were decided according to *in situ* measured temperature and dissolved oxygen concentration, DO, which were assessed by means of a Hydrolab DS4/SVR4.

Fixation. Ciliates were fixed with acid Lugol's iodine, decolourised with thiosulfate this is fate and post-fixed with 2% formalin (Sherr & Sherr 1993), or eventually with 7% (v/v) Bouin's fixative (Montagnes & Lynn 1987). Total picoplankton including autotrophic picoplankton, APP was fixed with 2% formalin (Strařkrabová *et al.*, 1999).

Quantification and identification of microorganisms. Ciliates were counted in the DAPI-stained samples (Porter & Feig 1980) and identified using a quantitative protargol staining (QPS) on cellulose-esters membranes (1.2 µm) according to Skibbe's (1994) modification of the Montagnes & Lynn (1987) method. Foissner *et al.* (1999) key, as well as the literature cited therein, was used for ciliate identification; however, higher taxa are presented according to Adl *et al.* (2005).

Autotrophic picoplankton (APP), particularly picocyanobacteria, were evaluated in the samples concentrated onto polycarbonate membranes (0.2 µm) and mounted in an immersion oil via autofluorescence (epifluorescence microscope Leica, Germany) using the CY3 filter-set (green excitation and red observation-light); the commonly used yellow fluorescence of APP upon AO and FITC sets (Callieri & Stockner, 2002) was not sufficiently intense.

Data analysis. For the ciliate stratification analysis, all data were used; in order to determine the annual pattern of development, weighted mean-numbers were calculated within the whole water column, and for the top 20 m and the below 35 m layers, representing the epilimnion and the anoxic hypolimnion during the stratification period, respectively.

RESULTS

A total of about 40 taxa of ciliate have been identified to genus and, when possible, to species level, covering nearly all higher taxa of Ciliophora (important species listed in Table 1). Apart from several abundant taxa present during the whole sampling period and distributed throughout the water column (scuticociliates, peritrichs and spirotrichs), most of the present taxa appeared in low numbers during most of the study period.

Average ciliate abundances in the whole water column ranged from undetectable numbers in January 2005 to 26 cells ml^{-1} in September 2006 (Fig. 1). The highest water column means of ciliates were observed in the late stratification period (September to November); when the assemblage was almost exclusively dominated by scuticociliates, however, mainly in the oxycline-anoxic layers (Figs. 1, 2). An absolute maximum of 54 cells ml^{-1} was observed in the surface in May 2004, when peritrichs colonizing *Nodularia* sp. filaments dominated the assemblage. During August to October, local maxima of over 40 cells ml^{-1} were found, as mentioned above, in micro-aerobic-anoxic layers. Near bottom ciliate numbers reached the maximum of 40 cells ml^{-1} in September 2005.

Peritrichs were the numerically dominant group in Alchichica (Fig. 2), contributing nearly 40% to the total numbers throughout the study period. They were characterised by small-sized taxa (<40 μm), either single-celled, non-attached (*Pelagovorticella natans* (Fauré-Fremiet, 1924) Jankowski, 1985, and *Vorticella aquadulcis* complex) or sessile *Rhabdostyla* sp. and unidentified *Vorticella* sp. Peritrichs contributed frequently >70% to the total ciliate abundance in the epilimnion. When *Rhabdostyla* sp. absolutely dominated the ciliate assemblage, it colonised a centric diatom, *Cyclotella alchichicana* Oliva *et al.*, 2006 and/or

filamentous cyanobacteria, *Nodularia* sp. (peaking March to May 2004 in epilimnion). Nearly all filaments of cyanobacteria were colonized, as well as diatoms, which frequently possessed ciliates at both sides of their centric cell. Around the oxycline, peritrichs abundances were of the similar value as those of spirotrichs; they were observed neither abundant in the anoxic hypolimnion nor around the oxycline.

Scuticociliates were the most abundant group in 2005 (68%) and throughout the study they formed 27% of the sampling average. Scuticociliates were found generally around the oxycline and in anoxic layers (Fig. 2), mainly represented by minute ciliates *Uronema nigricans* (Müller, 1786), *Cyclidium glaucoma* (Müller, 1773) and *Cinetochilum margaritaceum* Perty, 1852. They were also characteristic for the near-bottom ciliate assemblage, especially from August to October, when an anaerobic *Isocyclidium globosum* Esteban, Finlay & Embley, 1993 was observed (particularly in 2005).

Minute spirotrichs were observed to be distributed throughout the water column, and they formed about 10% of the total ciliate numbers (Fig. 2). Average sampling mean was about 15.0%, however, *Halteria grandinella* (Müller, 1773) Dujardin, 1841 solely contributed to 12.5%. Moreover, very small *Halteria* sp. and

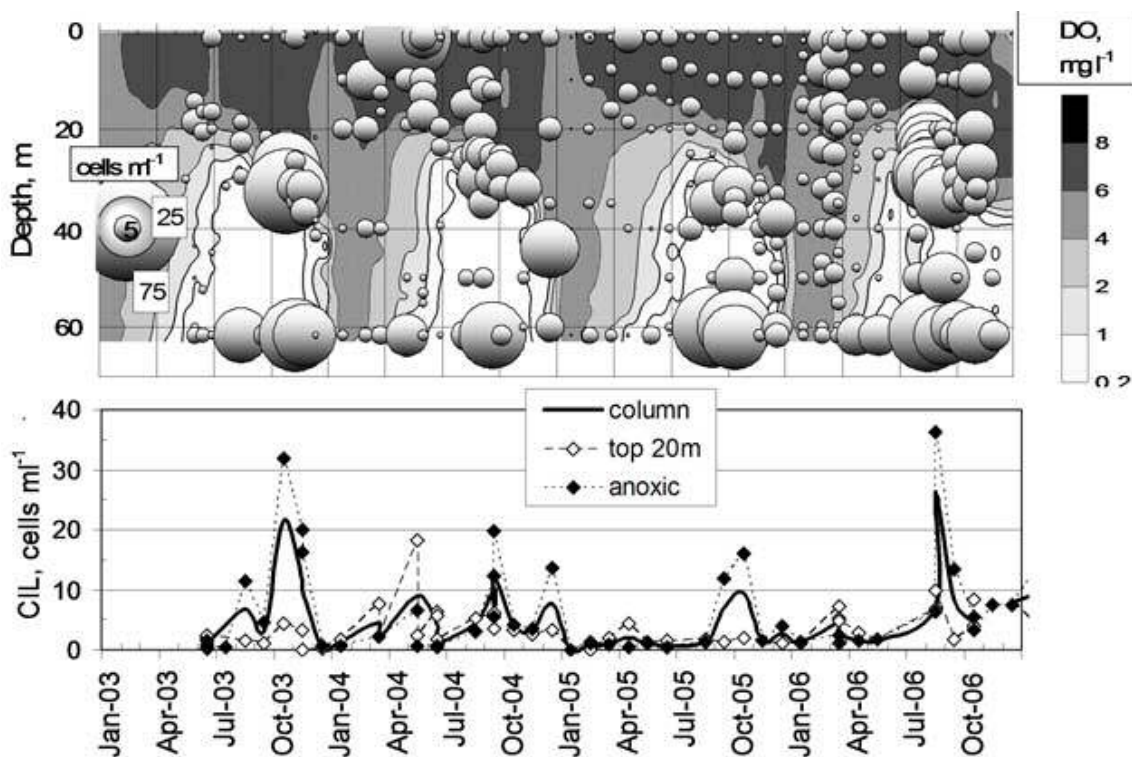


Figure 1. Dissolved oxygen concentrations, DO and total ciliate numbers in Lake Alchichica (upper panel); mean ciliate numbers in the whole water column, the top 20 m and bottom (lower panel).

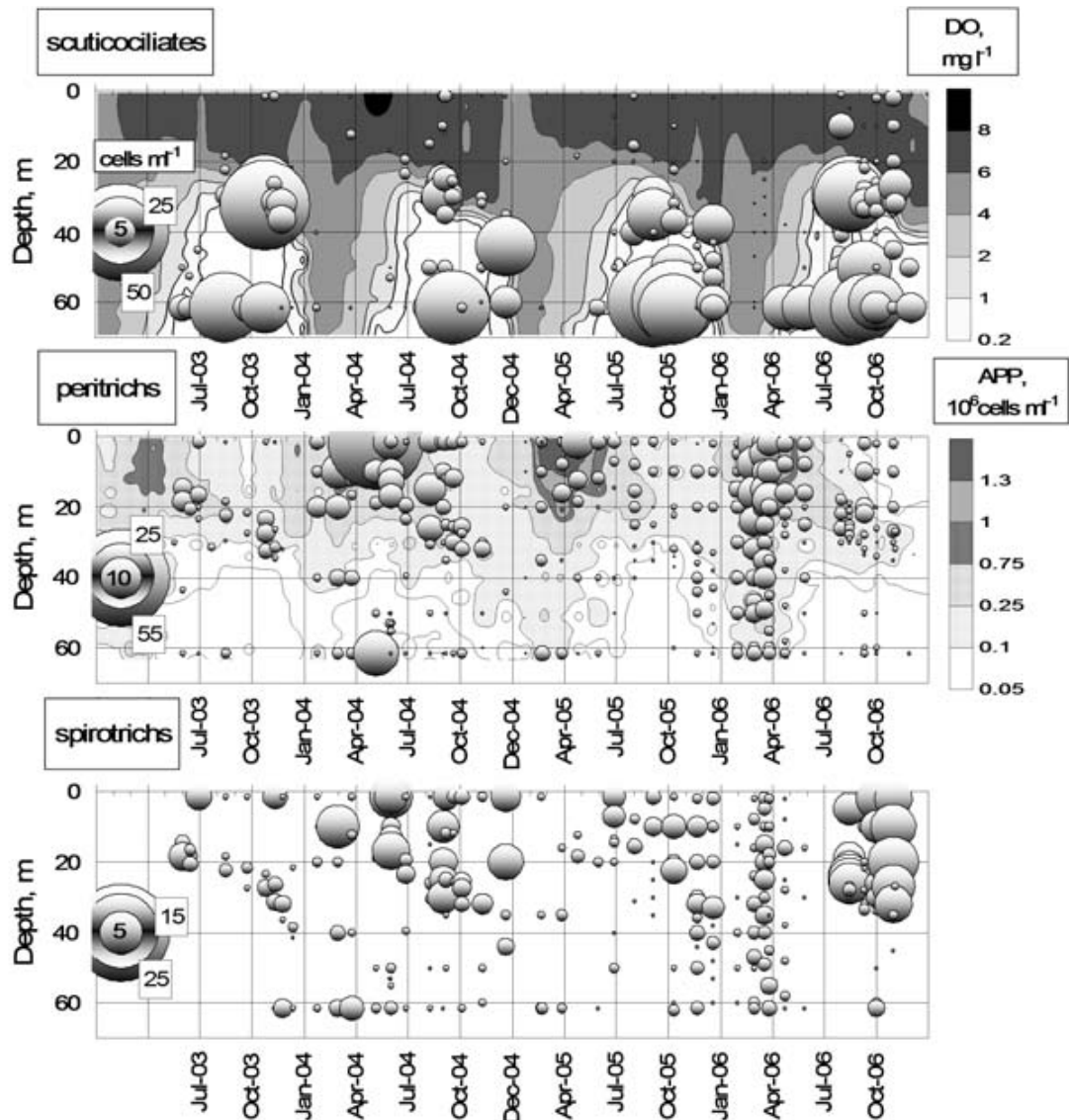


Figure 2. Dissolved oxygen concentrations and scuticociliate numbers (upper panel); autotrophic picoplankton, APP and peritrichous ciliate numbers (medium); spirotrichous ciliate numbers (lower panel).

Rimostrombidium sp. (with globoid macronucleus) were found. Typical stratification of temperature, dissolved oxygen and ciliate numbers are presented in Figure 3.

Among haptorids, *Belonophrya pelagica* André, 1914 (Fig. 4b-d), *Monodinium* sp. (Fig. 4e) and *Mesodinium acarus* Stein, 1862 were the most abundant species. However, from the point of view of biomass, *Phialina* sp. (Fig. 4a) was the most important, followed by *Lacrymaria* sp. and *Pelagolacrymaria* sp. They were concentrated in thermocline-oxyclyne layers and round the anoxic boundary, accompanied by mixotrophic hypotrich, *Euplotes* cf. *daidaleos* Diller & Kowaris, 1966 (Fig. 5a-f). In addition

to these groups, some very large ciliates, generally observed in micro-aerobic or anoxic conditions, particularly *Holosticha kessleri* Kessler (Wrzesniowski, 1877), *Uroleptus rattulus* Stein, 1859 (Fig. 5g) and *Chaetospora* sp. (Fig. 6h-j) showed very important contribution to the ciliate biomass. A minute *Litonotus* sp. was also found (Fig. 4f, g).

Among strictly anaerobic ciliates, *Isocyclidium globosum* (Esteban, Finlay & Emsley, 1993) and a minute *Caenomorpha* sp. (Fig. 6a-d) were the most abundant; *Epalxella* sp. and *Trimyema* sp. were found in considerable numbers at the end of the stratification period (November 2003 and 2006).

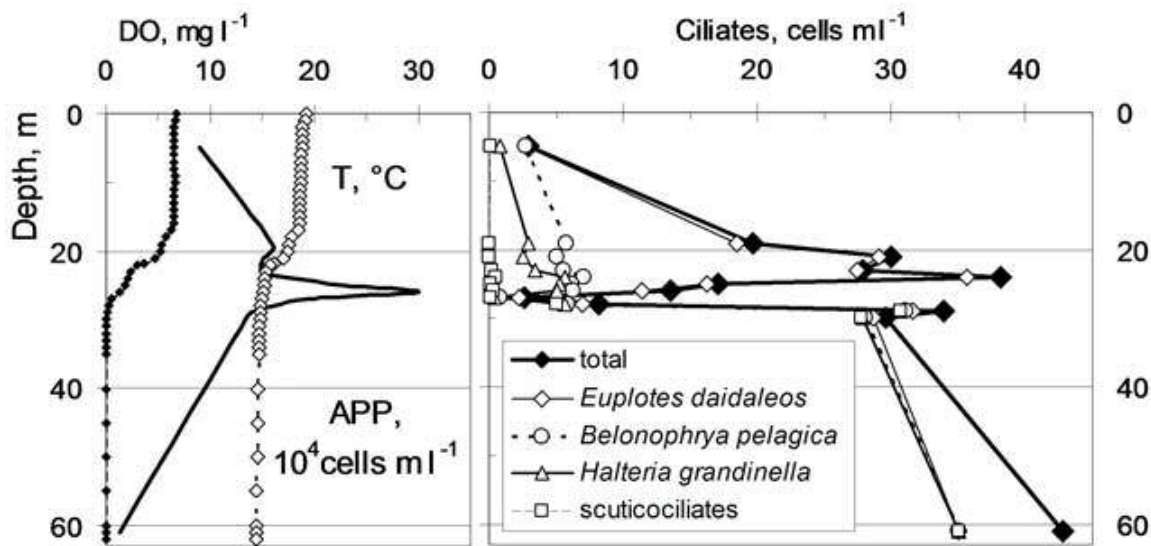


Figure 3. Stratification in Lake Alchichica, August 16, 2006: Temperature, dissolved oxygen concentrations and APP numbers (left); Cumulative ciliates numbers (right).

DISCUSSION

Ciliate abundance and species richness found in Alchichica did not markedly differ from those reported from the oligo- to mesotrophic environment (Gates, 1984; Taylor & Heynen, 1987; Beaver & Crisman, 1989; James *et al.*, 1995; Weisse & Müller, 1998; Foissner *et al.*, 1999; Callieri & Bertoni, 1999; Callieri *et al.*, 2002; Carrick, 2005; Macek *et al.*, 2006). Although the annual-average ciliate abundances varied nearly two-fold, the ciliate dynamics apparently followed a similar annual pattern.

Generally, the highest ciliate abundances (>10 cells ml⁻¹) were found during the late stratification period (mainly scuticociliates) while the ciliates were scarce during the mixing period (December through February); local maxima were observed in the stratification onset in May 2004 as the result of the attached peritrichous ciliate peak in the epilimnion, during the *Nodularia* sp. bloom.

Such dynamics differed from the known patterns in template dimictic water bodies, where ciliate maxima were generally concentrated to the metalimnion, reflecting either spring (following mixing) or summer phytoplankton peak in the epilimnion (e.g., Carrick, 2005; Macek *et al.*, 1994; Šimek *et al.*, 1990, 1995; Weisse & Müller, 1998). Numerically, free-swimming either omnivorous or algivorous ciliates, followed by peritrichs dominated.

In Alchichica, low ciliate abundances during the mixing period coincided with increasing APP numbers throughout the water column. During this period, the contribution of the different ciliate groups was distributed only within peritrichs and spirotrichs. The lake mixing was followed by the important peritrichous

ciliate peak whenever the ciliates found sufficient abundance of phytoplankters to be colonised: filamentous cyanobacteria *Nodularia* sp. and/or diatoms *Cyclotella alchichicana* throughout the water column, and *Chaetoceros elmorei* Boyer mainly in the thermocline. *Rhabdostyla* sp. and unidentified minute *Vorticella* sp. contributed for about 25% and 20% as a sampling mean in numbers and biomass, respectively. Typical pelagic colonial peritrichous genera such as *Epistylis* or *Zoothamnium* from oligotrophic-mesotrophic environment (Macek *et al.*, 1994; Müller *et al.*, 1991; Salbrechter & Arndt, 1994; Foissner *et al.*, 1999) were not found; however, *Pelagovorticella natans* and *Vorticella aquadulcis* complex were observed throughout the water column penetrating below the oxycline. The contribution of peritrichs to the total biomass was very high (compare, Macek *et al.*, 1994, 2000; Lugo *et al.*, 1998 with Salbrechter & Arndt, 1994; Weisse & Müller, 1998; Wille *et al.*, 1999; Callieri *et al.*, 2002; Macek, 2002; Macek *et al.*, 2006).

The dominance of peritrichs, spirotrichs and scuticociliates was found a common feature in freshwater systems and marine environments (e.g., James *et al.*, 1995; Šimek *et al.*, 1995). Minute (< 20 µm) picoplanktivorous heterotrophic spirotrichs such as oligotrichs (*Rimostrombidium brachykinetum* Krainer, 1995 and *R. humile* Petz and Foissner, 1992) and stichotrichs (*Halteria* spp.) dominated within bacterivorous ciliates in freshwater environments, at least during summer stratification period (Šimek *et al.*, 2000; Carrick 2005). Additionally, the peaks of *H. grandinella* and *Halteria* sp. have frequently been located at the food-rich and/or above bottom-layers (Foissner *et al.*, 1999; Macek, 2002; Macek *et al.*, 1996; Salbrechter & Arndt, 1994; Šimek *et al.*, 1995, 1996, 2000; Stabell, 1996; Weisse & Müller, 1998).

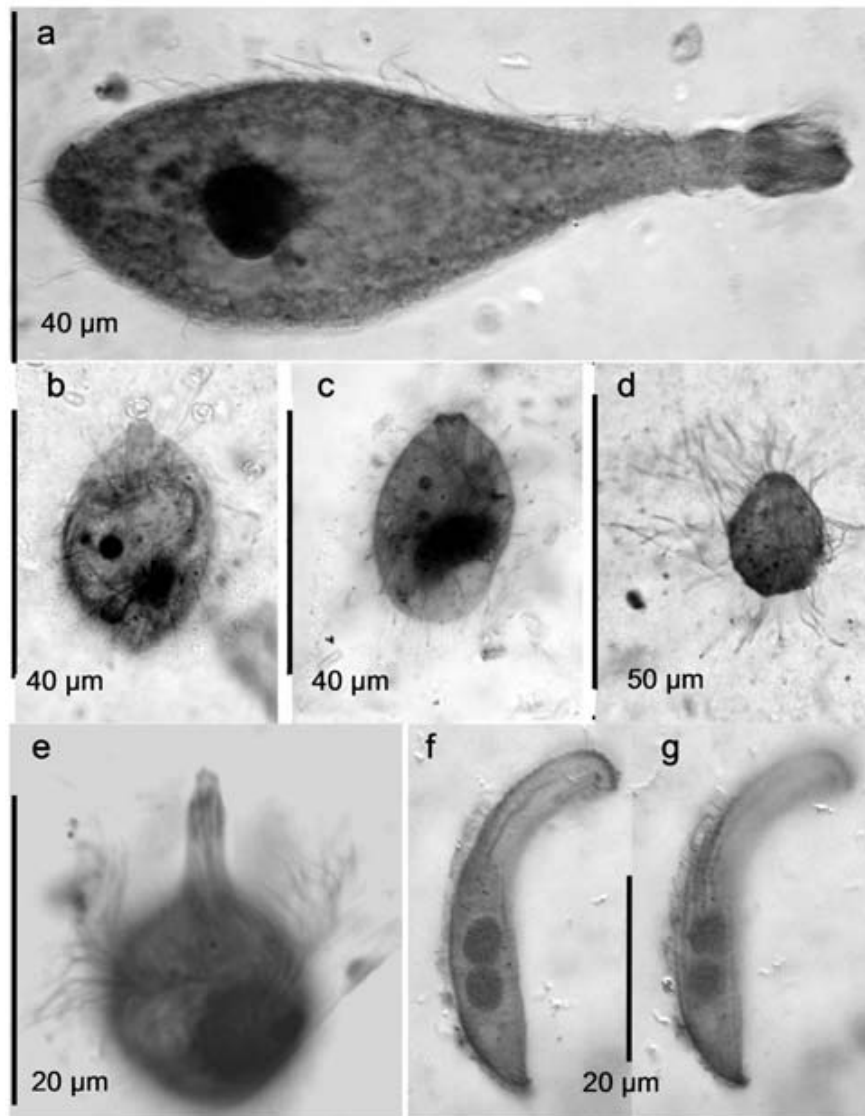


Figure 4. Ciliates found around the oxycline of Lake Alchichica (protargol staining): *Phialina* sp. (a); *Belonophrya pelagica* with contracted (b, c) and extended tentacles (d); *Monodinium* sp. (e); *Litonotus* sp. (f, g)

The predominance of large mixotrophic, fine- to coarse filter feeding ciliates was reported for oligotrophic lakes and coastal waters (Beaver & Crisman, 1989; Šimek *et al.*, 1996; Macek *et al.*, 2001, 2006). Large oligotrichs (like *Rimostrombidium lacustris* Petz and Foissner, 1992 or a mixotrophic *R. velox* Jankowski, 1978) were found in lakes with a well-distinguished pelagic zone (cf., Taylor & Heynen, 1987; Müller *et al.*, 1991; Salbrechter & Arndt, 1994; Weisse & Müller, 1998) but they were rather scarce in Alchichica. On the other hand, during the late stratification period, the peak of microaerobic/anoxic and/or mixotrophic species were found. The distribution of mixotrophic *Euplotes* cf. *daidaleos* and *Pelagothrix* sp. followed on a very fine way the

oxygen depletion below the thermocline, which dropped down 30 m. *Euplotes* cf. *daidaleos* frequently dominated in the oxycline while *Pelagothrix* sp. was repeatedly observed in low numbers throughout the water column. Its occurrence in anoxic water layers with sufficient light was in concordance with published data on the role of its symbionts in the ciliate distribution (Berninger *et al.*, 1986; Finlay *et al.*, 1996; Foissner *et al.*, 1999). A mixotrophy might support its growth in nearly anoxic environment such as it was observed either for prostomes (Finlay *et al.*, 1996) or strombidiids (Macek *et al.*, 2001); however, during August (2006), *Euplotes* sp. was found without an apparent presence of zoochlorelae.

Table 1. List of ciliates found in Alchichica and their ecological position.

Feeding behaviour	Taxon	Mixed column	Epilimnion	Oxyclyne	Hypolimnion
Free swimming picoplankton feeders	<i>Halteria grandinella</i> (Müller, 1773, Dujardin, 1841)	X		X	
	<i>Rimostrombidium</i> sp. (with globoid macronucleus)	X		X	
	<i>Cyclidium glaucoma</i> (Müller, 1773)		X	X	
	<i>Uronema nigricans</i> (Müller, 1786)			X	X
	<i>Cinetochilum margaritaceum</i> (Perty, 1852)			X	X
Attached fine filter feeders	<i>Pelagovorticella natans</i> (Fauré-Fremiet, 1924) Jankowski, 1985	X	X	X	
	<i>Vorticella aquadulcis</i> complex	X	X	X	
	<i>Rhabdostyla</i> sp.	X	X	X	
Mixotrophs	<i>Vorticella</i> sp.	X	X	X	
	<i>Pelagothrix</i> sp.	X		X	X
Algivorous	<i>Euplotes daidaleos</i> Diller & Kounaris, 1966			X	X
	<i>Prorodon</i> sp.	X	X	X	
	<i>Mesodinium acarus</i> Stein, 1862	X		X	
Flagellate hunters and coarse filter feeders	<i>Monodinium</i> sp.	X		X	
	<i>Phialina</i> sp.			X	
	<i>Holosticha kessleri</i> (Wrzesniowski, 1877)			X	
	<i>Uroleptus rattulus</i> Stein, 1859			X	
Raptorial feeders	<i>Chaetospira</i> sp.			X	X
	<i>Litonotus</i> sp.		X	X	
	<i>Lacrymaria</i> sp.			X	
Others	<i>Pelagolacrymaria</i> sp.			X	
	<i>Belonophrya pelagica</i> André, 1914		X	X	
	<i>Actinobolina</i> sp.		X	X	
Anaerobic filter feeders	<i>Isocyclidium globosum</i> (Esteban, Finlay & Embley, 1993)				X
	<i>Caenomorpha</i> sp.				X
	<i>Epalkella</i> sp.				X
	<i>Trimyema</i> sp.				X

Bacterial abundance in Alchichica was high enough to maintain the populations of scuticociliates (Peštová *et al.*, 2008). Scuticociliates were typically connected with phytoplankton decay (Müller *et al.*, 1991; Šimek *et al.*, 1995, 1996) following the summer peak, even though they were also found in very low numbers in the water column in the above timberline lakes

(*cf.*, Weisse & Müller, 1998; Callieri & Bertoni, 1999; Wille *et al.*, 1999; Macek *et al.*, 2002, 2006). In Alchichica, apparently, their peaks did not directly follow phytoplankton maxima, measured by Chl *a*, but could be related to the phytoplankton decay. Particularly, *Cinetochilum margaritaceum* was observed above the thermocline, *Uronema nigricans* around the oxyclyne

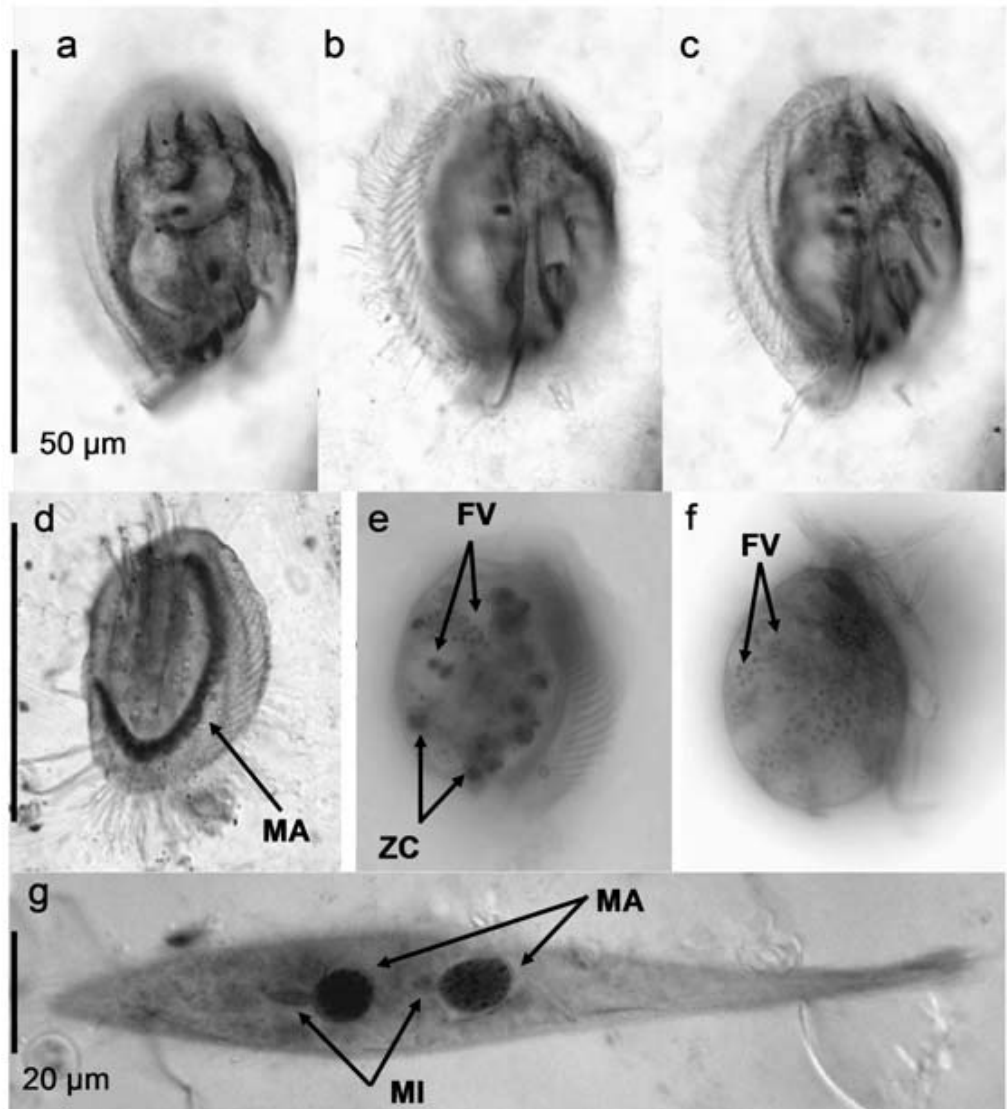


Figure 5. Ciliates found in the oxycline of Lake Alchichica: *Euplotes* cf. *daidaleos* in protargol staining, MA = macronucleus (a-d); *E. daidaleos* with ingested picocyanobacteria (FV = food vacuole) and symbionts (ZC = zoochlorella) visualised by autofluorescence (e, f); *Uroleptus rattulus* in protargol staining, MA = macronucleus, MI = micronucleus (g).

meanwhile *Cyclidium* and related genera penetrated into the anoxic hypolimnion. It is in concordance with data by Bernard & Fenchel (1996), which proved that *Uronema marina* (synonymic with *U. nigricans*) was not able to grow without the oxygen. A minute *Isocyclidium globosum* found at the lake floor, covered with symbiotic bacteria (Fig. 6f), had been first reported in a karstic lake (Esteban *et al.*, 1993).

Other anaerobic ciliates, particularly *Trimyema* sp. and *Caenomorpha* sp. were less important even though they dominated at the lake floor occasionally. Due to a peculiar quality

of anoxic water in Alchichica, we are lacking good protargol impregnated preparations but we could observe fluorescence of bacterial / archaeal symbionts of *Caenomorpha* sp. (Fig. 6d). Large anaerobic ciliates such as genera *Loxodes* or *Spirostomum*, were not found (Guhl & Finlay 1993; Macek *et al.*, 1994, 2000).

Raptorial haptorids could be found frequently in oligotrophic waters (Lugo *et al.*, 1998; Macek *et al.*, 1994, 2000); also in Alchichica, we found regularly the heterotrophic gymnostomes *Mesodinium acarus* and *Monodinium* sp. (Fig. 4e) throughout the year but normally in low numbers. Other gymnostomes were

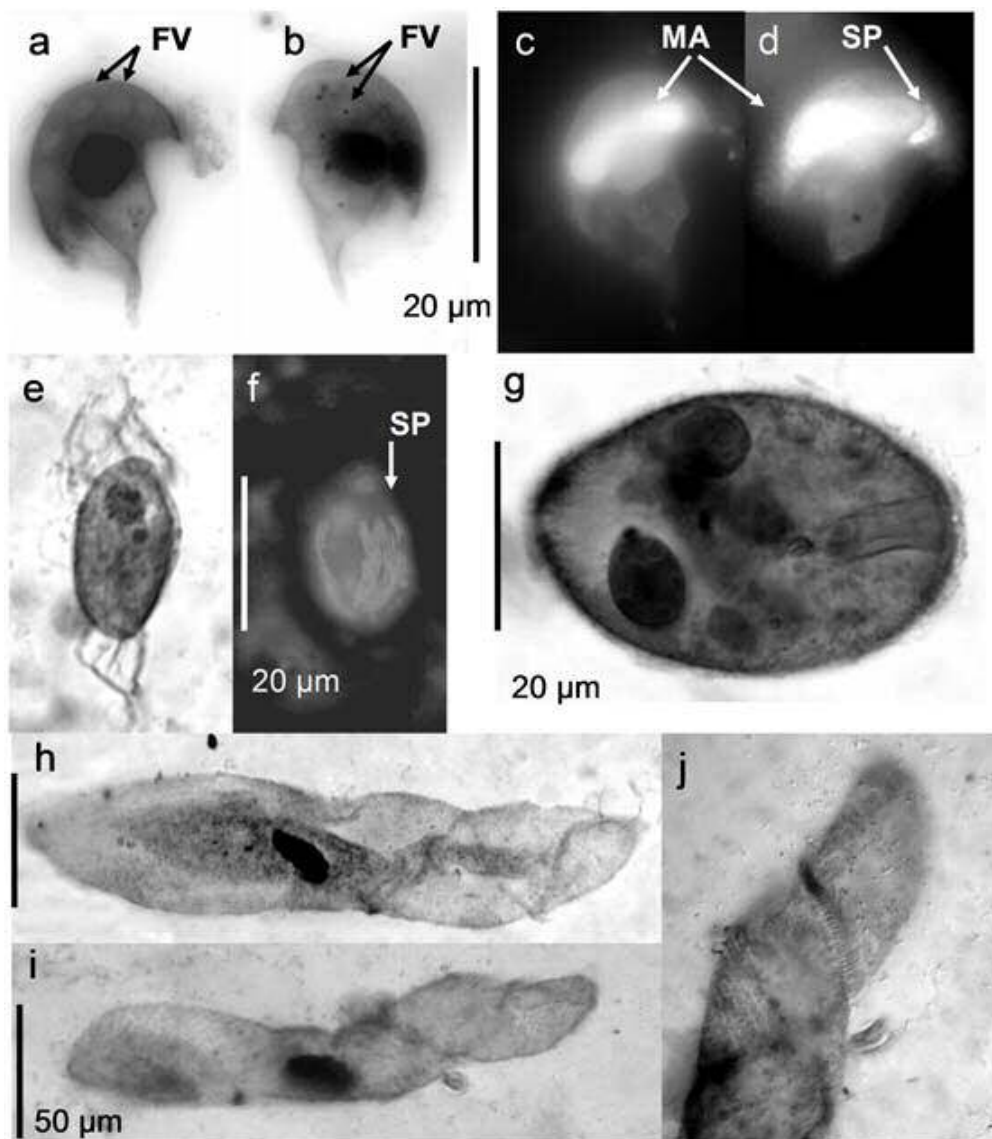


Figure 6. Ciliates found below the oxycline of Lake Alchichica: *Caenomorpha* sp. in DAPI staining (a-d) with stained macronucleus, MA, autofluorescing ingested prokaryots in foos vacuoles, FV and symbiotic prokaryots (SP); *Isocyclus globosum* in protargol staining (e) and with fluorescently labelled bacterial symbionts (f); *Pelagothrix* sp. (g) and *Chaetospira* sp. (h-j) in protargol staining

present in elevated numbers, particularly *Belonophrya pelagica* (Fig. 4b-d) or biomass, particularly *Phialina* sp. (Fig. 4a).

Among undoubtedly algivorous species, only prostomes of the genus *Prorodon* were found in Alchichica but in negligible frequency. In comparison with other reported data, *Balanion planctonicum* Foissner, Berger and Kohmann, 1994 and *Histiobalantium* spp. that are typical for oligo- to mesotrophic low-alkaline environments (Müller *et al.*, 1991; Salbrechter & Arndt 1994; Šimek *et al.*, 1995; Macek *et al.*, 1996; Weisse & Müller 1998; Wille *et al.*, 1999) were not found.

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