

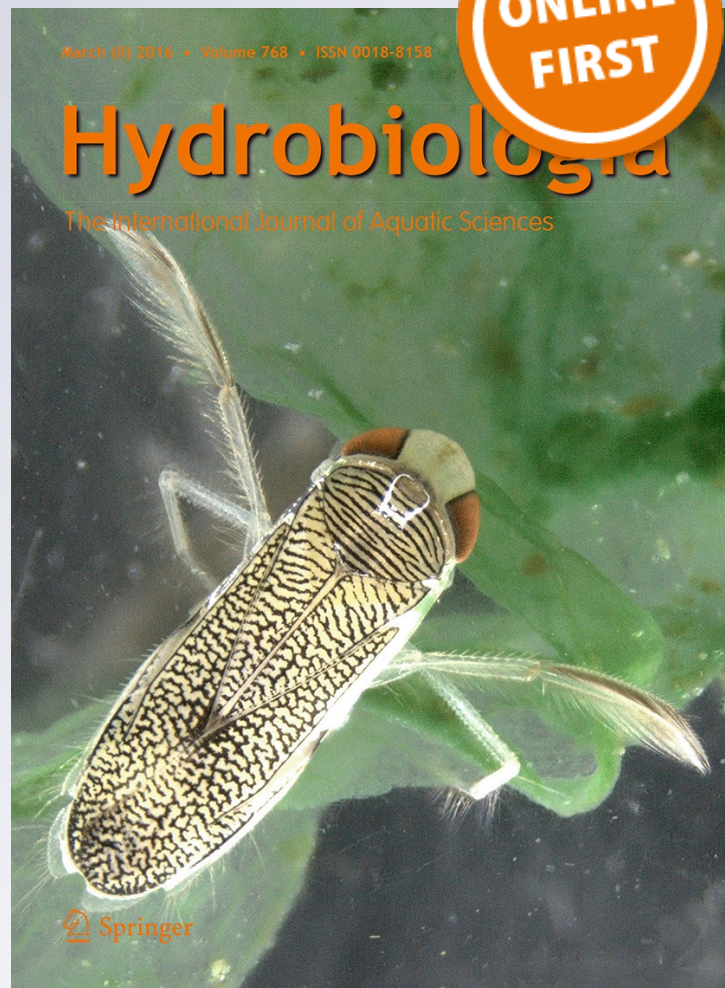
Drivers of highly diverse planktonic ciliate assemblages in peat bog pools from Tierra del Fuego (Argentina)

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Drivers of highly diverse planktonic ciliate assemblages in peat bog pools from Tierra del Fuego (Argentina)

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Abstract Peatlands often encompass shallow pools, wherein dystrophic and colored acid waters host a remarkably diverse biota, with ciliates likely playing a key role in their short trophic webs. In the *Sphagnum magellanicum*-dominated Rancho Hambre peat bog, a 2-year study was conducted in five pools with different morphometric and trophic characteristics, in order to identify main environmental variables driving ciliate species richness, abundance, biomass, and diversity. Overall species richness (125 taxa) was much higher than in northern Hemisphere counterparts. Deep minerotrophic pools hosted the richest communities, showing similar seasonal abundance patterns and the

highest species turnover. Although all pools shared the same dominant ciliates, similarity in taxonomic composition among them was generally low ($J = 0.22\text{--}0.35$). Moreover, IndVal analysis showed that rare and occasional species were highly indicative of different pools. Euryoecious, heterotrophic species, occurred in all sites, while mixotrophs were typical from shallow ombrotrophic pools. *Rimostrombidium hyalinum* was the most indicative species of a deep ombrotrophic pool. A CCA revealed that the abundances of potential ciliate preys, i.e., picophytoplankton, bacterioplankton, and heterotrophic flagellates, were the most significant regulators of abundances of this group. Therefore, ciliate structure and dynamics were influenced by pool morphometry and physical

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and chemical features, but foremost by interactions with other plankton communities.

Keywords Planktonic ciliates · Diversity · IndVal · Peat bog pools · Tierra del Fuego

Introduction

Peatlands are unique wetlands formed by accumulating dead organic matter or peat under particular environmental conditions such as low temperatures, high humidity, and abundant and evenly distributed precipitations (Roig & Roig, 2004). Their global distribution mainly involves northern temperate or cold climate areas (around 80% of global peatlands), while 15–20% are tropical or subtropical, and only a few are located in southern temperate or cold regions (Rydin & Jeglum, 2006). The areas where peat is actively produced, termed mires, are commonly classified into bogs, fens, and peat bogs according to hydrological, topographical, and floristic features (Roig & Roig, 2004). While minerotrophic fens usually have concave profiles and are fed by precipitation as well as by nutrient-rich, circumneutral underground sources, ombrotrophic peat bogs result from the accumulation of peat, frequently as *Sphagnum* mosses debris, are characteristically dome shaped and fed only by precipitation (Iturraspe, 2010). These nutrient-poor, acidic environments often encompass a number of shallow pools, wherein dystrophic and colored acid waters host a unique yet remarkably diverse biota (Mataloni, 1997) organized in commonly short trophic webs frequently dominated by micro- and mesozooplankton as top predators, with ciliates likely playing a key role in carbon transference along trophic compartments (Quiroga et al., 2013). In spite of this, ecological studies on ciliates from peat bog pools or lakes are scarce and restricted to the northern Hemisphere (Macek et al., 2001; Mieczan, 2007a, b, 2010a, b; Mieczan & Siczek, 2010; Mieczan & Tarkowska-Kukuryk, 2013). Most of these investigations identified low pH as a major cause of decreasing both species richness and abundance of ciliate communities, in agreement with those carried out in humic and acid mining lakes (Beaver & Crisman, 1981, 1989; Bienert et al., 1991; Kalinowska, 2000; Packroff, 2000). Moreover, ciliate abundances from several

peat bog pools also correlated to water temperature, total organic carbon, and total phosphorus (Mieczan & Siczek, 2010; Mieczan & Tarkowska-Kukuryk, 2013). Nevertheless, studies pertaining the interaction of biotic and abiotic factors as modeling variables of planktonic ciliate communities in these environments are almost unknown (Mieczan, 2010b; Mieczan & Tarkowska-Kukuryk, 2013).

In the southern area of Tierra del Fuego, the Andean ridges encompass a series of peatlands which include Rancho Hambre (54°47'S, 68°19'W). This is a typical dome-shaped, ombrotrophic peat bog (Roig & Roig, 2004) composed of a *Sphagnum magellanicum* Bridel dominated matrix, which holds a large number of pools of different size. Mataloni & Tell (1996) first characterized the phytoplankton communities in water hollows and the Lasifashaj River from this Fuegian peat bog, finding floristic differences among them on account of morphometric features and conductivity values. Between 2008 and 2010, a 2-year survey was conducted in five different sized-water bodies from Rancho Hambre peat bog in order to study their planktonic communities and to elucidate the main environmental variables shaping these. As a result of these investigations, González Garraza et al. (2012) observed that hydrological connectivity and pool morphometry dictated different patterns of changes in water level and temperature, which in turn modulated physical and chemical features. This resulted in high environmental diversity in both space and time, and investigated water bodies could be classified into two groups: acidic ombrotrophic pools and slightly acidic, minerotrophic ones. In the same pools, Lara et al. (2015) conducted an environmental DNA-based composition survey of the smallest size fraction (<3 µm) of planktonic eukaryotes. This study confirmed the structural differences among minerotrophic and ombrotrophic water bodies, with a prevalence of autotrophs as indicative species of minerotrophic pools and mixotrophs in ombrotrophic ones. Quiroga et al. (2013), in turn, found that albeit the structures of planktonic communities were similar in spring, in late summer, both abundance and biomass of the different trophic compartments differed according to pool size. In particular, abundances of heterotrophic flagellates were bottom-up regulated in spring, shifting to top-down control in late summer, with different metazoans and the ciliate *Pelagostrombidium fallax* (Zacharias) as putative main predators in these fishless pools.

As mentioned previously, the particular characteristics of peat bog pools and the environmental heterogeneity found in Rancho Hambre provide a special scenario to study the taxonomic composition, structure, and dynamics of planktonic ciliates. In fact, this is the first time an ecological approach focusing on ciliates from this particular kind of habitats is carried out in the southern Hemisphere. In this context, we aim at studying the diversity and dynamics of planktonic ciliates in limnetic environments representing a range of environmental features in a peat bog from Tierra del Fuego. We also aim at identifying main environmental drivers of ciliate structure and dynamics, in order to compare these results with those observed in communities from peat bog pools in other geographic locations. On this basis, we hypothesize that descriptors of planktonic ciliates from Rancho Hambre peat bog vary in space and time on account of pool morphometry (shallow, deep) and trophic status (ombrotrophic, minerotrophic). On the basis of previous investigations, we expect these differences to rely on distinct physical and chemical characteristics of the pools and structure and dynamics of other plankton communities.

Materials and methods

Samplings and sample processing

In order to account for the varying water table depths that characterize dome-shaped ombrotrophic peat bogs such as Rancho Hambre (Iturraspe, 2010), a transect was established across the bog. Among the many pools it intersected, five (RH1–RH5) were selected to represent different morphometric characteristics. These pools were sampled on eight occasions during two consecutive ice-free periods (October–April) between 2008 and 2010 (Fig. 1). Geographical coordinates were established with a Garmin Etrex GPS, and morphometric features of the pools indicated in Table 1 were measured as described in González Garraza et al. (2012). In large pools RH1, RH2, and RH4, three to four sampling points were selected according to its size: shore (1 or 2 points, corresponding to northern and/or southern shores), limnetic surface, and bottom. At each point, duplicate samples were taken with a wide-mouthed 1-l sampler for subsurface samples and with a 5-l van Dorn bottle for

bottom ones. In small, shallow pools RH3 and RH5 samples were only taken from the shore. Live as well as 2% Lugol-fixed duplicate samples were transported to the laboratory and preserved in cold and dark conditions. Fixed samples were allowed to settle for 24 h and then concentrated to a final volume of 120 ml. In order to identify ciliate species, live samples were observed immediately under stereoscopic and bright field microscopes, and were also used to establish raw cultures within a culture chamber at 5–10°C and 12/12-h light/dark cycle. To reveal the infraciliature and the nuclear apparatus, ciliates were picked from the samples and cultures with specially designed micropipettes, and fixed in Bouin solution to proceed with protargol silver impregnation according to Wilbert (1975). Countings of Lugol-fixed ciliates were made under an inverted microscope in 10-ml chambers, after homogenization and settling for 24 h, by scanning the whole bottom of the chamber (Utermöhl, 1958). Ciliate identifications were based on the comparison of live observations and protargol impregnations of individuals from cultures and Lugol-fixed samples. Live observations, protargol impregnations, and quantification of ciliates were performed by a single person (GK). Fresh live samples were observed on the same sampling date and the day after, while countings were performed within 3–6 months after sampling to avoid cell losses (Sime Ngando & Grolière, 1991). Taxonomic identifications were mainly made according to Kahl (1930–1935), Foissner et al. (1991, 1992, 1994, 1995), Foissner & Berger (1996), Berger (1999), and specific taxonomic papers. Classification follows Lynn (2008). Ciliate volumes were determined approximating the shape of Lugol-fixed cells to geometrical figures (Hillebrand et al., 1999), based on measurements of length and width of usually 30–50 individuals. The shrinkage correction of Putt & Stoecker (1989) for Lugol-fixed cells was applied and biomass was calculated using a carbon conversion factor according to Müller & Geller (1993).

Picoplankton (picophytoplankton and bacterioplankton) and heterotrophic flagellates (HF) were quantitatively sampled. Both qualitative and quantitative samples were taken for the analysis of nano- and microphytoplankton and metazooplankton. Quiroga et al. (2013) give a detailed account of the methods employed for the sampling, preservation, taxonomic identification, and quantitative analyses of each of these communities.

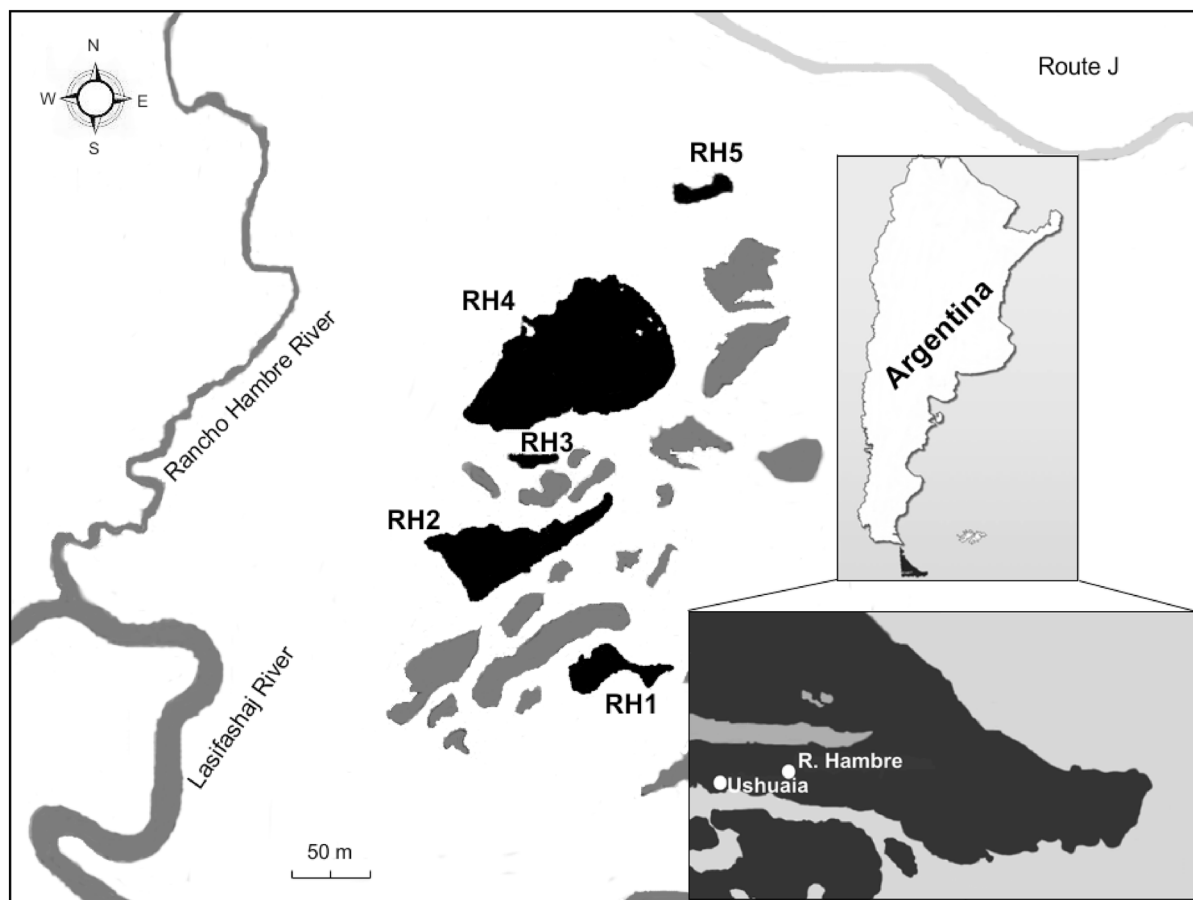


Fig. 1 Study site in Rancho Hambre peat bog, Ushuaia, Tierra del Fuego. The five pools investigated (RH1–RH5) are shaded black (Mataloni et al., 2015)

Environmental variables

Temperature, pH, dissolved oxygen, and conductivity were measured in situ with a multiparametric probe (HORIBA, Japan). Water samples for dissolved nutrient concentration measurements were filtered onto Millipore APFF filters (pore size 0.7 μm). Those for ammonium ($\text{NH}_4\text{-N}$) were preserved at pH 2 and 4°C and analyzed according to the salicylate method. Phosphate ($\text{PO}_4\text{-P}$) and nitrate ($\text{NO}_3\text{-N}$) samples were preserved at -20°C and analyzed using the ascorbic acid and cadmium reduction methods, respectively (APHA, 2005). Dissolved inorganic nutrients (DIN) were calculated as the sum of ammonia and nitrate concentrations. Unfiltered samples for total nitrogen (TN), total phosphorus (TP), and total hardness were preserved

at -20°C until analysis. TN and TP were determined by acid digestion with potassium persulfate and boric acid followed by $\text{NO}_3\text{-N}$ and $\text{PO}_4\text{-P}$ determinations (APHA, 2005). Total hardness was assessed by the calmagite colorimetric method. All measurements were carried out with a Hach spectrophotometer (Hach Company, USA) using the appropriate reactants for each analysis. Suspended solids were estimated by filtering the water samples onto ashed, pre-weighted Millipore APFF filters (pore size 0.7 μm). Dry mass was determined according to APHA (2005). During the second ice-free period (2009–2010) dissolved organic carbon (DOC) was determined from filtered water using the high temperature Pt catalyst oxidation method (Shimadzu analyzer TOC-5000A, SM 5310B technique) following the recommendations of Sharp et al. (1993).

Table 1 Geographical location, morphometric, physical, and chemical features of five pools from Rancho Hambre peat bog (RH1–RH5)

	RH1	RH2	RH3	RH4	RH5
Latitude (S)	54°44'52.87"	54°44'48.61"	54°44'46.75"	54°44'41.51"	54°44'39.35"
Longitude (W)	67°49'29.44"	67°49'31.66"	67°49'31.69"	67°49'31.69"	67°49'26.70"
Area (m ²)	1,824	5,976	137	16,190	542
Maximum depth (cm)	95	150	33	150	33
Temperature (°C)	8.8 (2.2–17.3)	8.6 (1.1–17.0)	11.8 (3.2–25.0)	8.5 (2.4–15.0)	10.6 (1.7–20.0)
pH	5.7 (5.0–7.1)	4.5 (3.8–5.5)	4.5 (3.6–5.4)	6.3 (5.8–7.0)	4.6 (4.1–5.4)
Conductivity (µS cm ⁻¹)	23.6 (13.6–50.0)	22.8 (8.7–40.0)	33.1 (10.0–82.0)	29.8 (16.0–60.0)	25.6 (5.5–50.0)
DO (mg l ⁻¹)	10.5 (8.2–14.0)	11.3 (7.6–14.4)	10.4 (8.7–12.9)	10.6 (7.6–12.2)	9.9 (8.6–11.5)
Susp. solids (mg l ⁻¹)	2.1 (0.7–3.7)	2.5 (0.9–8.3)	5.5 (0.4–19.7)	6.1 (1.6–23.9)	4.1 (0.3–10.9)
DIN (µg l ⁻¹)	46 (7–102)	53 (7–239)	55 (10–103)	44 (19–107)	36 (0–73)
TN (µg l ⁻¹)	5,317 (1,430–10,100)	6,293 (1,980–12,870)	7,305 (1,980–11,330)	6,859 (1,073–26,000)	9,479 (3,410–30,000)
PO ₄ -P (µg l ⁻¹)	62 (27–93)	58 (23–157)	61 (30–130)	34 (10–60)	31 (20–50)
TP (µg l ⁻¹)	206 (113–477)	172 (92–330)	169 (90–308)	164 (88–290)	195 (77–420)
Total hardness (mg equiv CaCO ₃ l ⁻¹)	25.6 (7.0–41.4)	24.2 (6.8–46.2)	22.0 (7.5–43.3)	30.5 (11.0–42.5)	22.3 (10.9–36.4)
DOC (mg l ⁻¹)	7.3 (5.4–9.2)	7.5 (5.1–9.0)	10.4 (2.8–13.4)	5.4 (4.4–7.0)	8.4 (3.9–11.6)

Mean values are followed by minimum and maximum observations in parentheses. *DIN* dissolved inorganic nitrogen, *DO* dissolved oxygen, *TN* total nitrogen, *TP* total phosphorus, *Susp. solids* suspended solids, *DOC* dissolved organic carbon. These data were partly published by González Garraza et al. (2012) and Mataloni et al. (2015)

Statistical analyses

Overall similarity in the taxonomic composition (i.e., the list of taxa recorded over the entire study period) of the five pools was evaluated by means of the Jaccard Similarity index, *J* (Magurran, 2004). For large pools (RH1, RH2, RH4), the internal variability of species richness, abundance, biomass, and diversity (Shannon and Wiener index, *H'*; Magurran, 2004) was assessed by means of a one-factor ANOVA with two independent replicates in each sampling point. Pools were taken as factors, with three levels in RH1 and RH2 (southern shore, limnetic surface, bottom) and four levels in RH4 (also northern shore was sampled). As these differences were not significant, duplicate samples from all points within each large pool were considered as grab samples. Hence, average values of species richness, abundance, biomass, and diversity per sampling date were compared by means of a one-factor ANOVA in which treatments represented the pools (Zar, 2010). These analyses were performed using the software PAST version 2.12 (Hammer et al., 2001). Species richness was previously log ($x + 1$)–

transformed in order to obtain a normal distribution of data. To evaluate the occurrence of indicator species of the trophic status of Rancho Hambre pools, an IndVal analysis was performed (Dufrene & Legendre, 1997). Samples were grouped based on morphometry and trophic status of the pools into deep minerotrophic RH1 and RH4, shallow ombrotrophic RH3 and RH5, and deep ombrotrophic RH2 according to Lara et al. (2015). Within these groups of samples, the indicator value (IndVal) of species or association of species (up to three species combinations) was computed using the 'multipatt' function in the indicpecies package for R (De Cáceres & Legendre, 2009). IndVal index ranges from 0 to 1. Values close to 1 are obtained by a combination of high mean abundance within a group compared to the other groups (specificity, referred to as A) and the presence in most samples of that group (fidelity, referred to as B; Borcard et al., 2011). For each group, the highest IndVal score was selected. To evaluate the correlations among all biotic and abiotic variables, the Spearman's rho test from PAST version 2.12 software (Hammer et al., 2001) was used. A detrended correspondence analysis (DCA) was run to

evaluate the response of the species to the environmental gradients. As this was unimodal, a canonical correspondence analysis (CCA) based on abundance raw data was performed using CANOCO 4.5 program (ter Braak & Šmilauer, 1998). A forward selection of environmental variables was done to extract synthetic gradients. Significance of the canonical axes was tested using Monte Carlo permutation test of samples (Lepš & Šmilauer, 2003). For all the above mentioned analyses, rare species occurring only in one sample with a frequency lower than 3% were removed.

Results

Abiotic features

Table 1 summarizes the abiotic features measured in each pool from Rancho Hambre. Pools RH1 and RH4 had inflows or outflows through natural superficial channels, but RH2, RH3, and RH5 were hydrologically isolated. This fact, together with low volume, accounted for the high variation ranges in temperature and conductivity observed in shallow pools RH3 and RH5. In general, pools could be characterized either as shallow ombrotrophic pools with low pH and total hardness (RH3, RH5) or deep minerotrophic pools with higher pH and total hardness (RH1, RH4). Deep ombrotrophic pool RH2 showed intermediate conditions. An extensive analysis on the variation of physical and chemical characteristics due to pool morphometry, and hydrological and meteorological features can be found in González Garraza et al. (2012).

Species richness, abundance, biomass, and diversity

A total of 125 ciliate species belonging to 24 orders were found in the five pools. The most species-rich orders were Haptorida (12), Prorodontida (9), and Peniculida (6), although most species in these orders were rare. In general, species richness was correlated with pH ($r = 0.6$, $P = 0.01$). Moreover, total species richness (recorded over the study period) was higher in minerotrophic than in ombrotrophic pools (Table 2). This difference was also significant for mean species richness over the study period ($F = 31.66$, $P < 0.05$, $df = 4$, $n = 40$). Only large minerotrophic pools

showed the same abundance dynamics in both sampling periods, with maximum values occurring in fall, while biomass varied little within and among pools, reaching maximum values in spring (Table 2; Fig. 2).

Shannon and Wiener diversity index had lower mean values and ranges in ombrotrophic than in minerotrophic pools (Table 2); however, such differences were not statistically significant ($F = 1.49$, $P > 0.05$, $df = 4$, $n = 40$) on account of large variations over time. As regard to the taxonomic composition, each pool had a particular ciliate assemblage ($J = 0.22$ – 0.35 ; Table 3), in spite of some of them being located a few meters apart from one another.

Structure and dynamics

Rancho Hambre pools were characterized by the presence of prorodontids, mainly *Urotricha* spp. and *Balanion planctonicum* (Foissner, Oleksiv & Müller), and strombidiids such as *Pelagostrombidium fallax*, which were common or dominant in all pools. In addition, choreotrichs like *Rimostrombidium hyalinum* (Mirabdullaev) dominated RH2 in autumn and pleuronematids (*Cyclidium* sp.) were common in RH5 (Table 2). Abundances of these common or dominant species varied widely in space and time (Fig. 3). Indeed, *Halteria grandinella* (O. F. Müller) occurred mainly in early spring in almost all pools and accounted for one case of wide dispersion range among sampling points (=replicates) in RH2 in October 08, due to higher numbers of this ciliate in the shore. *Pelagostrombidium fallax*, in turn, typically reached the highest abundances in summer (2.2 – 20.5 ind ml^{-1}). Minerotrophic pools were dominated by *Urotricha* spp., *P. fallax* in summer, and the small picoplanktivore *B. planctonicum* in late summer and autumn. In April 09, uneven spatial distribution of this latter species in RH1 caused a large dispersion of data in this pool, with higher values occurring in limnetic surface and bottom. Shallow ombrotrophic pools showed different dynamics in both sampling periods, but, in general, small picoplanktivores dominated in spring and autumn and were replaced by *P. fallax* in summer (Fig. 3).

Regarding trophic strategies (Table 3; Figs. 4, 5), most ciliates were small (10–30 μm) pico- to nanoplanktivores (*Urotricha* spp., *Cyclidium* sp., *H. grandinella*, *B. planctonicum*, and *R. hyalinum*). Several species of filter feeding hypotrichs and sessile

Table 2 Mean and total species richness (S), abundances, biomass, and Shannon and Wiener diversity index (H') in Rancho Hambre pools (RH1-RH5) over the study period

	RH1	RH2	RH3	RH4	RH5
S	19 (11–26)	9 (7–13)	7 (5–9)	16 (11–22)	8 (6–10)
ANOVA (S)	a	b	b	a	b
Total S	73	37	34	55	28
H'	1.3 (0.9–2.3)	0.9 (0.2–1.6)	0.9 (0.2–1.8)	1.3 (0.7–2.4)	1.0 (0.3–1.6)
Mean abundance (ind ml ⁻¹)	40.4 (2.9–151.9)	43.5 (6.6–101.8)	38.2 (0.4–208.0)	22.7 (0.7–66.7)	13.8 (1.3–42.2)
Mean biomass (µg C ml ⁻¹)	1.3 (0.3–2.8)	2.3 (0.4–10.1)	0.9 (0.02–2.4)	1.0 (0.07–2.6)	1.2 (0.2–3.2)
<i>Balanion planctonicum</i>	11.1 (0–88.5)	–	–	2.6 (1.4–14.9)	–
<i>Cyclidium</i> sp.	0.16 (0.02–0.6)	–	0.5 (0.3–2.0)	0.1 (0.02–0.2)	4.0 (9.6–22.5)
<i>Halteria grandinella</i>	0.4 (0–1.7)	1.6 (0–12.4)	0.006 (0–0.05)	0.2 (0–0.5)	0.2 (0–0.5)
<i>Pelagostrombidium fallax</i>	4.5 (0.02–18.9)	4.3 (1.2–8.5)	3.7 (0–14.9)	5.3 (0–17.8)	5.4 (0–20.5)
<i>Rimostrombidium hyalinum</i>	0.4 (0.03–0.8)	16.5 (0.2–96.4)	–	0.3 (0.2–1.1)	0.006 (0–0.05)
<i>Urotricha</i> spp.	22.7 (0.2–72.0)	18.0 (0.2–108.1)	33.0 (0–199.4)	1.4 (0.1–44.0)	2.9 (0–15.6)

Dominant and common ciliate mean abundances are expressed in ind ml⁻¹. Mean values are followed by minimum and maximum observations in parenthesis. Significant differences ($P < 0.05$) in S among pools are indicated with different letters (a, b)

– Absent

peritrichs were also found, probably associated to suspended particles or coming from other communities, such as benthos. In addition to the dominant *P. fallax*, large (60–130 µm) mixotrophic ciliates were occasionally present, such as *Limnostrombidium* sp., *Paramecium bursaria* (Ehrenberg), *Stentor* cf. *araucaus*, *Uroleptus willii* Sonntag, Strüder-Kypke & Summerer, *Stichotricha aculeata* Wrzesniowski, *Ophrydium versatile* (O. F. Müller), and *Thylakidium pituitosum* Foissner. These mixotrophs made a great contribution to total biomass in all pools, mostly in summer and early autumn (Fig. 4). In particular, and together with *P. fallax*, *S.* cf. *araucaus* and *T. pituitosum* contributed greatly to mean biomass in shallow ombrotrophic pools (Fig. 5c). Raptorial feeders belonging to the Haptorida also occurred but were mostly rare, and their contribution to total biomass was insignificant (Fig. 4). Only raptorial prorodontids (*Urotricha* spp.) made a great contribution to mean biomass due to their high abundances (Fig. 5a–c).

Influence of biotic and abiotic features on ciliate composition and abundances

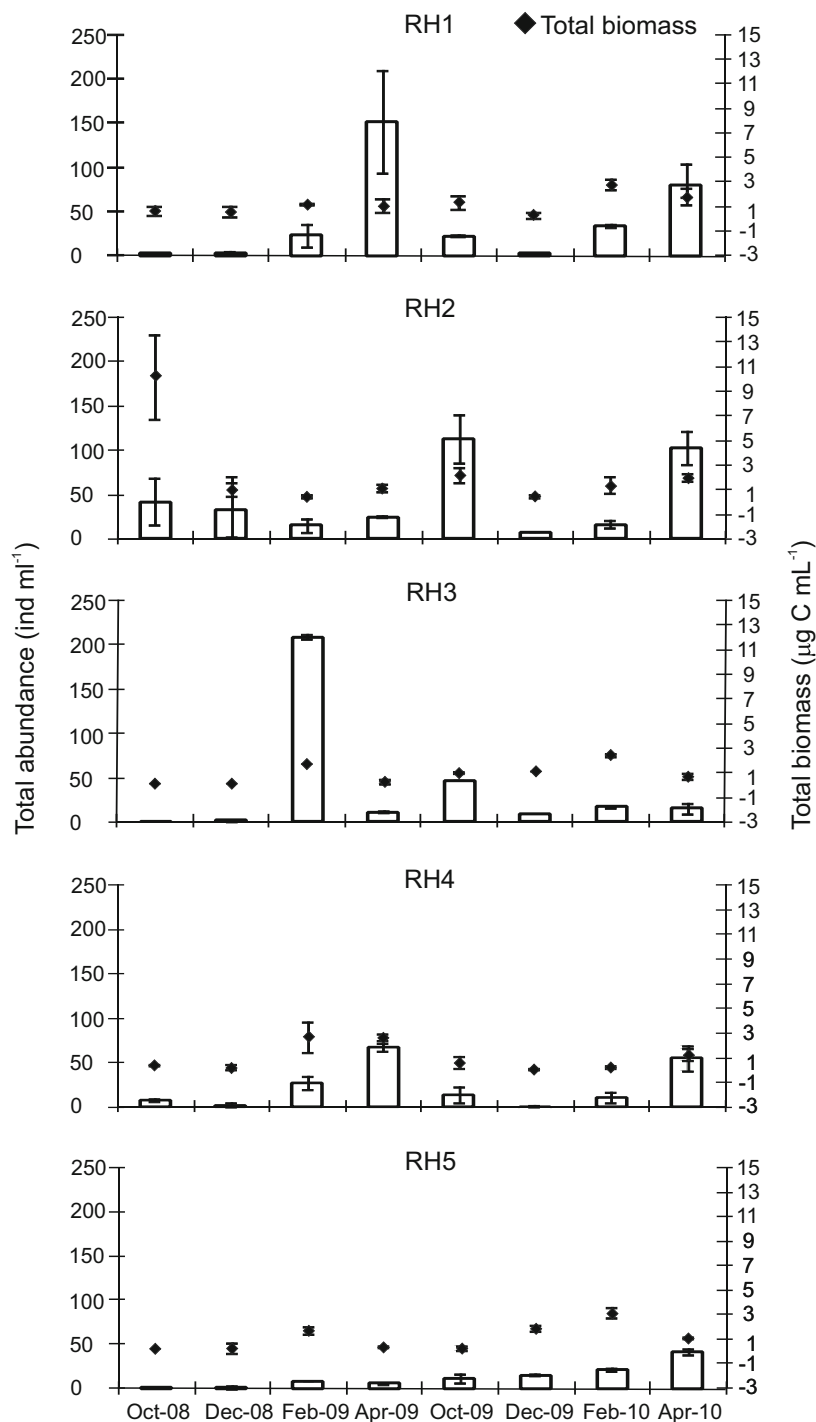
The influence of environmental variables and other plankton communities on ciliate species abundances was assessed through a canonical correspondence analysis. The first two axes shown in the CCA plots (Fig. 6a, b) based on biotic and abiotic features

explained 46.3% of the variability observed in the structure of ciliates, with a species-environment correlation of 0.88 that was highly significant ($P = 0.002$). According to the Monte Carlo permutation test, picophytoplankton abundances (eigenv. 0.66, $P = 0.02$) was the most influential variable on axis 1. Along the second axis, abundances of the different ciliates were mainly driven by the abundances of bacterioplankton and HF (eigenv. 0.38, -0.38, respectively). In turn, high bacterioplankton abundances were associated with summer samples. In particular, summer samples from large minerotrophic pools are placed in the upper left quadrant. In contrast, early spring and some autumn samples were associated to high HF and metazooplankton abundances and mostly placed in the lower right quadrant. Regarding the behavior of dominant taxa, abundances of pioneering *H. grandinella* were closely associated with the latter group of samples, while the filter feeding *Rimostrombidium hyalinum* was clearly associated with RH2 samples. Summer dominant *P. fallax*, in turn, is located in the upper left quadrant among most December and February samples.

Indicator species

According to the IndVal analysis, not only single species but also associations of species were indicators of pool morphometry and trophic status in Rancho Hambre peat

Fig. 2 Total abundance and biomass of ciliates in the five pools (RH1-RH5) from Rancho Hambre peat bog over the study period (October 08–April 10). Error bars indicate dispersion data among sampling points or replicates



bog. Interestingly, these associations involve both dominant and rare taxa. In particular, deep minerotrophic pools were characterized by the association of the euryoecious *H. grandinella* and different species of

hypotrichs ($A = 0.90$, $B = 0.81$, $\text{IndVal} = 0.73$, $P < 0.001$). On the other hand, the combination of the mixotrophs *P. fallax* and *Thylakidium pituitosum* was indicative of shallow ombrotrophic ones; in spite of

Table 3 Species list, abbreviations (abbrev.) used in the canonical correspondence analysis, occurrence in Rancho Hambre pools (+), and trophic characterization

Species	Abbrev.	RH1	RH2	RH3	RH4	RH5	Trophic charact.
<i>Acropisthium</i> sp.	acsp		+				RF
<i>Amphileptus</i> sp.	amsp	+					RF
<i>Aspidisca lynceus</i> (O.F. Müller)	asl	+					FF
<i>Aspidisca</i> sp.	assp	+	+		+	+	FF
<i>Balanion planctonicum</i> (Foissner, Oleksiv & Müller)	bap	+			+		RF
<i>Blepharisma</i> sp.	bsp				+		FF
<i>Bryometopus sphagni</i> (Penard)	brs					+	FF
<i>Bursaridium pseudobursaria</i> (Fauré-Fremiet)	bup			+	+		FF
<i>Bursellopsis</i> sp.	bursp		+				RF
<i>Chaenea</i> sp.	chasp	+		+			RF
<i>Chilodonella</i> sp.	chisp	+					RF
<i>Coleps</i> sp.	cosp	+	+	+		+	RF
<i>Colpidium</i> sp.	colsp				+		FF
<i>Colpoda steinii</i> Maupas	colpst				+		FF
<i>Colpoda</i> sp.	colpsp	+	+	+	+		FF
<i>Cyclidium</i> sp.	cysp	+	+	+	+	+	FF
<i>Dileptus</i> sp.	dilsp	+		+	+		RF
<i>Enchelyodon</i> sp.	ensp	+		+			RF
<i>Enchelys</i> sp.	enchsp	+	+	+	+		RF
<i>Epispathidium amphoriforme</i> (Greeff)	epiam		+		+	+	RF
<i>Euplotes</i> sp.	eusp		+		+	+	FF
<i>Frontonia atra</i> (Ehrenberg)	fronat		+				FF
<i>Frontonia</i> cf. <i>acuminata</i>	frona	+		+	+	+	FF
<i>Frontonia</i> sp. 1	fronsp1	+	+		+		FF
<i>Frontonia</i> sp. 2	fronsp2				+		FF
<i>Halteria grandinella</i> (O. F. Müller)	halgran	+	+	+	+	+	FF
Hypotrichs	hypo	+	+	+	+	+	FF
<i>Tachysoma</i> sp.	tachsp			+	+		FF
<i>Holophrya</i> sp. 1	holosp1	+	+			+	RF
<i>Holophrya</i> sp. 2	holosp2	+	+	+	+	+	RF
<i>Lacrymaria</i> sp. 1	lasp1	+			+		RF
<i>Lacrymaria</i> sp. 2	lasp2	+					RF
<i>Lagynophrya</i> sp.	lagsp	+	+		+	+	RF
<i>Lembadion lucens</i> (Maskell)	lemlu	+		+	+		FF
<i>Leptopharynx</i> sp.	lepsp			+			RF
<i>Limnostrombidium</i> sp.	limnsp		+				M
<i>Litonotus</i> sp.	litosp	+		+	+		RF
<i>Loxophyllum</i> sp.	loxosp	+		+			RF
<i>Mesodinium acarus</i> Stein	mesoa		+				RF
<i>Metopus</i> sp.	metosp	+					FF
<i>Monodinium</i> sp.	monosp	+					RF
<i>Ophrydium versatile</i> (O. F. Müller)	ophv					+	M
<i>Oxytricha</i> sp.	oxysp	+	+	+			FF
<i>Paramecium aurelia</i> complex	para	+	+		+		FF

Table 3 continued

Species	Abbrev.	RH1	RH2	RH3	RH4	RH5	Trophic charact.
<i>Paramecium bursaria</i> (Ehrenberg)	parb	+			+		M
<i>Parasterkiella thompsoni</i> (Foissner)	parat	+	+	+	+	+	FF
<i>Pelagostrombidium fallax</i> (Zacharias)	pelaf	+	+	+	+	+	M
<i>Plagiopyla nasuta</i> Stein	plan			+	+		FF
<i>Platyophrya</i> sp.	plasp	+		+	+		RF
<i>Pleuronema</i> sp.	pleusp	+					FF
<i>Podophrya fallax</i> Dingfelder	podof	+					DF
<i>Podophrya</i> sp.	podosp	+					DF
<i>Rimostrombidium hyalinum</i> (Mirabdullaev)	rimohy	+	+		+	+	FF
<i>Sphaerophrya</i> sp.	sphasp				+		DF
<i>Stentor coeruleus</i> Ehrenberg	stenco				+		FF
<i>Stentor</i> cf. <i>araucanus</i>	stena	+		+	+	+	M
<i>Stentor</i> sp.	stensp2				+		FF
<i>Stichotricha aculeata</i> Wrzesniowski	stia				+		M
<i>Strobilidium caudatum</i> (Fromentel)	stroc				+		FF
<i>Stylonychia</i> sp.	stysp	+					FF
<i>Tetrahymena pyriformis</i> complex	tetrap	+		+	+	+	FF
<i>Thylakidium pituitosum</i> Foissner	thyp	+		+		+	M
<i>Tokophrya</i> cf. <i>infusioformis</i>	toki			+			DF
<i>Trachellophyllum</i> sp.	trachsp	+			+		RF
<i>Uroleptus willii</i> Sonntag, Strüder-Kypke and Summerer	urolw	+		+	+	+	M
<i>Uronema</i> sp.	uronsp	+	+		+		FF
<i>Urotricha</i> sp. 1	urosp1	+	+	+	+	+	RF
<i>Urotricha</i> sp. 2	urosp2	+	+	+	+	+	RF
<i>Urotricha</i> sp. 3	urosp3		+				RF
<i>Urotricha</i> sp. 4	urosp4				+		RF
<i>Vorticella</i> sp. 1	vortsp1	+	+	+	+	+	FF
<i>Vorticella</i> sp. 2	vortsp2		+	+	+	+	FF
No of unidentified ciliates	–	27	9	3	10	4	–

Unidentified ciliates occurred only once and were not shared by different pools

DF Diffusion feeder, FF filter feeder, M mixotrophic, RF raptorial feeder

having a high specificity, fidelity of this group of species to these environments was low ($A = 0.99$, $B = 0.38$, $\text{IndVal} = 0.37$, $P = 0.014$). Finally, as expected, *R. hyalinum* was the most indicative species of deep ombrotrophic pool RH2 ($A = 0.98$, $B = 1.00$, $\text{IndVal} = 0.98$, $P < 0.001$), showing the highest fidelity to this environment as well.

Discussion

In spite of the uniqueness of peat bog communities, which renders them excellent biogeographic indicators

(Mataloni, 1997), diversity and ecology of ciliates from peat bog pools have been scarcely investigated globally, and there are only few comparable studies with the present one (Macek et al., 2001; Mieczan, 2007a, b, 2010a, b; Mieczan & Siczek, 2010). Notably, Rancho Hambre pools turned out very ciliate rich, with 125 species belonging to 24 orders, in contrast with the findings of Mieczan (2007a, b, 2010a, b) and Mieczan & Siczek (2010) from several *Sphagnum* pools with different pH and nutrient upload (between 9 and 16 species in each peat bog, and a total of 36 in four different peat bogs). In agreement with these authors, in our study, species richness was positively correlated

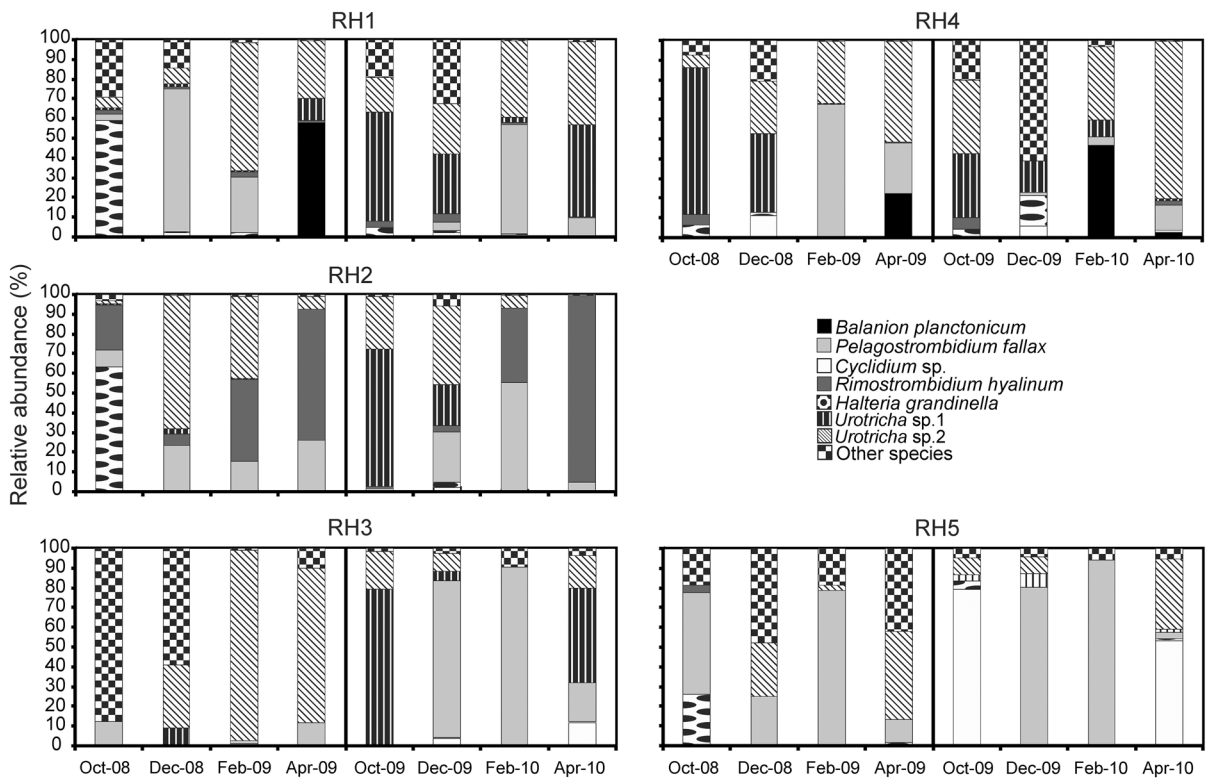


Fig. 3 Relative abundance of dominant ciliates in five pools (RH1–RH5) from Rancho Hambre peat bog over the study period (October 08–April 10)

with pH, with the lowest values in most acidic pools. Regarding mean abundances, Rancho Hambre pools showed similar values to those recorded by Mieczan (2007a, b, 2010a) and Mieczan & Siczek (2010) (13.8–43.5 vs. 5–60 ind ml⁻¹, respectively). However, one of the most acidic pools had the highest abundance due to a peak of *Urotricha* spp. and reached comparable values to those recorded by Macek et al. (2001) in a deep bog lake from Germany (290 and 660 ind ml⁻¹). The abundance peak of *Urotricha* spp. in such an acidic environment is in line with Weisse & Stadler (2006) proving that several small *Urotricha* species are able to tolerate wide pH ranges. Although pH is a main driver of ciliates occurrence in these environments, the mechanisms involved are still not clear, as Weisse & Stadler (2006) found that even under simplified experimental conditions, the ciliate response to this parameter combined direct and food quality mediated effects.

With respect to biomass, the maximum value in our study was higher than that recorded by Macek et al. (2001), who found similar species to those occurring

in Rancho Hambre pools (10.1 vs. 0.66 µg C ml⁻¹ and 0.99 µg C ml⁻¹, respectively). In agreement with Mieczan (2007a, b), the highest biomass was observed in one of the most acidic pools from Rancho Hambre.

Ciliate abundances followed the same variation pattern in minerotrophic pools throughout the studied period, suggesting more predictable environmental conditions in these hydrologically stable water bodies (González Garraza et al., 2012). In spite of being very near from one another, each pool had a particular ciliate assemblage mostly defined by rare and occasional species, as observed for phytoplankton communities from these same pools (Mataloni et al., 2015). This further supports the idea that a high landscape-driven environmental variability exists in Rancho Hambre pools, which plays a key role in shaping the composition of their plankton communities. Large and deep minerotrophic pools showed the highest mean and total species richness, and were characterized by euryoecious and widely distributed species, such as *H. grandinella*, several hypotrichs,

Fig. 4 Relative biomass of raptorial feeder, mixotroph, and filter feeder ciliates in five pools (RH1-RH5) from Rancho Hambre peat bog over the study period (October 08–April 10). Biomass of diffusion feeders was negligible, therefore not included

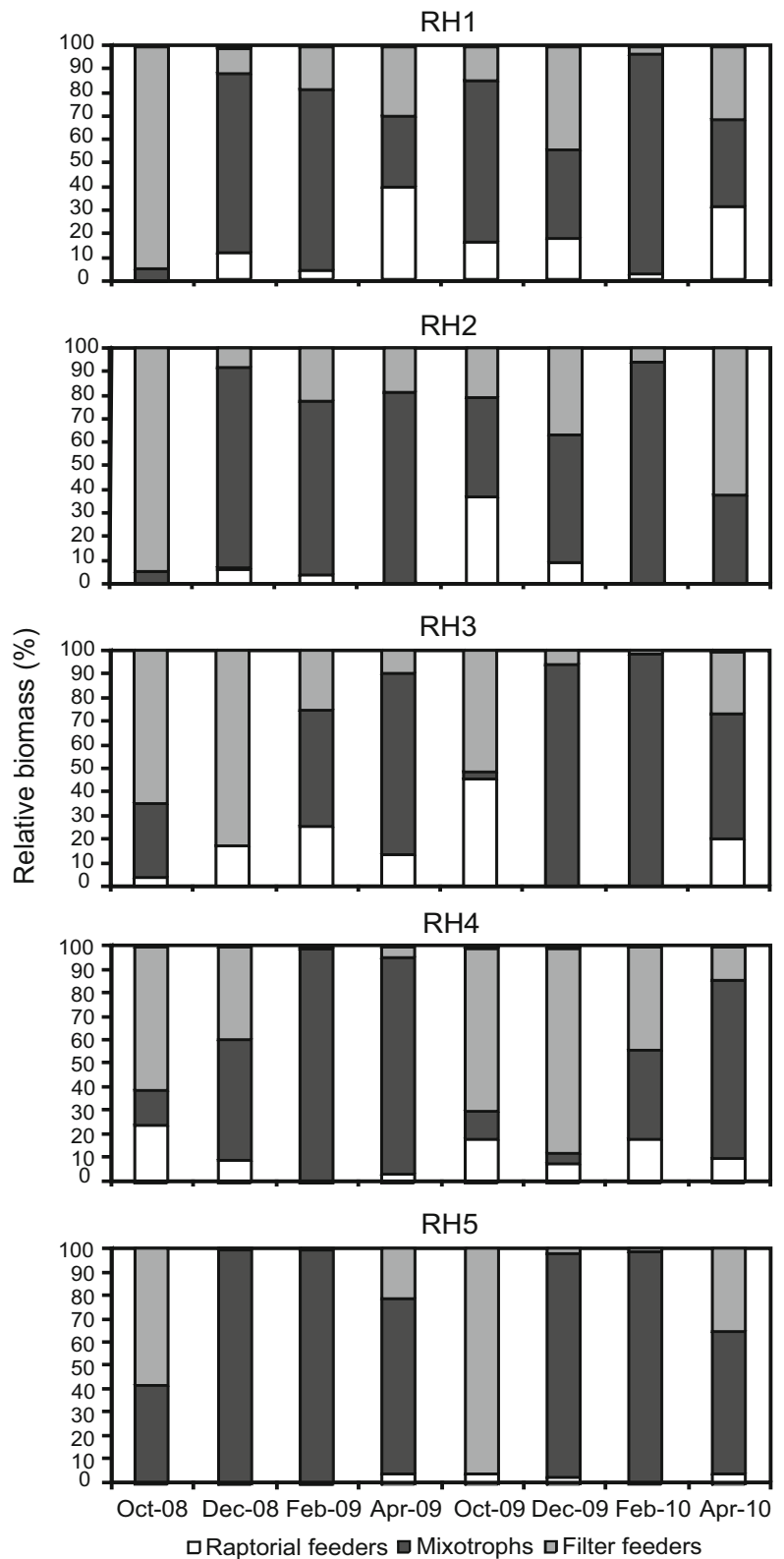
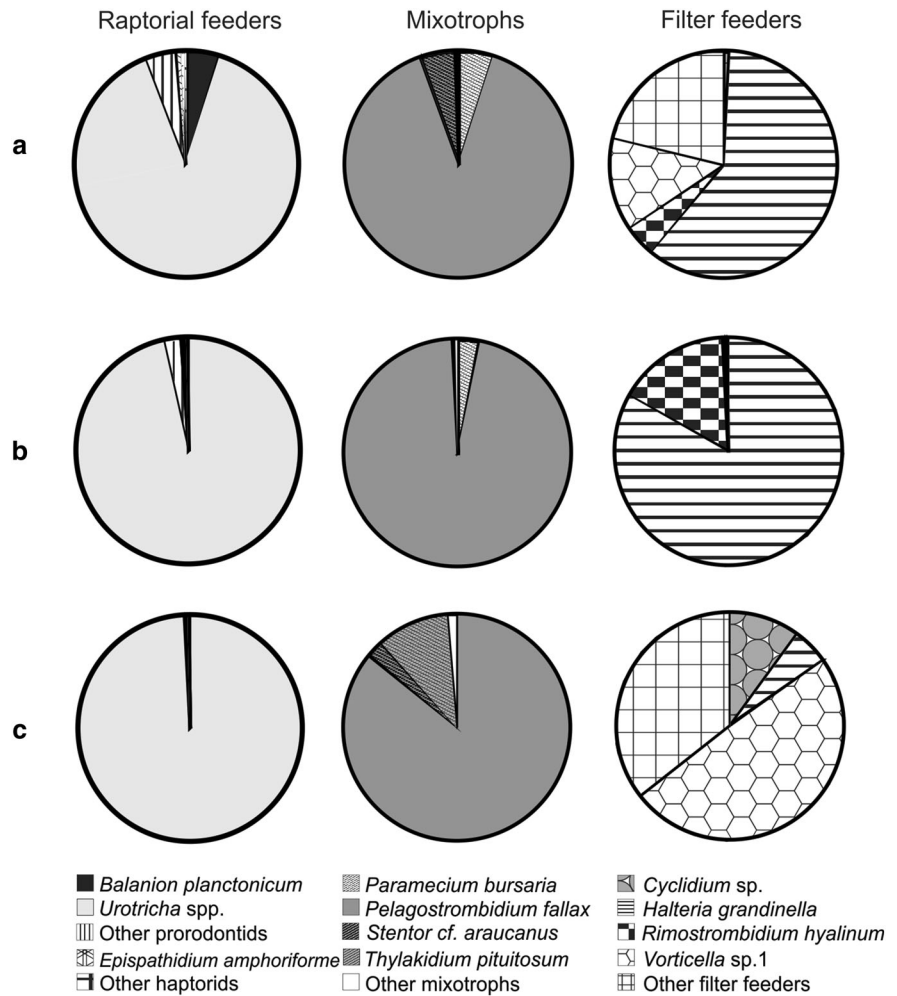


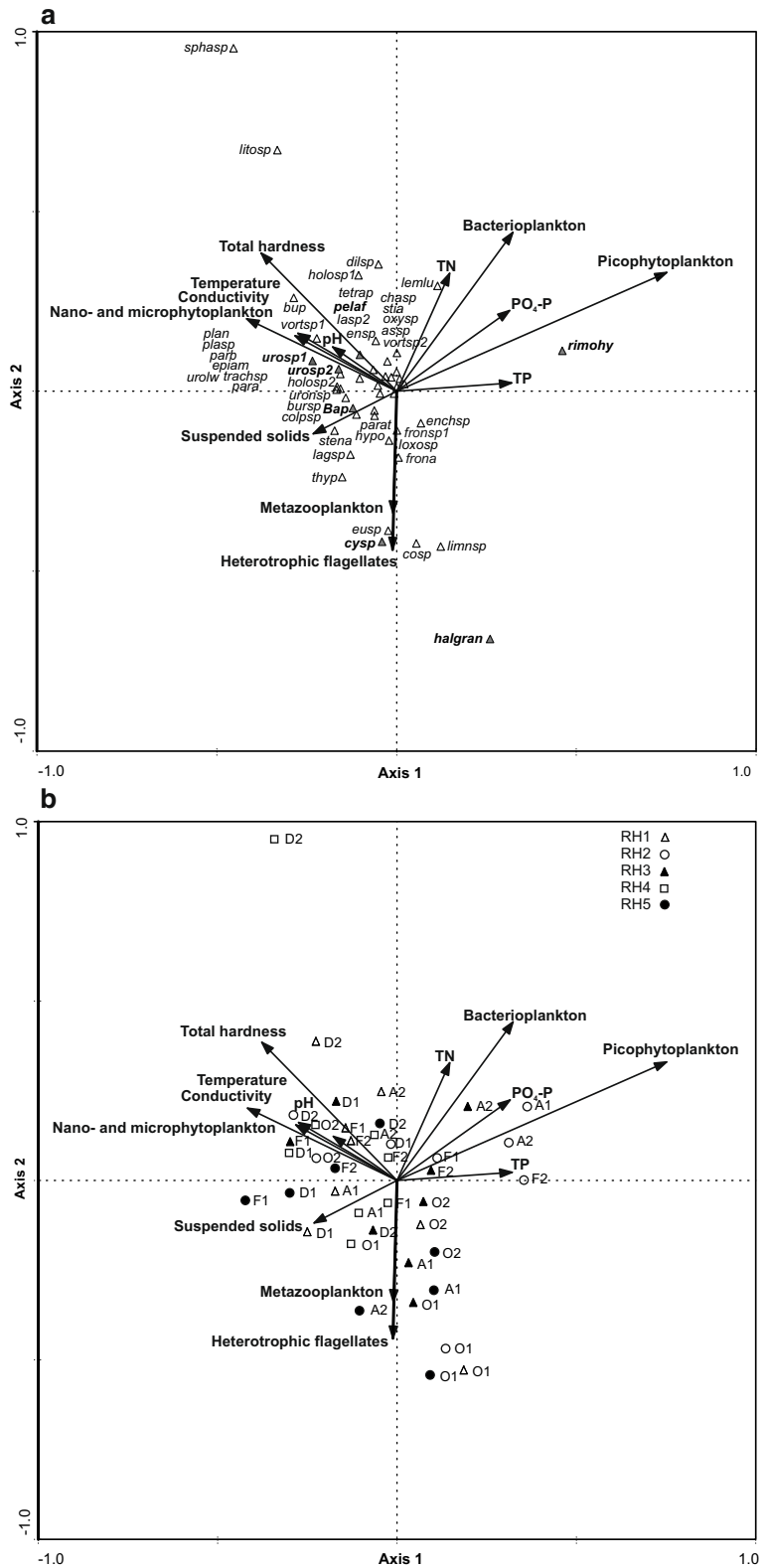
Fig. 5 Relative contribution of taxa to mean biomass of different trophic groups of ciliates in Rancho Hambre pools. **a** Minerotrophic (RH1, RH4), **b** deep ombrotrophic (RH2), and **c** shallow ombrotrophic (RH3, RH5) pools



Urotricha spp., *B. planctonicum*, *Paramecium aurelia* complex, and *P. bursaria*, among others (see Foissner et al., 1999 for distribution and autecological data on these species), while shallow ombrotrophic pools were characterized by large mixotrophic ciliates such as *T. pituitosum*, *Stentor* cf. *araucanus*, and *P. fallax*. The two former species host hundreds of green symbiotic algae (Foissner & Wölfl, 1994; Kreutz & Foissner, 2006), while *P. fallax* maintains “sequestered” plastids from the algae it ingests (Foissner et al., 1999). In addition to this obvious trophic advantage, algal symbionts are known to synthesize UV sunscreen compounds or act as a physical barrier against UV (Sonntag et al., 2007; Summerer et al., 2009), rendering mixotrophy further convenient in these shallow, well-lit environments, which are submitted

to very strong spring UV radiation (Searles et al., 2001). In fact, large mixotrophs made a great contribution to total biomass mostly in summer and early autumn in Rancho Hambre pools, with *P. fallax*, *Stentor* cf. *araucanus*, and *T. pituitosum* making the greatest contribution to mean biomass typically in shallow ombrotrophic pools, which were exposed to higher light penetration. Interestingly, these ciliates were indicative species of these shallow ombrotrophic environments. Mixotrophs belonging to the same genera than those found in Rancho Hambre have been recorded in peat bog pools or lakes from other geographic locations in the northern Hemisphere, e.g., *Pelagostrombidium mirabile* (Penard), *Limnostrombidium viride* (Stein), and *Rimostrombidium velox* (Fauré-Fremiet) (Macek et al., 2001; Mieczan,

Fig. 6 Canonical correspondence analysis based on ciliate species abundances and biotic and abiotic features in Rancho Hambre pools (RH1-RH5). **a** Ordination of species over two first canonical axes, **b** ordination of samples based on biotic and abiotic variables. Species labels are shown in Table 3, and dominant species are shaded black with gray triangles; sample labels indicate sampling month (*O* October, *D* December, *F* February, *A* April) and year (*I* first, *2* second); *TN* total nitrogen, *TP* total phosphorous, *PO₄-P* phosphate concentration



2007b). Lara et al. (2015) studied the molecular diversity of small (<3 µm) eukaryotes in these Rancho Hambre pools by IlluminaHi-Seq approach and also found mixotrophs to be more frequent in ombrotrophic environments. Remarkably, although OTUs corresponding to ciliates were present in low frequencies, four ciliate sequences were among the 5% best minerotrophy indicators, and another one was among the 5% best ombrotrophy indicators. Thus, also in a wider context, less frequent taxa proved again to be more valuable as indicators of trophic conditions. However, the most remarkable ciliate indicator species was the picoplanktivore *R. hyalinum*, which was present in all deep pools but typically occurred more frequently and reached the highest abundances in the deep, ombrotrophic RH2. *Rimostrombidium hyalinum* has hitherto been regarded as a rare species, which was originally described from a pisciculture pond in Uzbekistan and then only retrieved from a eutrophic lake from Austria (Foissner et al., 1999). Further morphological, ontogenetic, and molecular studies are needed to find out whether *R. hyalinum* from Rancho Hambre is indeed the same species and in order to characterize its autecology accurately. In fact, this finding would not be exceptional, since the geographical distribution of an Antarctic hypotrich, *Parasterkiella thompsoni* (Foissner), has been widened and the species redescribed based on isolates from Rancho Hambre pools (Küppers et al., 2011). It is also worth mentioning that *Uroleptus willii*, a mixotrophic planktonic hypotrich, has been retrieved here for the first time since its original description by Sonntag et al. (2008) from an oligo-mesotrophic lake from Austria. Therefore, from a biogeographical point of view, this study provides a novel insight into the diversity and distribution of a group of protists which has been long disregarded mainly because of under-sampling, the existence of largely unexplored geographical regions (i.e., South America), misidentifications, and the lack of interdisciplinary work of trained taxonomists assessing for (morpho)species diversity (Foissner et al., 2008).

With regard to the influence of environmental variables on ciliate community structure, in addition to pH as a driver of species richness (Beaver & Crisman, 1982; Packroff, 2000; Mieczan, 2007a, b, 2010a), total organic carbon and conductivity strongly influenced ciliate abundances in peat bog pools from Poland (Mieczan, 2007a, b, 2010a). Yet, taxonomic

composition and abundance of ciliates in Rancho Hambre were also strongly influenced by abundances of other plankton communities, e.g., RH2 was characterized by high abundances of *R. hyalinum* in close association to picophytoplankton abundance. Šimek et al. (1995) found *R. hexakinetum*, a similar-sized congeneric species, to be a highly efficient filter feeder with an elevated uptake rate of picoplankton. On the other hand, Quiroga et al. (2013) found a positive correlation between temperature and nano- and microphytoplankton abundances in all pools from Rancho Hambre. In the present study, these communities appeared associated with high abundances of *Urotricha* spp. and *P. fallax*, suggesting that the mentioned ciliates probably fed on these planktonic fractions. Indeed, Šimek et al. (1996) found that this latter species can feed on a wide range of phytoplankton sizes.

In spring, relatively high abundances of *H. grandinella* were associated to heterotrophic flagellates and metazooplankton. Although this species is the main bacterivore ciliate in eutrophic lakes (Šimek et al., 1995), in Rancho Hambre both *H. grandinella* and another bacterivore ciliate, *Cyclidium* sp., were negatively related to bacterioplankton abundances, in agreement with the observations of Tadonlécé et al. (2005) from boreal humic lakes. In fact, Šimek et al. (1998) suggested that *Cyclidium* sp. and metazooplankton could be the top-down regulators of heterotrophic nanoflagellates in an acidic bog lake, which also appeared in close association in Rancho Hambre. During that season, metazooplankton was mainly composed by micro-filter feeding nauplii (Quiroga et al., 2013), which are known to feed on ciliates in other freshwater environments (Adrian & Schneider-Olt, 1999). Moreover, adult and nauplii of several microcrustaceans are able to capture and feed on *H. grandinella*, in spite of its jumping escape behavior (Archbold & Berger, 1985), suggesting that this ciliate could also be top-down regulated. Raptorial ciliates that feed on other ciliates (e.g., haptorids) rarely occurred in Rancho Hambre pools and also had a negligible contribution to total biomass as to have an impact on picoplanktivorous ciliates. Indeed, small prorodontids (mostly *Urotricha* spp. and *B. planctonicum*) rather than haptorids, made the greatest contribution to biomass of raptorial ciliates due to their high abundances. All these observations would support the hypothesis that cascading trophic regulation would

play an important role in these environments, in line with the findings of Mieczan (2010b) of clear vertical distribution patterns of ciliates in a raised bog, with metazoans (copepods and rotifers) being the main regulators of protozoan communities in surface waters. Clearly, laboratory and/or field controlled experiments in Rancho Hambre pools are needed to confirm or dismiss the importance of the bottom-up versus top-down regulating mechanisms discussed here.

In conclusion, our results coincide with observations on other plankton communities from the same pools from Rancho Hambre (Quiroga et al., 2013, 2015; Lara et al., 2015; Mataloni et al., 2015) in that plankton communities are very species rich, mainly in minerotrophic pools. Albeit all pools shared the same dominant ciliates, and euryoecious, widely distributed species, were conspicuous in minerotrophic as well as in ombrotrophic environments, rare and occasional species were highly indicative of the trophic status of these pools. In particular, shallow ombrotrophic environments were mainly characterized by the occurrence of mixotrophs. The most particular environment was the deep ombrotrophic pool RH2, where picophytoplankton abundance was the main regulator of ciliate structure. Accordingly, the most distinctive indicator species occurred in this pool. In general, and in agreement with observations by Quiroga et al. (2015) on the prokaryotic communities from Rancho Hambre, both abiotic features and trophic relationships interact to produce a stronger environmental filtering in ombrotrophic pools. To what extent each of these factors contributes to shape ciliate structure and dynamics in Rancho Hambre peat bog remains to be answered through in situ controlled experiments.

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