

# Towards a comprehension of *Ceratium* (Dinophyceae) invasion in Brazilian freshwaters: autecology of *C. furcoides* in subtropical reservoirs

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**Abstract** *Ceratium* species are not a common component of freshwater phytoplankton in South America. However, these dinoflagellates have often been observed in many water bodies over the past two and a half decades. We investigated *Ceratium furcoides*' abundance and morphological variation during its initial phase of colonization (2012–2013) in two subtropical reservoirs in southern Brazil in order to explore which environmental factors were related to the occurrence, persistence and bloom formation of this dinoflagellate in those environments. Biomass of *C. furcoides* showed a strong seasonal pattern, in which warm seasons led to an increase in population

density, resulting in cell-size reduction, while in the cold seasons cells increased in volume. Maximum densities over 2,500 cells ml<sup>-1</sup> were observed in spring–summer periods in both reservoirs. *C. furcoides*' abundance in the studied reservoirs was associated, primarily, with a combination of optimal conditions of temperature, organic matter, and pH, and secondarily, with nutrient availability. The possible factors for the successful colonization performed by *C. furcoides* across distinct Brazilian waterbodies include good swimming performance, low herbivory pressure, and ability to form dense blooms, as strategies that allow maintenance of populations and effective dispersal.

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## Introduction

Biological invasion is a central subject in management and conservation of natural landscapes. Well-established species can cause negative effects in the invaded ecosystems, such as loss of biological diversity, extinction of native species, changes in community dominance, and ecosystem alterations (Mooney & Cleland, 2001; Catford et al., 2012). Studies of macroscopic organisms are frequent, whereas the microbiological invasion is harder to detect and

therefore much less documented (Elbrächter, 1999; Litchman, 2010; Leuret et al., 2013). Several microalgae species, in particular potentially harmful ones, are quickly expanding their geographic distribution (e.g., Elbrächter, 1999; Edwards et al., 2001; Hoppenrath et al., 2007; Lilly et al., 2007; Blanco & Ector, 2009; Sukenik et al., 2012). The dispersion of these species can be intensified by human activities (Nagai et al., 2007). Moreover, studies indicate that human-altered ecosystems, especially impoundments, favor the invasive species' spread (Johnson et al., 2008). Therefore, they are key-environments for understanding the processes governing colonization, establishment, and expansion of exotic species.

The dinoflagellate genus *Ceratium* Schrank is considered to be invasive in South American freshwaters (Boltovskoy et al., 2013). Species of this genus have rarely been reliably recorded in this region until the 1990s, when *C. hirundinella* (O. F. Müller) Dujardin started in southern Chile and spread 2,000 km northward in 10 years (Mac Donagh et al., 2005; Boltovskoy et al., 2013). In Brazil, the colonization by *Ceratium* was particularly distinct: it started in 2000s and the primary species was *C. furcoides* (Levander) Langhans, which was recorded in rivers and reservoirs from the southeastern (Santos-Wisniewski et al., 2007; Matsumura-Tundisi et al., 2010), northeastern (Oliveira et al., 2011), and southern regions (Cavalcante et al., 2013; Jati et al., 2014). Since Brazil, *C. furcoides* has been detected in other countries such as Colombia (Bustamante-Gil et al., 2012) and Argentina (Meichtry de Zaburlin et al., 2014), suggesting that this species has expanded in a radial pattern, first in Brazil, and then reaching areas not previously invaded by *C. hirundinella* (Boltovskoy et al., 2013; Cavalcante et al., 2013).

*Ceratium* species are not toxic; however, high biomasses may be harmful to ichthyofauna during bloom decay due to oxygen depletion from bacterial consumption (Smayda, 1997). Moreover, they can cause odor and taste in drinking water and clog filters during water purification, and are therefore considered prejudicial in monitoring programs of watersheds destined for public consumption (Ewerts et al., 2013).

Ecological studies were largely conducted in north temperate regions, especially of *Ceratium hirundinella* (e.g., Dottne-Lindgren & Ekbohm, 1975; Moore, 1977; Heaney & Talling, 1980; Nicholls et al., 1980; Chapman et al., 1985; Padišák, 1985; Grigorszky

et al., 2003). The autecology of *Ceratium furcoides* is poorly understood and probably much of the information related to *C. hirundinella* in the literature in fact corresponds to *C. furcoides*, due to the morphological similarity of these species (Calado & Larsen, 1997). *C. furcoides* is often found co-occurring with other *Ceratium* species, at low abundance in temperate systems, but occasionally it was the representative or dominant species in relation to total *Ceratium* density, with blooms occurring during the summer in those regions (Canter & Heaney, 1984; Hickel, 1988; Lindström, 1992). According to Heaney et al. (1988) and Bustamante-Gil et al. (2012), *C. furcoides*' ecology is also very similar to *C. hirundinella*: both organisms tolerate wide environmental variation, but prefer conditions of high nutrient availability, temperatures between 15 and 25°C, thermal stratification, and pH higher than 8 (Heaney & Talling, 1980; Lindström, 1992). Laboratory experiments conducted with strains of *C. furcoides* have supported some of these environmental preferences, demonstrating optimal growth at temperatures of 14–25°C (Butterwick et al., 2005) and phototactic and chemosensory behavior of this species in response to photon irradiance and several chemical gradients (Clegg et al., 2003, 2004). However, some studies have shown a different seasonal pattern than that found in temperate systems for *C. hirundinella*, with winter dominance during water mixing (Pérez-Martínez & Sánchez-Castillo, 2001, 2002). Besides population fluctuations in terms of abundance, seasonal variation on morphometric characters (called “cyclomorphosis”) is also reported in the literature for ceratioid dinoflagellates (Huber-Pestalozzi, 1950; Pollinger, 1988; Lindström, 1992; Gligora et al., 2003). High morphometric variation in *Ceratium* is not only considered to be an adaptive characteristic for environmental changes, especially temperature (Popovský & Pfister, 1990; Lindström, 1992), but also seems to be related to biotic pressures, such as herbivory, and resistance to mechanical damage by filtering zooplankton (Hamlouli et al., 1998; Bertolo et al., 2010).

With the fast expansion of *Ceratium* in South American systems, research investigating its ecological requirements and tolerance levels is necessary to understand its potential dispersal and possible impacts on those ecosystems. Some studies have already been published (on *C. hirundinella*: Mac Donagh et al., 2005; Parodi et al., 2007; Silverio et al., 2009; on *C.*

*furcoides*: Bustamante-Gil et al., 2012; Silva et al., 2012), but the knowledge is still diffuse. In this study, we investigated *C. furcoides*' abundance and morphological variation during its initial phase of colonization (2012–2013) in two subtropical reservoirs in southern Brazil in order to explore which environmental factors were related to the occurrence, persistence, and bloom formation of this dinoflagellate in those environments. These findings, together with other similar studies performed in the region, are a crucial first step toward understanding the invasive success of *Ceratium* in South American water systems.

## Materials and methods

The present study was conducted in two subtropical reservoirs located in the city of Caxias do Sul, in southern Brazil. This region is characterized by a warm temperate climate without a dry season (Cfa, Kottke et al., 2006), annual mean temperature of 16°C, and total annual precipitation between 1,800 and 2,200 mm (Becker et al., 2009a). Faxinal and Maestra reservoirs (Fig. 1) are two unconnected systems included in the Taquari-Antas river basin and are used as a water supply by SAMAE (Serviço Autônomo Municipal de Água e Esgoto), the company responsible for limnological monitoring of these systems.

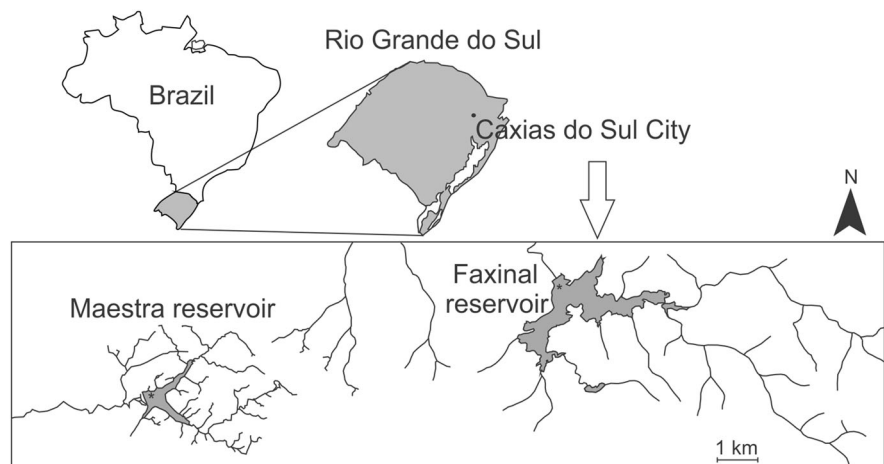
Faxinal reservoir (29°05'00"S; 51°03'30"W) was constructed in 1992. It is a warm monomictic and meso-eutrophic system, with surface area of 3.1 km<sup>2</sup>,  $z_{\max}$  30 m, and retention time of 191 days (Becker et al., 2009b). In contrast, Maestra reservoir

(29°06'37"S; 51°09'51"W) is less studied than the former. The reservoir was built in 1968, has a surface area of 0.54 km<sup>2</sup>,  $z_{\max} \approx 25$  m, and is regarded as a eutrophic system (SAMAE, unpublished data).

Samples derived from the phytoplankton monitoring program performed by SAMAE were preserved with Lugol's iodine solution. Samples were gathered weekly near the water intake, from the surface layer (0–0.5 m), in both reservoirs, in 2012 and 2013. Simultaneously, physical and chemical parameters were measured; the analytical methods of APHA (1998) were followed. Temperature, dissolved oxygen, pH, and conductivity were measured by a Horiba U-10 multiparameter probe; turbidity was measured by a HACH 2100P turbidimeter. Organic matter was estimated by titration method. Nutrient (ammonium, nitrite, nitrate, and phosphate) and metal (iron and manganese) concentration analyses were performed in a PHARO 300 UV/VIS spectrophotometer, using Merck's colorimetric test kits. Precipitation data were obtained from Caxias do Sul meteorological station (OMM: 83,942, at ca. 20 km from both reservoirs), available from the National Institute of Meteorology website (INMET, 2014).

Using analysis of the monitoring data previously provided by SAMAE, only subsamples containing *Ceratium* cells were selected for the present study, resulting in 91 sample units. To estimate abundance, 1–8 ml aliquots were concentrated by sedimentation, depending on the *Ceratium* concentration in the samples. At least 100 cells were counted at low magnification ( $\times 100$ ) on the entire area of a Sedgewick-Rafter chamber, using an Olympus CH-2 light microscope.

**Fig. 1** Map of Faxinal and Maestra reservoirs and their main tributaries. Asterisks indicate sampling stations



Two morphotypes were considered based on the number of antapical horns: two or three. Species identification was determined according to Cavalcante et al. (2013).

In this study, we arbitrarily assumed bloom cells densities above 1,000 cells ml<sup>-1</sup> (Kawabata & Kagawa, 1988; Guerrero & Echenique, 1997; Mac Donagh et al., 2005; Hart & Wragg, 2009; Silverio et al., 2009), because densities above this threshold had a distinct ecological importance in the studied period.

Ten cells were measured per month from both reservoirs ( $n = 240$ ). The equation used to estimate the cell volume of *C. furcoides* is the same as that employed in European monitoring programs (e.g., INAG, 2011). Biomass was estimated from biovolume calculations, assuming a specific gravity of 1 mm<sup>3</sup> l<sup>-1</sup> = 1 mg l<sup>-1</sup> (Wetzel & Likens, 2000). Cell volumes were also used to evaluate cyclomorphosis.

One-way analysis of variance (ANOVA) was carried out to test seasonal differences of cell densities and volumes, with post hoc Tukey's test to compare means. Pearson correlation was used to find relationships among cell biomass, cell volume, and environmental variables. The aforementioned univariate analyses were performed using the software Statistica 7.1<sup>®</sup>. Principal component analysis (PCA) was performed to determine spatial and temporal patterns in the physical and chemical data sets, using correlation to produce a cross product matrix (data not log transformed). This analysis was performed on PC-ORD 6.08<sup>®</sup>.

## Results

### Physical and chemical variables

Precipitation data showed that on a seasonal basis, winter and spring constituted the rainy seasons in 2012 and 2013 in this region, with monthly average of 200 and 193 mm, respectively. The highest precipitation sampled was 68.3 mm on November 12, 2013, whereas the accumulated precipitations during the weeks before sampling were 214.8 mm on August 27, 2013 (winter), 197.3 mm on November 12, 2013 (spring), and 189.2 mm on January 2, 2013 (summer).

Both reservoirs were very distinct of each other in relation to the majority of the environmental variables (Table 1). The PCA ordination for 12 abiotic variables explained 55.21% of data variability in the first two

axes (Fig. 2); only dissolved oxygen was not plotted. Manganese ( $r = -0.87$ ), nitrite ( $r = -0.86$ ), and phosphate ( $r = -0.83$ ) were the principal variables in the composition of axis 1 (32.18%), while pH ( $r = 0.88$ ), temperature ( $r = 0.84$ ), and organic matter ( $r = 0.77$ ) were the most important variables for axis 2 (23.02%). The PCA's diagram presented a clear seasonal pattern in the ordination of the units, but secondarily we can see the units grouped by reservoir into each season, highlighting the limnological distinction between these reservoirs, especially regarding to nutrient availability.

### *Ceratium furcoides* occurrence and abundance

Cells of *C. furcoides* were registered for the first time in Maestra in September 2012 and remained throughout the studied period. After detected introduction, it occurred in low densities, with the first growth peak in late October, followed by recurrent blooms throughout the summer with a maximum recorded density of 2,680 cells ml<sup>-1</sup> (Figs. 3, 4). New blooms were observed in early fall and mid-November and December 2013.

In Faxinal reservoir, *C. furcoides* only was registered in phytoplankton counts in April 2013 (7 months after the colonization in Maestra), with low densities. The density rose sharply in early October and reached maximum density in mid-November (2,819 cells ml<sup>-1</sup>) (Figs. 3, 4). No cysts were observed in the samples from either reservoir during the study period.

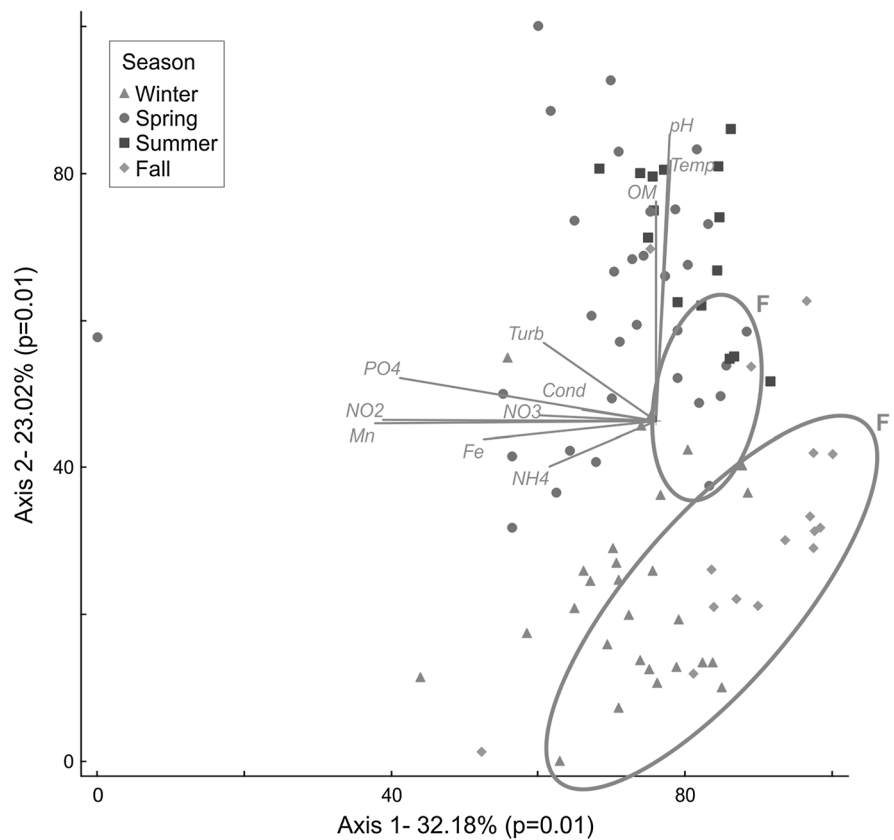
Neither density nor biomass was significantly different between reservoirs (ANOVA,  $P > 0.05$ ). On the other hand, density was significantly different between seasons (ANOVA,  $F = 18.05$ ,  $P < 0.01$ ). Tukey test presented differences (mean log density in cells ml<sup>-1</sup>) between spring (2.53)–summer (2.91) and fall (1.83)–winter (1.42).

Direct and inverse correlations among abiotic variables and biomass suggested some patterns (Table 2). Biomass peaks occurred in temperatures higher than 15°C; below 15°C, the biomass dropped. High organic matter values were also related to *C. furcoides* biomass. Cell maxima were observed when organic matter was higher than 8 mg l<sup>-1</sup>. The pH showed a similar pattern in promoting bloom: *C. furcoides* bloomed at alkaline pH (8.5–10 in Maestra, 8–9 in Faxinal) except on November 12, 2013 in Faxinal, when the biomass peak was recorded

**Table 1** Range, mean values, and standard deviation of physical and chemicals variables of Faxinal and Maestra reservoirs, during *Ceratium* occurrence in 2012 and 2013

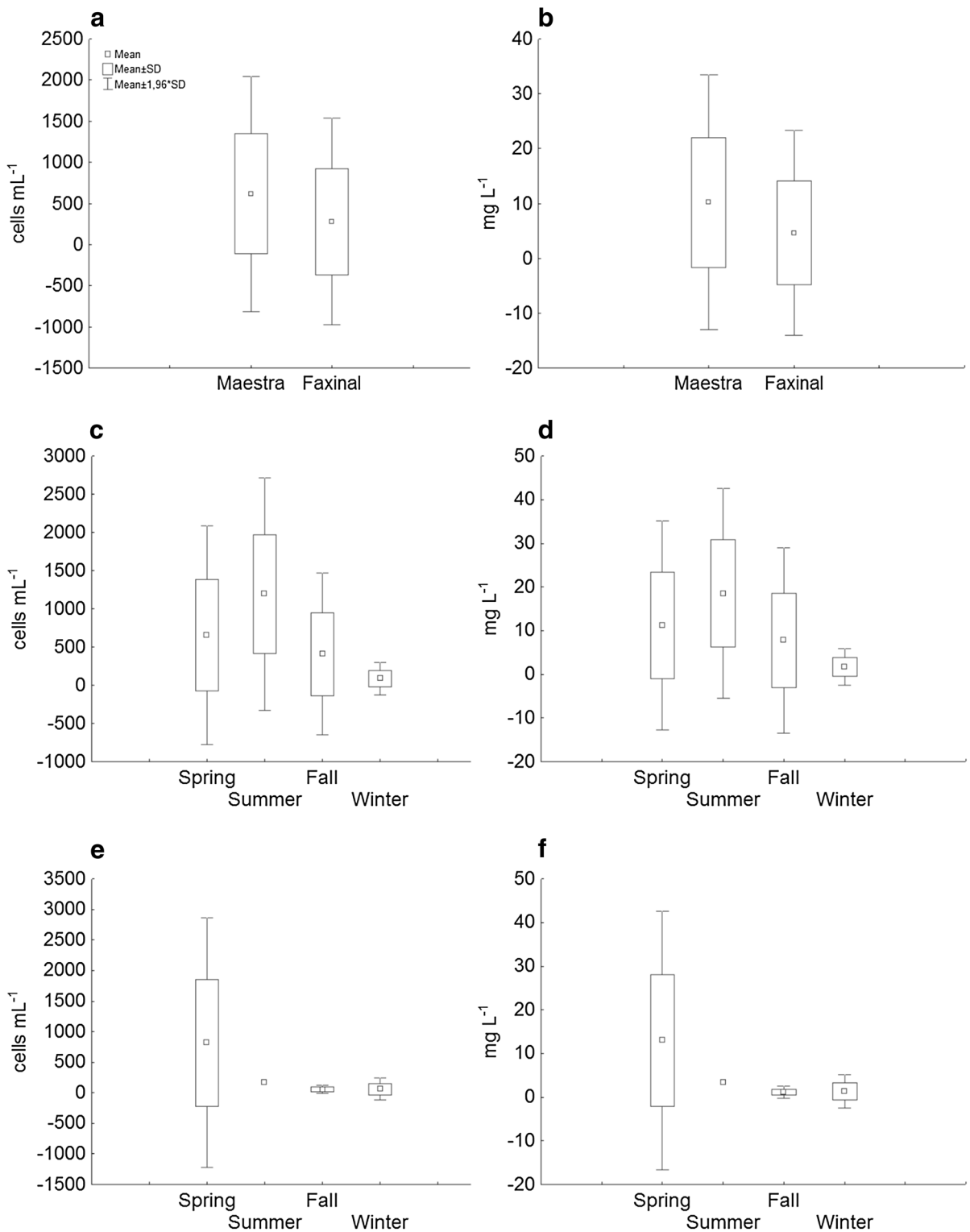
	Faxinal (n = 35)				Maestra (n = 56)			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Temperature (°C)	11.8	25.8	17.6	3.7	11.4	26.9	19.6	4.2
Turbidity (NTU)	3.4	41.2	15.2	8.0	6.0	96.7	23.4	15.3
pH	6.0	9.4	7.6	0.9	6.3	10.5	8.5	1.2
Conductivity ( $\mu\text{S cm}^{-1}$ )	31.2	50.2	39.1	5.2	54.3	79.6	64.2	6.2
Dissolved oxygen ( $\text{mg l}^{-1}$ )	3.60	11.34	7.74	1.85	1.70	11.05	7.97	2.12
Organic matter ( $\text{mg l}^{-1}$ )	2.20	15.90	6.37	3.21	2.00	19.80	9.02	5.49
$\text{NH}_4$ ( $\text{mg l}^{-1}$ )	0.01	0.29	0.09	0.07	<0.01	0.80	0.15	0.16
$\text{NO}_3$ ( $\text{mg l}^{-1}$ )	<0.2	0.35	0.05	0.09	<0.2	1.28	0.57	0.32
$\text{NO}_2$ ( $\text{mg l}^{-1}$ )	0.02	0.05	0.03	0.008	0.01	0.10	0.04	0.02
$\text{PO}_4$ ( $\text{mg l}^{-1}$ )	<0.01	0.09	0.02	0.02	<0.01	0.29	0.06	0.04
Fe ( $\text{mg l}^{-1}$ )	0.12	1.43	0.54	0.30	0.12	1.83	0.48	0.24
Mn ( $\text{mg l}^{-1}$ )	0.04	0.46	0.21	0.11	0.02	0.93	0.25	0.14

**Fig. 2** PCA ordination diagram for the abiotic variables and sampling units of Faxinal and Maestra reservoirs during *Ceratium* occurrence. See Table 2 for variables abbreviations. Ellipsoids correspond to Faxinal (F) grouped samples

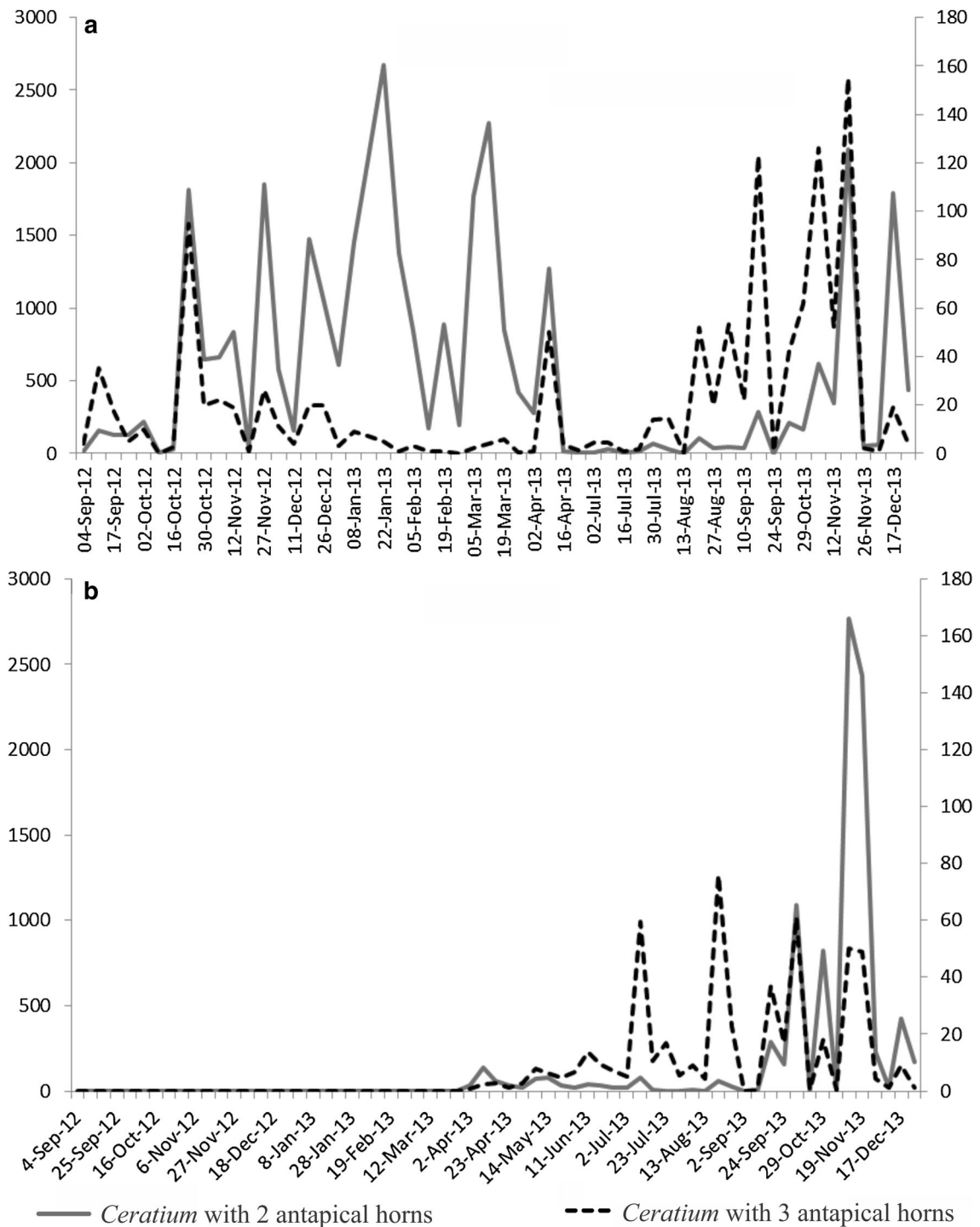


(40.39  $\text{mg l}^{-1}$ ), and when pH abruptly decreased to 6.1. *C. furcoides* was abundant in periods of low conductivity in both reservoirs; however, biomass peaks occurred at 54 to 64  $\mu\text{S cm}^{-1}$  in Maestra and

approximately half of these values (33–37  $\mu\text{S cm}^{-1}$ ) in Faxinal. Turbidity was related more to biomass in Faxinal, and *Ceratium* peaks occurred with the highest values observed of that variable (25–41 NTU).



**Fig. 3** Density and biomass variation of *Ceratium furcoides*. Total variation of density (a) and biomass (b) in both reservoirs; density and biomass by season at Maestra (c and d, respectively) and Faxinal (e and f)



**Fig. 4** Cell density (cells ml<sup>-1</sup>) of *Ceratium furcoides* with two (solid line) and three (dashed line) antapical horns in Maestra (a) and Faxinal (b) reservoirs during 2012–2013

Phosphate was an important factor for *Ceratium* growth in Faxinal, where blooms occurred when phosphate reached concentrations higher than  $0.05 \text{ mg l}^{-1}$ . Regarding nitrate concentrations, *C. furcoides* biomass showed a distinctive pattern between reservoirs. In Maestra, which had high nitrate availability, high biomass values were inversely related to nitrate concentrations; in Faxinal, which had lower nitrate availability, blooms were associated with higher nitrate concentrations. Precipitation on the sampling day and during the week prior had different interactions in the reservoirs, with no direct effects in Maestra but positive correlation in Faxinal. Heavy rainfalls occurred during the week of January 2, 2013 (189.2 mm) interrupting the continuous summer bloom in Maestra; in Faxinal, the highest cumulative precipitation value (197.3 mm) coincided with the *Ceratium* peak on November 12, 2013. Dissolved oxygen (DO) was not significantly correlated with *C. furcoides* abundance; however, both reservoirs had presented a trend to well-oxygenated water column throughout the studied period ( $\text{DO} > 5 \text{ mg l}^{-1}$ ).

### *Ceratium* morphometric variation

In both reservoirs, cells having two antapical horns were more common than those with three antapical horns during most of this study. The abundance of three-antapical-horned cells was higher in Maestra during the spring (maximum  $155 \text{ cell ml}^{-1}$  on November 2013) and in Faxinal, during the winter (Fig. 4). Biomass of this morphotype was significantly correlated with nitrate, nitrite, phosphate, and manganese (Table 2).

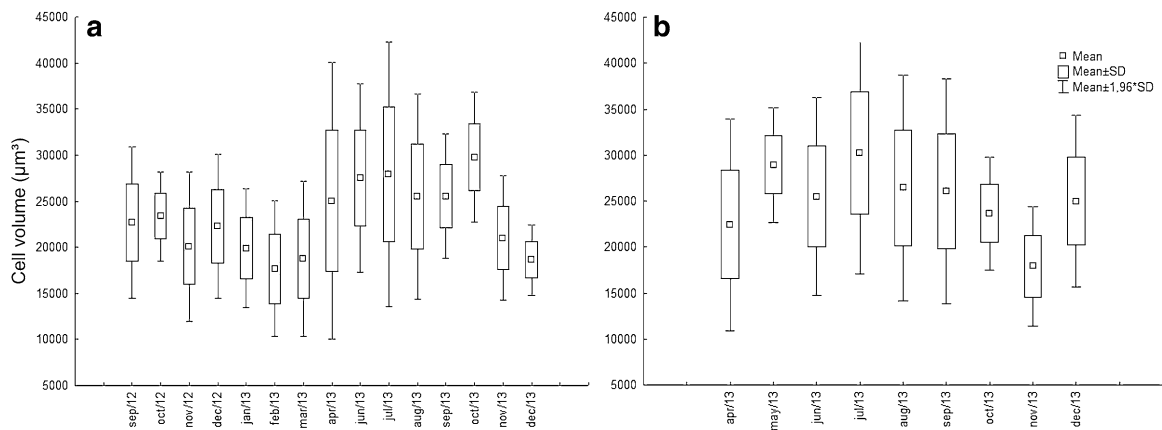
The mean cell volume showed seasonal variation during this study (Fig. 5; ANOVA,  $F = 8.309$ ,  $P < 0.01$ ). In warm seasons (spring–summer), the cells were smaller than in cold seasons (fall–winter). However, the abundance (Figs. 3, 4) had the opposite pattern, showing inverse correlation between cell volume and cell density ( $r = -0.70$ ,  $P < 0.05$ ). Regarding abiotic data, cell volume was negatively correlated with temperature ( $r = -0.70$ ), pH ( $r = -0.72$ ), organic matter ( $r = -0.66$ ), and turbidity ( $r = -0.47$ ).

**Table 2** Pearson correlation values ( $P < 0.05$ ) between *Ceratium furcoides* biomass and environmental variables (B2 biomass of two antapical horns cells, B3 biomass of three antapical horns cells, TB total biomass, Temp temperature,

Turb turbidity, Cond conductivity, OM organic matter, Pday precipitation on the sampling day; Pweek precipitation accumulated over a week)

	Temp	Turb	pH	Cond	OM	NO <sub>3</sub>	NO <sub>2</sub>	PO <sub>4</sub>	Fe	Mn	Pday	Pweek
Bloom periods ( $n = 15$ )												
B2			0.58		0.80	-0.60			-0.53			-0.52
B3							0.52					
TB			0.58		0.79	-0.57			-0.52			
Two reservoirs ( $n = 91$ )												
B2	0.51	0.34	0.50		0.79			0.24			0.22	
B3						0.26	0.44	0.40		0.26		
TB	0.49	0.34	0.49		0.79			0.25			0.23	
Maestra ( $n = 56$ )												
B2	0.56		0.56	-0.38	0.82	-0.34						
B3						0.30	0.48	0.43				
TB	0.54		0.55	-0.39	0.81	-0.32						
Faxinal ( $n = 35$ )												
B2		0.72		-0.38	0.68	0.65		0.65			0.51	0.34
B3										0.38		
TB		0.72		-0.37	0.68	0.64		0.65			0.50	0.34





**Fig. 5** Monthly variation of the cell volume of *Ceratium furcoides* in Maestra (a) and Faxinal (b) reservoirs

## Discussion

*C. furcoides* cells are 123–322 µm long (Popovský & Pfister, 1990) and, despite being a conspicuously large organism of the phytoplankton community, have never been found in Brazilian environments until 2003 (Cavalcante et al., 2013). From the southeastern region, where it was first detected, its distribution has expanded northwards and southwards. In state of Rio Grande do Sul (southern Brazil), *C. furcoides* has been recorded in many reservoirs and rivers since 2011. In July 2012, it was detected in Jacuí River, ca. 150 km distant from Maestra reservoir (Cavalcante et al., 2013); these environments probably have been colonized from the same invading population (2 months after registered in reservoir).

Faxinal and Maestra phytoplankton have been sampled since 2002, when a monitoring program was implemented (Frizzo et al., 2004) according to the standards of the Ministry of Health (BRASIL, 2004). In these reservoirs, there is a historical occurrence of cyanobacterial blooms of the genus *Dolichospermum* (Ralfs ex Bornet et Flahaut) Wacklin, Hoffman et Komárek and *Microcystis* Kützing ex Lemmermann (Frizzo et al., 2004; Yunes et al., 2005). Other studies were performed in those systems, for example, Becker et al. (2009a, b), revealing the important role of physical processes in the seasonal gradient in selecting for phytoplankton functional groups and Cardoso et al. (2010), which studied the dinoflagellate assemblages in reservoirs from Caxias do Sul City (including Faxinal and Maestra) in 2002–2006. None of these studies found *C. furcoides* in those environments. The

absence of *C. furcoides*, confirmed by extensive previous studies and monitoring program; its rapid expansion as soon as it was first reported; and the aggressive behavior of this dinoflagellate, quickly reaching high biomass in those systems, are strong evidence of the invasive nature of this microorganism.

High densities of *Ceratium* are usually recorded in the literature as ordinary events in annual phytoplankton fluctuations of many temperate waterbodies (Table 3). The major bloom-forming species is *C. hirundinella*. Only a few papers described the bloom dynamics of *C. furcoides* (Canter & Heaney, 1984; Lindström, 1992). However, the majority of these density peaks were under 1,000 cells ml<sup>-1</sup> (Padisák, 1985; Lindström, 1992; Pérez-Martínez & Sánchez-Castillo, 2002; Carty, 2003). In subtropical environments, *Ceratium* spp. tend toward higher population growth, as found for *C. hirundinella* in Argentina (Silverio et al., 2009) and South Africa (Hart & Wragg, 2009), and for *C. monoceras* Temponeras in the boundary between Macedonia and Greece (Temponeras et al., 2000a). In South America, populations of *C. furcoides* were observed at a maximum of 41 cells ml<sup>-1</sup> during the spring in Riogrande II reservoir (Bustamante-Gil et al., 2012), of 29 cells ml<sup>-1</sup> during the winter in Furnas reservoir (Silva et al., 2012), and of 15 cells ml<sup>-1</sup> during the fall in Yacyretá reservoir (Meichtry de Zaburlin et al., 2014). Matsumura-Tundisi et al. (2010, p. 828, Table 2) found a maximum density of 21,455 cells ml<sup>-1</sup> during the winter in Billings reservoir, but there is probably a typographical error since the same data (plotted in Fig. 1, p. 826 from that paper) do not exceed 25 cells

**Table 3** The densest blooms of *Ceratium* spp. recorded in the scientific literature

Environment	Bloom-forming species	Maximum density (cells ml <sup>-1</sup> )	Season	Reference
South America				
Faxinal and Maestra reservoirs, southern Brazil	<i>C. furcoides</i>	2,819	Spring–summer	Present study
Paso de las Piedras reservoir, east-central Argentina	<i>C. hirundinella</i>	2,000	Mid-summer	Guerrero & Echenique (1997)
Río Tercero reservoir, central Argentina	<i>C. hirundinella</i>	1,244	Late summer	Mac Donagh et al. (2005)
Sumampa and Las Pirquitas reservoirs, northwestern Argentina	<i>C. hirundinella</i>	5,634	Winter	Silverio et al. (2009)
North America				
Heart Lake, southeastern Canada	<i>C. hirundinella</i>	1,300	Summer	Nicholls et al. (1980)
Europe				
Lake Erken, southeastern Sweden	<i>C. hirundinella</i>	416	Late summer	Dotne-Lindgren & Ekbohm (1975)
Esthwaite Water, northern England	<i>C. hirundinella</i>	370	Late summer	Chapman et al. (1985)
Lake Sempach, central Switzerland	<i>C. hirundinella</i>	380	Summer	Pollinger et al. (1993)
Blelham Tarn, northern England	<i>C. furcoides</i>	ca. 485	summer	Canter & Heaney (1984)
Lake Plußsee, northern Germany	<i>C. furcoides</i>	670	Summer	Hickel (1988)
Laje Doirani, Macedonia, Greece	<i>C. monoceras</i>	3,339	Spring	Temponeras et al. (2000a, b)
Asia				
Ishitegawa reservoir, Southern Japan	<i>C. hirundinella</i>	1,300	Summer	Kawabata & Kagawa (1988)
Small pond in Tsukuba, east-central Japan	<i>C. hirundinella</i>	925.5	Late spring	Xie et al. (1998)
Africa				
Albert Falls Dam, eastern South Africa	<i>C. hirundinella</i>	over 5,000	Summer	Hart & Wragg (2009)
Oceania				
Chaffey Dam, eastern Australia	<i>C. hirundinella</i>	ca. 520	Summer	Baldwin et al. (2003)

ml<sup>-1</sup>. The densities that we observed, with peaks of 2,680 and 2,819 cells ml<sup>-1</sup> during spring–summer in Maestra and Faxinal, respectively, represent the densest bloom ever reported for *C. furcoides* (Table 3).

*C. furcoides* was a perennial form in the phytoplankton of Faxinal and Maestra during this study, with bloom formation at temperatures between 15 and 27°C just as *C. hirundinella* was in Río Tercero reservoir (Mac Donagh et al., 2005). In temperate systems, *Ceratium* spp. occurred during warm and stratified waters in a few summer months, completely disappearing from water column in cooler seasons (Heaney & Talling, 1980; Pollinger, 1988). In the subtropical lake Kinneret, *C. hirundinella* reached maximum density during the spring but declined in summer, at temperatures higher than 25°C (Pollinger

& Hickel, 1991). Despite the seasonality difference, the optimum range of temperature for *Ceratium* growth is similar, between 12 and 23°C (Heaney et al., 1988; Popovský & Pfister, 1990). This seems to be a crucial factor for the distribution of these dinoflagellates throughout the year in subtropical reservoirs, such as Faxinal and Maestra. In these environments, the temperatures were moderate, seldom reaching the extreme temperatures assigned to *Ceratium* growth. On the other hand, in a Spanish reservoir, *C. hirundinella* occurred throughout the year with highest densities during mixing periods of fall–winter at temperatures of 7–14°C (Pérez-Martínez & Sánchez-Castillo, 2002), demonstrating a high tolerance of this species to temperature variation.

In this study, the occurrence and growth of *C. furcoides* in the reservoirs of Caxias do Sul were

controlled, primarily, by a combination of optimal conditions of temperature, organic matter, pH, and dissolved oxygen. Secondly, although this species tolerates a wide range of conductivity and nutrient content, *Ceratium* abundance was associated with nutrient availability, especially phosphate and nitrate. Similar results were found by Grigorszky et al. (2003), for dinoflagellates in Hungarian water bodies, and Cardoso et al. (2010), in the same subtropical reservoirs of Caxias do Sul. The high biomass of *C. furcoides* was associated with high values of organic matter. Despite the potential autocorrelation between these variables, we did not reject the contribution of other planktonic (phyto- and zoo-) organisms to organic matter, favoring a nutritional alternative by mixotrophy (Olrik, 1994). Mixotrophy has never been demonstrated in *C. furcoides* and is a controversial topic concerning this genus (Gaines & Elbrächter, 1987; Hansen & Calado, 1999). However, it is a feature sometimes recorded for *C. hirundinella* (Dodge & Crawford, 1970) and well documented in marine relative species (Bockstahler & Coats, 1993; Jacobson & Anderson 1996, Jacobson 1999), and probably can occur in *C. furcoides*. Regarding pH, *Ceratium* peaks were registered in alkaline conditions, as in other recorded maxima (Lindström, 1992; Guerrero & Echenique, 1997; Temponeras et al., 2000b; Carty, 2003; Mac Donagh et al., 2005; Silverio et al., 2009; Matsumura-Tundisi et al., 2010). Only in an atypical event in Faxinal on November 12, 2013 did the highest cell abundance of *C. furcoides* occur at low pH, coinciding with highest accumulated precipitation and high values of turbidity and nutrients, especially nitrogen compounds. The heavy rainfall could have been responsible for pH reduction, as well as have provided input of nutrients from runoff or sediment to the water column. We postulate that in a mesotrophic system, nutrient availability can be an important factor for *Ceratium* growth, even at slightly acidic pH. Similar patterns were observed with *C. hirundinella* in Lake Biwa, suggesting that *Ceratium* abundance was controlled by nitrogen availability (Nakano et al., 1999). Well-oxygenated waters, such as those of Faxinal and Maestra reservoirs, are also an important factor for *Ceratium* development (Pollinger, 1988; Mac Donagh et al., 2005). Previous studies have showed that *C. furcoides* cells can swim toward high concentrations of O<sub>2</sub> in water column, filling their physiological requirements for oxygen during

respiration and accelerating metabolic activity and growth (Clegg et al., 2004). In mesotrophic systems showing low phosphorus content, as in Faxinal reservoir, *C. furcoides* abundance was associated with phosphorus peaks (Wu & Chou, 1998; Bustamante-Gil et al., 2012; Silva et al., 2012). Under eutrophic conditions, as in Maestra reservoir, phosphorus content was not a correlated factor for *Ceratium* growth (van Ginkel et al., 2001). However, Mac Donagh et al. (2005) showed high densities of *C. hirundinella* in a very low phosphorus context. It is stated that *Ceratium* spp. can obtain phosphorus from multiple sources when conditions of P-limitation exist in the epilimnion, by vertical migration (James et al., 1992; Olrik, 1994). Sexual reproduction (gamete fusion) of *C. furcoides* in Lake Plußsee was linked to low nitrogen and phosphorus levels (Hickel, 1988). The contrasting behavior of *Ceratium* species in divergent lake types (with different climatic, morphometric, geological, hydrological, and trophic features) explains the existence of ecotypes of these species adapted to diverse environmental conditions and exhibiting high intra- and inter-population morphological variability (Salmaso, 2003).

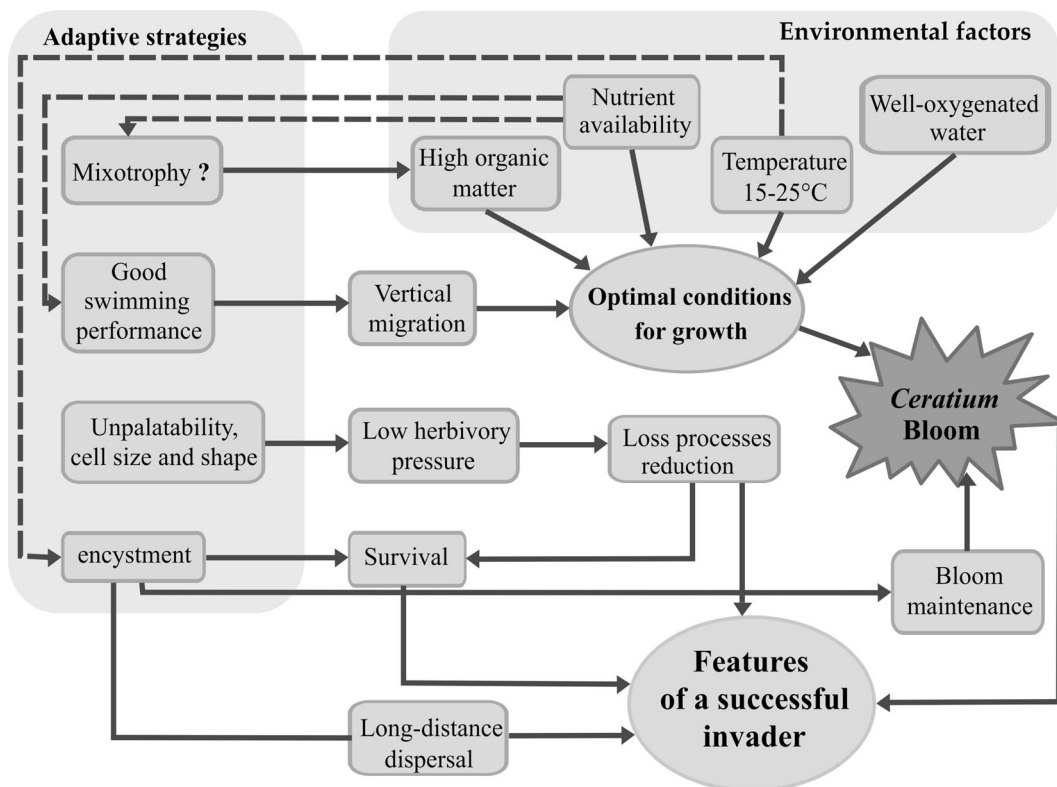
Incidence of three-antapical-horned cells was higher in Faxinal during the winter and in Maestra during the following spring, correlating with the highest mean cell volume. Throughout the spring–summer blooms, *C. furcoides* with two antapical horns was the dominant morphotype, in accordance with previous studies (Dotne-Lindgren & Ekbohm, 1975; Hickel, 1988; Lindström, 1992). Lindström (1992) pointed out that large cells, generally having three antapical horns, probably consist of forms adapted to low temperatures. However, it cannot be concluded that temperature directly affects the density of cells with different numbers of antapical horns (Dotne-Lindgren & Ekbohm, 1975). We found significant correlation between three-antapical-horned cell abundance and nutrient concentrations, in accordance with previous studies (Kimmel & Holt, 1988). Hamlaoui et al. (1998) have found that the proportion of three-horned cells tended to increase at high levels of nutrient content, but this effect was not statistically significant. No study has ever shown an association between three-antapical-horned cells and manganese like the positive correlation observed in Faxinal. However, experimental studies are necessary to verify the real influence of this micronutrient on the growth

of the third antapical horn. Recent studies have also demonstrated that biotic pressure, especially protection against physical contact with the filtering apparatus of grazers, plays a strong role on morphological variability in *Ceratium* (Bertolo et al., 2010).

In the Faxinal and Maestra reservoirs, warm seasons promoted population increases, while in cooler seasons cells increased in volume. Similar seasonal cell-size variation was observed for different populations of *Ceratium* species (Dottne-Lindgren & Ekbohm, 1975; Lindström, 1992; Gligora et al., 2003). Temperature is a key factor in the cell-size dynamics for *Ceratium* spp. (Huber-Pestalozzi, 1950). *C. furcoides* biomass peaks (smaller cells) were also inversely related to iron content. It is known that iron can bind with phosphorus and make it unavailable for phytoplankton consumption. Other studies have demonstrated increasing cell volume in dinoflagellates at P-depletion, probably due to cell-division inhibition

resulting in large cells (Flaim et al., 2010). In the present study, *Ceratium* abundance and cell volume had similar temporal distribution in both reservoirs. In contrast, the reservoirs were typically different, especially regarding to nutrient availability. These findings can be explained by the high tolerance to various environmental conditions ascribed to this dinoflagellate (Pollinger, 1988).

The major *Ceratium* features that promote its wide environmental tolerance were summarized in Fig. 6. *Ceratium* species are considered excellent competitors among freshwater phytoplankton due to intrinsic features, such as good swimming performance, enabling the cells to perform vertical migration in order to find optimal conditions of light and nutrients for their growth (Heaney & Talling, 1980); low herbivory pressure due to their size and shape (Xie et al., 1998); presumable mixotrophy, as a nutritional alternative for growing even under inorganic nutrient depletion (Olik,



**Fig. 6** A synthesis diagram showing relationships among environmental conditions, adaptive strategies and invasion success of *Ceratium furcoides*. Solid arrows represent direct

relation while dashed arrows indicate inverse relation. A question mark indicates a biological process that needs confirmation for this species

1998; Salmaso, 2003); and resting cyst production, which ensures the survival, bloom maintenance, and dispersal capacity of these species (Pollinger, 1988). We assume that these adaptive strategies are critical in understanding the invasive success demonstrated by *Ceratium* in Brazilian freshwaters (Fig. 6). Future studies should demonstrate the effects of each of these biological processes in the population dynamics of *C. furcoides* in Brazilian reservoirs.

Previous studies on the dinoflagellate communities of reservoirs from Caxias do Sul suggested that the lack of dinoflagellate blooms in those reservoirs was related to nutrient limitation and consequent competition among phytoplankton (Cardoso et al., 2010). Now, it is possible to conclude that the initial lack of blooms was related to the absence of highly tolerant and excellent competitor populations, such *Ceratium* species. *C. furcoides* performed a rapid colonization: it bloomed in Maestra just over a month after the first appearance and colonized Faxinal (ca. 10 km away) only 7 months later. Dense blooms performed by *C. furcoides* suggested that this species had found ideal conditions for growing in both subtropical reservoirs, with favorable limnological and climatic characteristics, probable low competition with native species, and absence of natural predators and parasites.

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