







Invasion and establishment of *Ceratium furcoides* (Dinophyceae) in an urban lake in Porto Alegre, RS, Brazil

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ABSTRACT

Ceratium furcoides has received attention due its invasive behavior in South America and consequent alterations in local phytoplankton communities. Pedalinhos Lake had been dominated by chlorophytes until 2015, when the first occurrence of this dinoflagellate was detected. In order to investigate the colonization process of this species, we monitored the meteorological variables and phytoplankton abundance of this urban lake on a weekly basis from September 2015 to September 2018. At the beginning of the invasion process (Year 1), a peak density of 10,170 ind.mL⁻¹ was recorded, with a significant decrease to 23 ind.mL⁻¹, indicating an initial, unstable process of adaptation, with notable oscillation and reduction of cyanobacterial blooms. At this time, abundance of *C. furcoides* revealed inverse correlations with cyanobacteria, temperature, and insolation. In Year 2 there were a stabilization of the density of *C. furcoides* accompanied by increased cell size. Year 3 (starting in September 2017) was again marked by oscillations in the density of this dinoflagellate. This study contributes to improved understanding of the adaptation process of this dinoflagellate in an invaded environment and its effects on the local phytoplankton community.

Keywords: dinoflagellate, invasive species, shallow lake, subtropical, Southern Brazil

Introduction

The ecosystemic importance of phytoplankton is incontrovertible, particularly because of its key role as primary producers in the aquatic food web. There are several factors that can change the balance of a phytoplankton community, such as bioinvasion, which tends to reshape the relationships between local species (Catford *et al.* 2012). Impacts range from niche alterations, which imply changes in predation and reproduction, local extinction of native species, and physical and chemical changes in the environment (Mooney & Cleland 2001).

The genus *Ceratium* is typically found in temperate and subtropical lakes in the Northern Hemisphere (Carty 2014; Moestrup & Calado 2018). In South America, where these algae had not previously occurred, reports began to appear in the 1990s and increased through the 2000s (Cavalcante *et al.* 2013). The first occurrence of *Ceratium furcoides* in Brazil dates from 2007 in the state of Minas Gerais (Santos-Wisniewski *et al.* 2007), while in the state of Rio Grande do Sul it has only been observed starting in 2011 (Cavalcante *et al.* 2013).

Since then, there has been a series of papers publishing new occurrences of this algae in many Brazilian freshwater systems (Oliveira *et al.* 2011; Cassol *et al.* 2014; Jati *et*

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al. 2014; Moreira *et al.* 2015; Campanelli *et al.* 2017) and a number of studies trying to understand the invasive behavior and the environmental factors that might favor the persistence and high abundance of *C. furcoides* in different tropical and subtropical systems. Matsumura-Tundisi *et al.* (2010) showed that a bloom of *C. furcoides* in a tropical hypereutrophic reservoir (Billings reservoir, São Paulo - Brazil) was related to mild temperatures (19–21 °C) and water column turbulence. *Ceratium* bloom was accompanied by elevated densities of cyanobacteria. Silva *et al.* (2012) stated that high abundance of *C. furcoides* in a tropical reservoir was linked to higher temperatures and high nutrient and organic matter content originating from untreated domestic sewage. Nishimura *et al.* (2015) associated the initial phase of *C. furcoides* colonization in two tropical reservoirs (Billings and Guaramiranga reservoirs, São Paulo- Brazil) with excessive organic matter and historical cyanobacteria blooms. At that time, a high biovolume of *C. furcoides* was found at all points sampled, except at oxygen depleted sites. Cavalcante *et al.* (2016) have demonstrated seasonal patterns in abundance, cell volume, and morphology of this dinoflagellate in two subtropical reservoirs from southern Brazil. Finally, Crossetti *et al.* (2019) showed that a *C. furcoides* invasion disrupted cyanobacterial dominance in some periods in a tropical shallow eutrophic reservoir, modifying the temporal pattern of this community. There are few studies dealing with the interactions between phytoplankton species during a *C. furcoides* invasion. Because it is a tolerant, highly variable species, which ensures its invasive success (Cavalcante *et al.* 2016), a better understanding of the relationships between *C. furcoides* and the native phytoplankton community in different freshwater environments is necessary.

This study monitored the arrival and establishment processes of *Ceratium furcoides* in an urban lake of Porto Alegre (state of Rio Grande do Sul, Southern Brazil) for three years to investigate relationships between this species, phytoplankton assemblages, and meteorological variables (temperature, insolation, precipitation, wind velocity, humidity) to understand the colonization success and its impact on the local phytoplankton community. As the climate in southern Brazil is quite different from the climate where this species is originally found, we focused on how the seasonal climatic variation in a subtropical and shallow environment can affect the occurrence of this invasive species.

Materials and methods

Pedalinhas Lake is a shallow artificial urban lake (mean depth 0.98 m and maximum depth 1.5 m) built in the 1930s and located in Farroupilha Park (30°02'S 51°13'W) in the city Porto Alegre, state of Rio Grande do Sul. The park has an area of 37.51 ha and is managed by Municipal Secretary for the Environment. It is widely frequented by

the population and suffers various human interventions, such as improper discharge of waste and trash. The region has a humid subtropical climate, Cfa (Kottek *et al.* 2006), an annual thermal amplitude of more than 30 °C, and the rainfall is evenly distributed throughout the year, with maximum precipitation in winter (INMET unpubl. res.).

Historically, the phytoplankton community in Pedalinhas Lake has been semiannually studied by biology researches from the Federal University of Rio Grande do Sul (UFRGS), and they reported chlorophytes as the dominant group for many years. In May 2015 *Ceratium furcoides* (Levander) Langhans was observed for the first time in the lake, which motivated this research.

Daily meteorological data (precipitation, air temperature, solar radiation, relative humidity, and wind velocity) from September 2015 to September 2018 were obtained from Porto Alegre Meteorological Station (maintained by INMET, the National Meteorological Institute). In the same period, weekly samples of subsurface water were taken from the lake in the morning (10 am), chosen randomly (into the four quadrants North, East, South, West in the lake) in each month (four weeks). Samples were fixed in 4 % formalin, quantified under an inverted microscope using 1 mL Sedgwick-Rafter chambers (400x magnification). Individuals of *C. furcoides* were counted as well as chlorophytes, euglenophytes, and cyanobacteria — the most representative algal groups in that environment. Other groups represented less than 5 % of total phytoplankton and were not considered here. Twenty individuals of *C. furcoides* were measured per sample to estimate cell volume, which was calculated based on the cingulum width applied to the linear regression equation proposed by Cavalcante *et al.* (2018). Descriptive analyses were performed with the data to observe their temporal patterns (seasonal and interannual). Correlation analyses (r-Pearson, $p < 0.05$) were calculated from biotic and meteorological data on seasonal and annual scales to investigate the tendencies among them that could be influencing the development of the invasive species. Both analyses were performed in the software Statistica® version 7.1.

Non-metric multidimensional scaling (NMDS) ordination was used to evaluate the temporal similarities between the meteorological variables for the samples ($n = 151$) based on the Sorensen (Bray–Curtis) distance matrix. The number of dimensions (3) was chosen to minimize the stress, *i.e.*, to maximize the rank correlation between the calculated similarity distances and the plotted distances. A Principal Component Analysis (PCA) of phytoplankton densities was processed with the transformed data matrix [$\log(x + 1)$] using analysis of variance and covariance to access the main temporal tendencies of those communities for the samples ($n = 151$) regarding their variability over the three years studied. A Detrended Correspondence Analysis (DCA) was performed to verify the length of the gradients generated from the biotic matrix (untransformed data). The Canonical Correspondence Analysis (CCA) was used to investigate the



environmental variables that drove the temporal patterns of the phytoplankton community in the lake. These multivariate analyses were performed using the software PC-ORD version 6.08 for Windows (McCune & Mefford 2011).

Results

Variation of temperature (minimum, maximum, and mean, °C), insolation (h), daily and accumulated precipitation (mm), wind velocity (m.s^{-1}) and relative humidity (%) were statistically investigated in seasonal

approach (Fig. 1). In general, the meteorological variables showed strong seasonality, which is expected for that subtropical region. Precipitation, when considering only sampling days, showed maxima in fall (90.6 mm) and spring (49.9 mm) of 2017 (Fig. 1E). However, when the precipitation was calculated based on the seven days before sampling (accumulated precipitation), spring of 2015 and 2017 showed mean values above 40 mm (Fig. 1F) and constituted the rainiest seasons in this monitoring period. Additionally, the highest wind velocity amplitudes were recorded in the spring, with a maximum in 2016 (4.46 m.s^{-1}) and a minimum (0.16 m.s^{-1}) in 2017 (Fig. 1G).

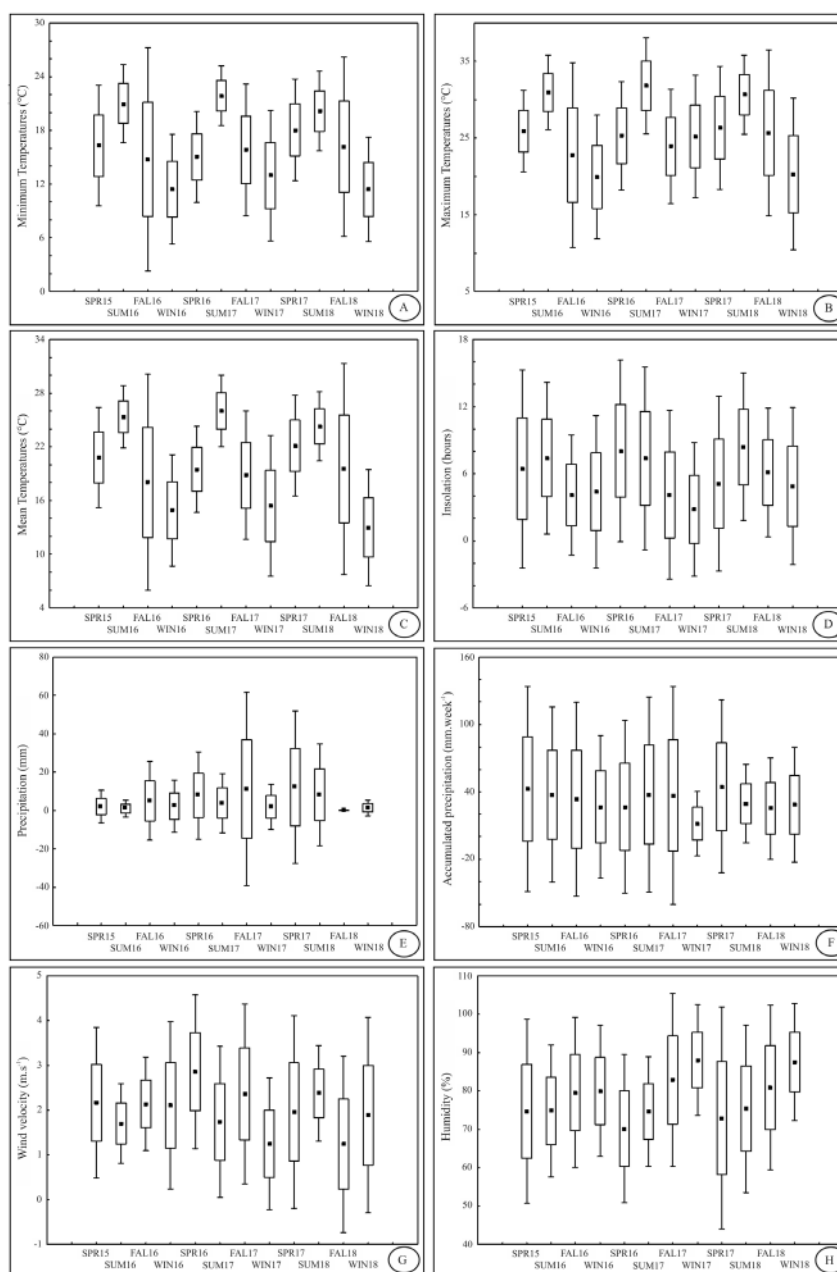


Figure 1. Meteorological variables shown on a seasonal scale (SPR = Spring, SUM = Summer, FAL = Fall, WIN = Winter, 15-18 – years from 2015 until 2018): **A.** Minimum temperature; **B.** Maximum temperature; **C.** Mean temperature; **D.** Insolation; **E.** Precipitation; **F.** Accumulated precipitation; **G.** Wind Velocity; **H.** Humidity. (Square = mean; Bar = mean \pm SD; Line = mean \pm 1.96*SD; SD = standard deviation).

The ordination axes in the non-metric multidimensional scaling (NMDS) (final solution with three dimensions, stress for the all three years analyzed gave a mean of 9.9 and a maximum of 10.4), indicated that the meteorological variables with a seasonal pattern were determinant in ordering the samples, where the temperature, more related to spring and summer, opposed humidity, more related to winter and fall (Fig. 2).

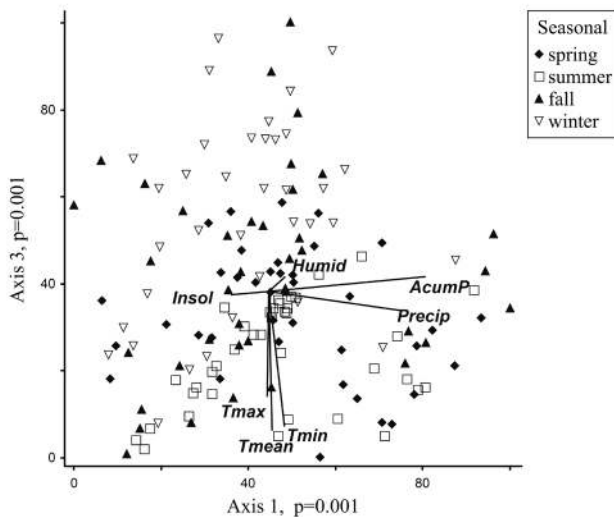


Figure 2. Non-metric Multidimensional Scaling (NMDS) ordination diagram for the meteorological variables and samples ($n=151$) on a seasonal scale. See Table 2 for variable abbreviations (AcumP = Accumulated precipitation for the week).

Ceratium furcoides was observed in Pedalinhos Lake throughout the studied period except on July 27th, 2018 (Fig. 3). In September 2015 oscillations in abundances of the exotic species were observed, with maximum density recorded in November 2015 ($10,170 \text{ ind.mL}^{-1}$; Fig. 3A). Between March (late summer) and September (early spring) of 2016, densities remained high. In August 2016, the second highest peak of *C. furcoides* density was recorded ($7,853 \text{ ind.mL}^{-1}$). From September 2016 to October 2017, *C. furcoides* abundance remained low and stable, but from November 2017 it oscillated again with small peaks in November 2017 ($1,912 \text{ ind.mL}^{-1}$), January 2018 ($2,942 \text{ ind.mL}^{-1}$), and May to July 2018 ($1,500\text{--}1,900 \text{ ind.mL}^{-1}$) (Fig. 3).

The population of *C. furcoides* showed three clearly distinct phases during these first years of colonization in Pedalinhos Lake (Fig. 4). In terms of biovolume, *C. furcoides* showed patterns similar to those recorded for cell density, with a stable period from winter 2016 to winter 2017, then decreasing in size in fall and winter of 2018 (Fig. 4B).

The phytoplankton community also varied as a result of *Ceratium* colonization (Fig. 5). Year 1 (spring 2015–winter 2016) was marked by instability of the phytoplankton community and exhibited the greatest density variation of the studied period (Figs. 4, 5A).

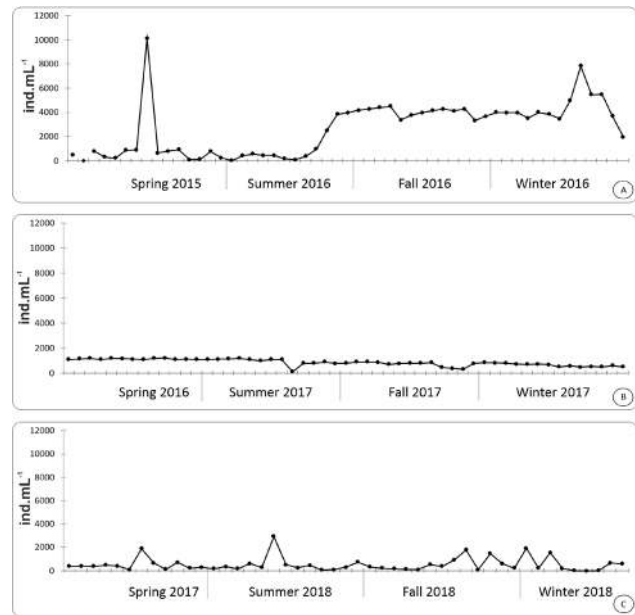


Figure 3. *Ceratium furcoides* density on each sampling date: A. year one; B. year two; C. year three.

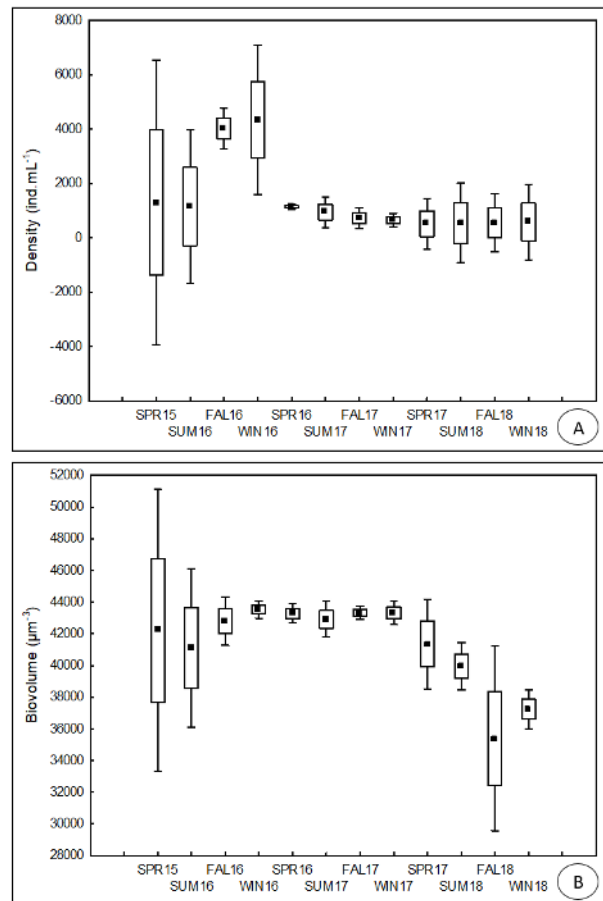


Figure 4. Density and biovolume of *C. furcoides* on a seasonal scale. See Figure 1 for seasonal abbreviations. (Square = mean; Bar = mean \pm SD; Line = mean \pm 1.96*SD; SD = standard deviation).

Year 2 (spring 2016–winter 2017) indicated the stability of the exotic species in the environment with phytoplankton structure (richness, density and diversity) seasonally constant (Fig. 5). Year 3 (spring 2017–winter 2018) was again characterized by oscillations in both *Ceratium* density and phytoplankton structure (Fig. 5), however with lower variation than Year 1 (Fig. 4A). The phytoplankton community was represented mainly by the species of *Microcystis* Lemmermann (only representatives of Cyanophyceae), *Phacus* Dujardin (Euglenophyceae), and species into 19 genera of chlorophytes, mainly desmids.

Density of *C. furcoides* was positively correlated with chlorophyte abundance in the majority of the studied period and with euglenophytes during summer 2016 and spring 2017 (Tab. 1). Inverse correlation was found between abundances of *C. furcoides* and cyanobacteria during 2016. Throughout

Year 2, all phytoplankton groups correlated with each other as a result of community stability in this period. The Principal Component Analysis (PCA) ordered the phytoplankton community on axis 1 (87.6%, $p < 0.001$) in an annual gradient, separating Cyanophyceae in the opposite direction to *Ceratium* and other phytoplankton groups (Fig. 6).

In Year 1, temperature and insolation were inversely correlated with *C. furcoides* density, although it was significant only in the spring samples ($p < 0.05$, Tab. 2). In contrast, positive correlations between these variables and cyanobacterial density were found for the same period. In Year 2, insolation and wind velocity showed positive correlation with *C. furcoides*. The other phytoplankton groups showed different environmental preferences by having significant correlations with distinct climatic variables. In Year 3, no significant correlation was established between

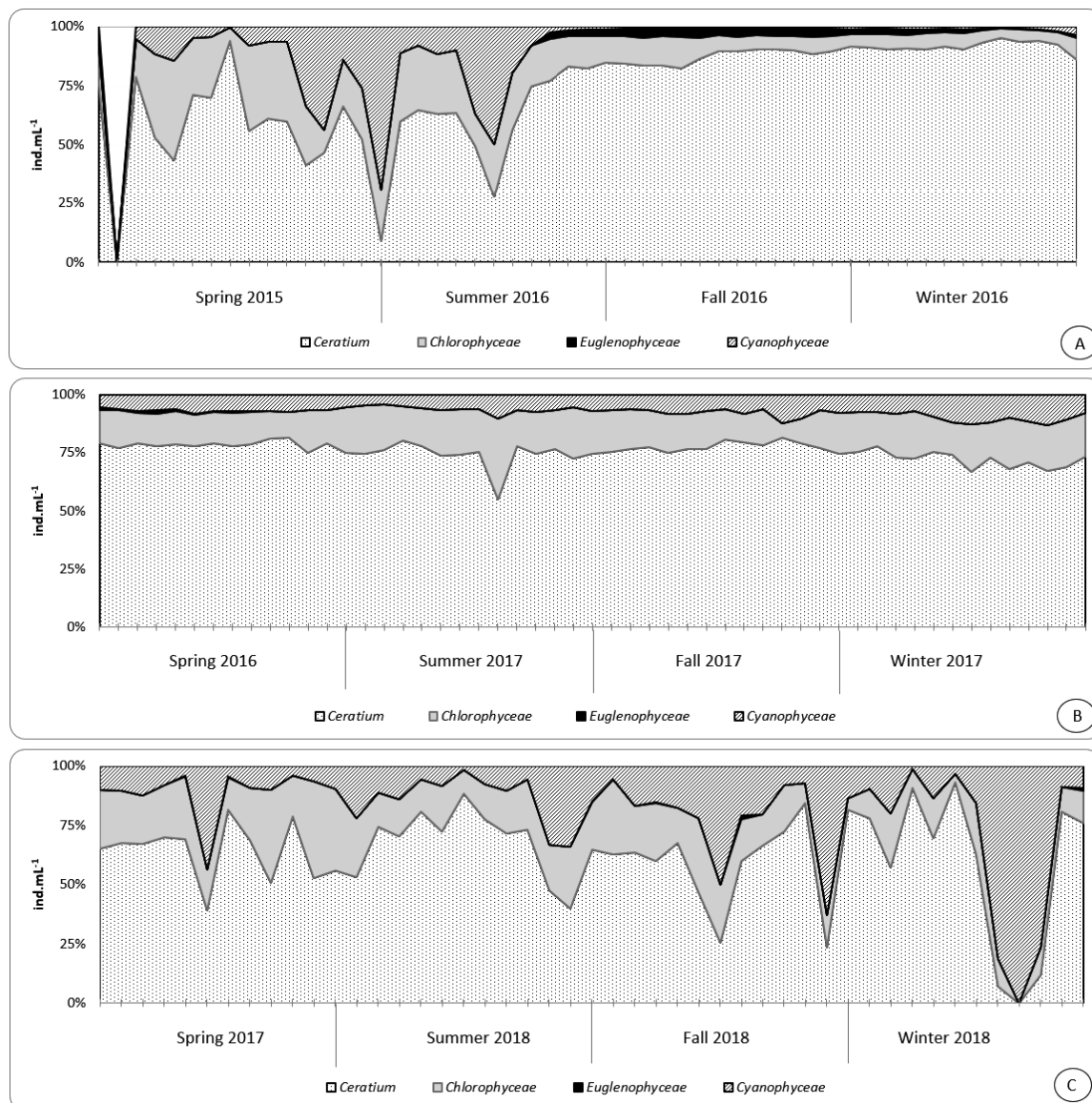


Figure 5. Densities of phytoplankton on each sampling date: **A.** year one; **B.** year two; **C.** year three. Dotted area = *C. furcoides*; Grey area = Chlorophytes; Black area = Euglenophyceae; Striped area = Cyanophyceae.

C. furcoides density and meteorological variables, except a negative correlation with insolation during summer.

Canonic Correspondence Analysis (CCA) presented a low percentage of variance explanation for axes 1 and 2 (11.2%, $p < 0.014$) but a clear seasonal separation of samples (Fig. 7). The spring-summer units were ordered by the mean temperature ($r = -0.67$) and wind velocity ($r = 0.57$), which were mostly related to *Ceratium* and chlorophyte densities. Inversely, insolation ($r = -0.42$) and air humidity ($r = -0.36$) ordered the fall-winter samples, being more related to cyanobacteria abundance.

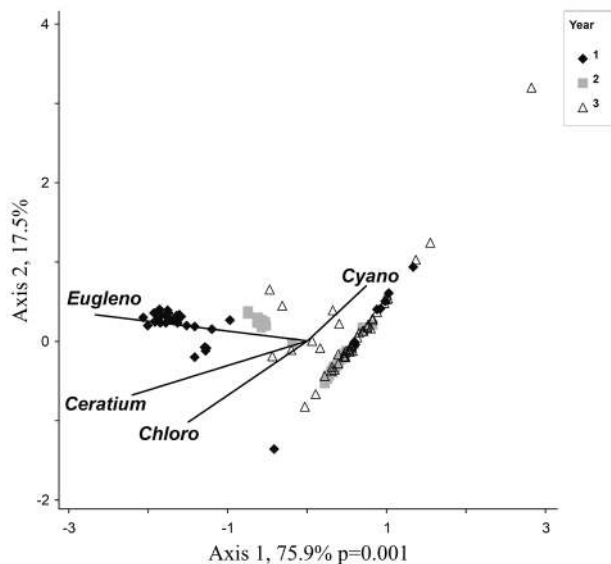


Figure 6. PCA (Principal Component Analysis) ordination diagram for the phytoplankton on an annual scale. See Table 2 for phytoplanktonic group abbreviations.

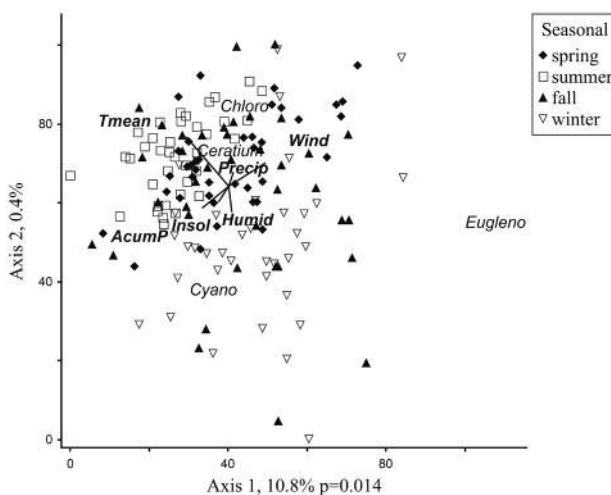


Figure 7. CCA (Canonical Correspondence Analysis) ordination diagram for the phytoplankton on a seasonal scale. See Table 2 for variable and phytoplanktonic group abbreviations.

Discussion

This study aimed to elucidate the population dynamics of *Ceratium furcoides* in the early stages of an invasion in an urban lake and to verify the changes in the local phytoplankton community during this event. The colonization process by *C. furcoides* in different water bodies from South America is still unclear, although there is an increasing number of publications on this subject. Factors such as climate change (Oliveira *et al.* 2011), hydrological regime (Matsumura-Tundisi *et al.* 2010; Bustamante-Gil *et al.* 2012; Meichtry-de-Zaburlin *et al.* 2016; Crossetti *et al.* 2019), nutrient availability (Almanza *et al.* 2016; Campanelli *et al.* 2017), untreated sewage discharge (Silva *et al.* 2012), and passive transport of cysts (Moreira *et al.* 2015) have been explored as important for establishing this algae in different aquatic systems. Meichtry-de-Zaburlin *et al.* (2016) have demonstrated the potential distribution of *C. furcoides* in South America as mainly concentrated in the tropical and subtropical regions of southern-southeastern Brazil, southeastern Paraguay, and northeastern Argentina. In this model, the main factors that determine the potential distribution of *C. furcoides* are water thermal stability and an annual mean temperature between 18 and 22 °C (Meichtry-de-Zaburlin *et al.* 2016). In addition, Cavalcante *et al.* (2016) compared data on *Ceratium* spp. blooms recorded across the globe and showed that subtropical systems tend to have better conditions for the development of massive *Ceratium* blooms. The aquatic systems of southern Brazil are, therefore, vulnerable to the establishment of *C. furcoides* and studies in this region are fundamental for understanding this bioinvasion phenomenon.

Ceratium furcoides persisted in Pedalinhos Lake since its initial detection, as in many studies carried out in Brazil up to that point (Silva *et al.* 2012; Cavalcante *et al.* 2016; Crossetti *et al.* 2019). The high ecophysiological adaptability of this dinoflagellate allows its survival in a wide range of environmental conditions, which contributes strongly to its invasive success (Cavalcante *et al.* 2016). It was absent only in one sample (July 27th, 2018) over three consecutive years. At that time, the temperature had dropped sharply, with a high of only 15 °C on the sampling day, associated with cold fronts that brought heavy rains. Turbulence caused by high precipitation is a disturbance factor that usually reduces flagellate abundance in aquatic systems (Pollinger & Zemel 1981). Under similar conditions, high precipitation also caused the fall in density of *C. furcoides* in a eutrophic reservoir of southern Brazil (Cavalcante *et al.* 2016) but it can persist at depth, by vertical migration, or as a cyst in sediment (Lindström 1992).

Many authors have demonstrated relevant relationships between *C. furcoides* abundance and climatic variables, since *C. furcoides* colonization shows strong seasonal dynamics (Hickel 1988; Pollinger 1988; Lindström 1992; Cavalcante *et al.* 2016). In this study, inverse correlations were found

Table 1. Correlations between the phytoplanktonic groups (Ce = *Ceratium furcoides*, Ch = chlorophytes, Eu = Euglenophyceae, Cy = Cyanophyceae) shown on seasonal and annual scales (ND = no detected, values in bold are significant, $p < 0.05$).

	n=51	Ce	Ch	Eu	Cy		n=53	Ce	Ch	Eu	Cy		n=47	Ce	Ch	Eu	Cy
Spring 2015	Ce	1.00				Spring 2016	Ce	1.00				Spring 2017	Ce	1.00			
	Ch	0.64	1.00				Ch	0.07	1.00				Ch	0.85	1.00		
	Eu						Eu	0.01	0.01	1.00			Eu	0.82	0.69	1.00	
	Cy	-0.54	-0.45		1.00		Cy	0.50	-0.05	-0.22	1.00		Cy	0.39	0.15	0.24	1.00
Summer 2016	Ce	1.00				Summer 2017	Ce	1.00				Summer 2018	Ce	1.00			
	Ch	0.97	1.00				Ch	0.86	1.00				Ch	0.73	1.00		
	Eu	0.98	0.95	1.00			Eu	ND	ND	ND			Eu	0.05	0.64	1.00	
	Cy	-0.60	-0.70	-0.51	1.00		Cy	0.79	0.66	ND	1.00		Cy	-0.33	-0.18	0.05	1.00
Fall 2016	Ce	1.00				Fall 2017	Ce	1.00				Fall 2018	Ce	1.00			
	Ch	0.34	1.00				Ch	0.91	1.00				Ch	0.55	1.00		
	Eu	0.44	0.51	1.00			Eu	ND	ND	ND			Eu	-0.02	0.26	1.00	
	Cy	0.38	0.38	0.01	1.00		Cy	0.83	0.72	ND	1.00		Cy	0.24	-0.01	0.19	1.00
Winter 2016	Ce	1.00				Winter 2017	Ce	1.00				Winter 2018	Ce	1.00			
	Ch	0.67	1.00				Ch	0.55	1.00				Ch	0.78	1.00		
	Eu	-0.32	-0.06	1.00			Eu	ND	ND	ND			Eu	0.00	0.29	1.00	
	Cy	-0.29	-0.52	-0.69	1.00		Cy	-0.50	-0.59	ND	1.00		Cy	-0.31	-0.49	-0.13	1.00
Year 1	Ce	1.00				Year 2	Ce	1.00				Year 3	Ce	1.00			
	Ch	0.51	1.00				Ch	0.76	1.00				Ch	0.63	1.00		
	Eu	0.53	0.53	1.00			Eu	0.48	0.14	1.00			Eu	0.07	0.21	1.00	
	Cy	-0.70	-0.48	-0.63	1.00		Cy	0.56	0.34	0.38	1.00		Cy	-0.14	-0.23	-0.04	1.00

between *C. furcoides* density and temperature and insolation during spring-summer periods. In this subtropical region, during the spring, minimum temperatures are close to the optimum for this species (12–23 °C, Heaney *et al.* 1988), while maximum temperatures (often around 25 °C) correspond to the period of population decline (Pollinger & Hickel 1991). During summer, mean temperatures were also around 25 °C. Wind velocity, which was positively related to density of *C. furcoides* in spring-summer periods and negatively related during fall-winter periods, promotes water column mixing and increases turbulence in the system. It is known that dinoflagellates of the genus *Ceratium* have preference for stable and thermally stratified environments (Ollrik 1994).

Invasive species can cause serious impacts in the native phytoplankton community, changing its structure and dynamics, and causing in local extinctions due to competitive exclusion (Mooney & Cleland 2001). Understanding the ecological interactions between native and exotic species over the colonization and establishment process is important to assess the extent of these impacts on invaded systems (Crossetti *et al.* 2019). Although there are few studies analyzing alterations in phytoplankton communities after the first report of *C. furcoides* (Crossetti *et al.* 2019), many studies uncovered valuable clues as to how the phytoplankton has changed in response to this invasion in different tropical and subtropical aquatic systems. In most cases, the invaded freshwater systems have presented historical blooms of cyanobacteria and the arrival of *Ceratium* seems to overturn the cyanobacterial dominance (Nishimura *et al.* 2015; Cavalcante *et al.* 2016; Crossetti *et al.* 2019). In other cases, *C. furcoides* blooms were found accompanied by cyanobacterial blooms (Silva *et al.* 2012;

Almeida *et al.* 2016). Almanza *et al.* (2016) found that the phytoplankton community presented lower diversity and species richness during the colonization process performed by *C. furcoides* in a Chilean eutrophic lake.

The present study used a weekly sampling of the phytoplankton community for three years after the initial detection of *C. furcoides*. This wide temporal scale allowed the observation of three distinct phases of *Ceratium* colonization and establishment in Pedalinhos Lake. During Year 1, *C. furcoides* caused destabilization of the community, with high peak densities alternating with high cyanobacterial abundance in spring and summer. The initial alternation suggested that both have different strategies relative to environmental resources. While *C. furcoides* prevailed in intermediate temperature conditions (up to 25 °C), floating cyanobacteria like *Microcystis* preferred higher insolation and temperature (Ollrik 1994) and these factors are probably related to the competition between dinoflagellates and cyanobacteria in the Pedalinhos Lake.

During fall and winter, *C. furcoides* dominated the phytoplankton community entirely, resulting in a very low occurrence of cyanobacteria and an atypical increase in euglenophyte (*Phacus* and *Euglena*) abundance. It is recognized that *Microcystis* reduces the penetration of light into water column, inhibiting the growth of other phytoplankton groups by light limitation (Xiao *et al.* 2018). Inversely, *Ceratium* are flagellate organisms with diffuse blooms at different depths in the lake (Pollinger 1988; Crossetti *et al.* 2019, Jaramillo-Lodoño 2018). Thus, when these dinoflagellates replace *Microcystis* by competition, there is a commensurate increase in water transparency, favoring other flagellate groups, such as euglenophytes (Crossetti *et al.* 2019).

Table 2. Correlations between the phytoplanktonic groups (Ce = *Ceratium furcoides*, Ch = chlorophytes, Eu = Euglenophyceae, Cy = Cyanophyceae) and meteorological variables (Precip = precipitation, Tmax = maximum temperature, Tmin = minimum temperature, Insol = insolation, Tmean = mean temperature, Humid = humidity, Wind = wind velocity; Acc Precip= accumulated precipitation) shown o seasonal and annual scales (ND = no detected, values in bold are significant, $p < 0.05$).

	n=51	Ce	Ch	Eu	Cy		n=53	Ce	Ch	Eu	Cy		n=47	Ce	Ch	Eu	Cy
Spring 2015	Precip	0.19	0.50	ND	-0.10	Spring 2016	Precip	-0.03	0.11	0.40	0.27	Spring 2017	Precip	-0.15	-0.06	-0.20	-0.14
	Tmax	-0.59	-0.32	ND	0.64		Tmax	-0.39	0.08	-0.39	-0.23		Tmax	-0.30	0.01	-0.20	-0.34
	Tmin	0.02	0.33	ND	0.43		Tmin	-0.11	0.31	0.05	0.19		Tmin	0.28	0.54	0.07	0.36
	Insol	-0.47	-0.56	ND	0.12		Insol	-0.43	-0.21	-0.46	-0.46		Insol	-0.34	-0.58	-0.16	0.29
	Tmean	-0.33	-0.05	ND	0.61		Tmean	-0.41	0.01	-0.29	-0.13		Tmean	-0.01	0.31	-0.10	0.05
	Humid	0.41	0.50	ND	-0.04		Humid	0.29	0.15	0.37	0.12		Humid	0.39	0.28	0.38	0.26
Summer 2016	Wind	0.50	0.56	ND	-0.27	Summer 2017	Wind	0.69	0.22	0.00	0.49	Summer 2018	Wind	-0.29	-0.36	-0.51	-0.36
	Precip	-0.30	-0.32	-0.25	0.40		Precip	-0.04	0.14	ND	-0.42		Precip	0.49	0.67	0.66	-0.20
	Tmax	-0.02	0.08	-0.09	-0.16		Tmax	-0.36	-0.45	ND	-0.11		Tmax	-0.37	-0.53	-0.45	0.03
	Tmin	-0.57	-0.57	-0.63	0.44		Tmin	-0.56	-0.33	ND	-0.40		Tmin	0.16	0.25	0.09	0.24
	Insol	0.46	0.47	0.42	-0.30		Insol	0.12	-0.15	ND	0.27		Insol	-0.56	-0.81	-0.59	-0.16
	Tmean	-0.37	-0.32	-0.44	0.20		Tmean	-0.30	-0.38	ND	-0.22		Tmean	0.11	-0.13	-0.36	-0.23
Fall 2016	Humid	-0.25	-0.37	-0.28	0.25	Fall 2017	Humid	-0.01	0.17	ND	-0.18	Fall 2018	Humid	0.07	0.41	0.49	0.57
	Wind	0.69	0.75	0.66	-0.49		Wind	0.15	-0.03	ND	0.06		Wind	0.48	0.60	0.32	-0.38
	Precip	0.00	0.24	0.30	0.17		Precip	-0.85	-0.76	ND	-0.73		Precip	0.04	-0.07	-0.09	-0.21
	Tmax	0.07	0.78	0.48	0.31		Tmax	0.70	0.85	ND	0.55		Tmax	-0.16	0.07	0.14	0.16
	Tmin	0.36	0.83	0.54	0.35		Tmin	-0.12	0.13	ND	-0.08		Tmin	-0.05	0.20	0.37	-0.09
	Insol	-0.18	0.11	-0.35	0.16		Insol	0.68	0.62	ND	0.61		Insol	-0.19	-0.05	-0.29	-0.18
Winter 2016	Tmean	0.22	0.84	0.53	0.31	Winter 2017	Tmean	0.11	0.31	ND	0.15	Winter 2018	Tmean	0.00	0.23	0.23	-0.11
	Humid	0.42	-0.08	0.26	0.25		Humid	-0.63	-0.59	ND	-0.70		Humid	-0.15	-0.33	0.35	0.26
	Wind	-0.22	-0.21	-0.31	-0.20		Wind	0.21	-0.02	ND	0.31		Wind	0.17	0.02	0.01	0.08
	Precip	-0.14	-0.28	0.31	-0.20		Precip	0.02	-0.38	ND	0.61		Precip	0.36	0.39	-0.23	0.12
	Tmax	0.32	0.25	-0.19	0.01		Tmax	0.09	0.20	ND	-0.02		Tmax	-0.08	-0.17	0.28	-0.15
	Tmin	-0.33	-0.23	0.18	-0.10		Tmin	-0.08	-0.20	ND	0.51		Tmin	0.02	-0.23	0.34	0.11
Year 1	Insol	0.28	-0.07	-0.57	0.68	Year 2	Insol	0.40	0.03	ND	-0.44	Year 3	Insol	0.01	0.22	0.55	-0.10
	Tmean	0.05	-0.04	0.05	-0.09		Tmean	-0.24	-0.24	ND	0.54		Tmean	-0.04	-0.15	0.65	0.01
	Humid	-0.13	-0.02	0.27	-0.45		Humid	0.14	0.44	ND	0.04		Humid	-0.27	-0.47	-0.51	-0.22
	Wind	-0.61	-0.81	-0.14	0.59		Wind	0.06	0.26	ND	0.27		Wind	0.05	0.36	0.91	-0.07
	Precip	0.10	0.20	0.24	-0.12		Precip	-0.22	-0.33	0.15	-0.25		Precip	0.12	0.36	-0.04	-0.05
	Tmax	-0.47	0.11	-0.27	0.51		Tmax	0.10	0.39	-0.22	-0.17		Tmax	-0.14	0.10	0.02	-0.21
Year 2	Tmin	-0.41	0.18	-0.18	0.50	Year 3	Tmin	-0.19	-0.13	-0.06	-0.19	Year 3	Tmin	0.05	0.37	0.16	-0.15
	Insol	-0.31	-0.11	-0.27	0.28		Insol	0.36	0.26	0.05	0.19		Insol	-0.25	-0.29	-0.09	-0.09
	Tmean	-0.48	0.14	-0.25	0.53		Tmean	0.19	0.35	-0.09	-0.22		Tmean	0.00	0.31	0.09	-0.20
	Humid	0.27	0.08	0.17	-0.13		Humid	-0.46	-0.30	-0.23	-0.20		Humid	0.05	-0.07	0.20	0.06
	Wind	0.25	0.27	0.10	-0.25		Wind	0.39	0.05	0.35	0.26		Wind	0.09	0.13	0.09	-0.03
	Acc Precip	-0.13	0.07	0.00	0.14		Acc Precip	-0.15	-0.17	-0.03	-0.37		Acc Precip	-0.05	0.01	-0.11	0.13

Year 2 was marked by stability in the phytoplankton community, with little variation in the relative contributions of each group over the year. *C. furcoides* presented moderate densities (never above 1,300 ind.mL⁻¹) but dominated the phytoplankton community throughout the period. In general, there was a reduction in the total density of phytoplankton in Year 2, during which each phytoplankton group showed distinct relationships with environmental variables. The stability of *C. furcoides* populations was also observed in terms of biovolume, with an expressive increase in the mean biovolume of *C. furcoides* in Year 2, indicating an increase in cell size in this period. In early stages of colonization, high cell densities are a consequence of high metabolic rates for cell division and result in smaller cells. In periods of low population growth, cells tend to invest in volume (Cavalcante *et al.* 2016).

In Year 3, cyanobacterial populations seemed to adapt to the environmental disturbance promoted by *C. furcoides* colonization. Although our data are not conclusive to infer competition, we can observe a clear pattern in the peaks and troughs of *C. furcoides* coinciding inversely with the density of cyanobacteria. During this period there was also a reduction in the abundance of green algae, beginning in fall and drastically declining in the winter. Chlorophytes are common components of freshwater phytoplankton in Brazilian tropical and subtropical lakes and usually co-occur with *Ceratium* blooms (Cassol *et al.* 2014; Hackbart *et al.* 2015). In general, chlorophytes are opportunistic organisms, which grow rapidly and depend on high concentrations of nutrients and light intensity (Ollrik 1994). We may propose the hypothesis that the intense oscillation in abundance

between *C. furcoides* and species of *Microcystis* promoted an unfavorable condition for the growth of chlorophytes in that period.

In several Brazilian reservoirs, harmful bloom-forming cyanobacteria have been a major problem for water quality (Yunes *et al.* 2003; Moura *et al.* 2018). These environments dominated by cyanobacteria have progressively modified their phytoplankton community due to *Ceratium* invasion (Nishimura *et al.* 2015; Crossetti *et al.* 2019). On the one hand, the reduction of toxic blooms of dominant cyanobacteria seems to be positive. On the other, *Ceratium* invasion brings structural modifications in native communities with many potential losses, such as reduction of biodiversity (Almanza *et al.* 2016) and hypoxia in the water column due to decay of dinoflagellate blooms causing massive kills of aquatic organisms (Camparelli *et al.* 2017; Morales 2016), and may be a problem for conventional water treatments of public water supplies (Almeida *et al.* 2016). However, in this urban and shallow lake it is clear that the *Ceratium* invasion was interacting with the original phytoplankton community of the lake because it was positively and significantly correlated with chlorophytes almost the entire time. Monitoring and long-term studies, in different environments, are the best way to understand the effects of *Ceratium* invasion in Brazilian waterbodies.

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