Invasion of *Ceratium furcoides* in subtropical lakes in Uruguay: Environmental drivers and fish kill record during its bloom

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**Abstract** The invasive freshwater dinoflagellate *Ceratium furcoides* is extending its distribution in South America with increasing environmental impacts associated with its bloom. We here report two events related to *C. furcoides* distribution expansion in Uruguay: (1) the main environmental drivers (physical and chemical factors, extreme wind events and zooplankton composition) of the first appearance and bloom of *C. furcoides* in 2012 in a subtropical eutrophic shallow lake (Lake Blanca, Uruguay); and (2) a fish kill event of *Prochilodus lineatus* observed during a bloom of *C. furcoides* in 2016 in a deep eutrophic lake (Puente de las Americas, Uruguay). The bloom of *C. furcoides* in Lake Blanca started in spring 2012 (December) after a clear water period with high phytoplankton species replacement after a cyanobacterial bloom of *Raphidiopsis raciborskii*. Extreme wind during this period may have initiated the bloom of *C. furcoides* by enhanced cysts resuspension from the sediments. High nutrient availability and low zooplankton grazing, further allowed *C. furcoides* to expand and reach over 96% of the phytoplankton biomass. In Lake Puente de las

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Americas, we registered the fish kill of the large-sized benthic Prochilodus lineatus during a bloom of C. furcoides. This bloom caused the oxygen depletion in the hypolimnion and the gills from these fish exhibited massive accumulations of C. furcoides cells compared to the ones collected in non-bloom conditions. Concurring to other studies our results suggest that the C. furcoides bloom likely caused the fish kill of P. lineatus by asphyxia. Our study is the earliest register of a bloom of C. furcoides in Uruguay (in 2012) and discusses the potential environmental effects of its bloom in subtropical lakes.

Keywords  Phytoplankton · Dinoflagellate bloom · Prochilodus lineatus · Eutrophication · Massive fish mortality

Introduction

Ceratium furcoides (Levander) Langhans 1925 is a freshwater dinoflagellate species which has recently expanded its geographic distribution range to southern South America where it is currently considered invasive (Boltovskoy et al. 2013; Macêdo et al. 2021a; Meichtry de Zaburlín et al. 2016). In South America, C. furcoides was first registered in Colombia (Bustamante Gil et al. 2012; Ramírez et al. 2005) and since then it has rapidly extended its southern distribution to Brazil (Amorim & do Nascimento Moura 2021; Cassol et al. 2014; Cavalcante et al. 2013, 2016; Jati et al. 2014; Macêdo et al. 2021a; Matsumura-Tundisi et al. 2010; Moreira et al. 2015; Santos-Wisniewski et al. 2007; Silva et al. 2012), Bolivia (Morales 2016), Argentina (Boltovskoy et al. 2013; Bordet et al. 2017; Meichtry de Zaburlín et al. 2014; Salusso & Moraña 2014) and Chile (Almanza et al. 2016). In 2015, it was registered in one of the arms on the Argentinean side of the binational reservoir of Salto Grande on the Uruguay River (31° 21’ S; 57° 91’ W) (Bordet et al. 2017) and the risk of expansion in Uruguay was emphasized as being high (Macêdo et al. 2021b; Meichtry de Zaburlín et al. 2016). However, the origin of C. furcoides in South America is still uncertain. Accattatis et al. (2020) found that the genetic sequence of the ribosomal 18S gene is identical to Asian sequences, and, consequently, more related to the North American variants than to those from Europe where it was first described (Levander 1894). In a recent study, Macêdo et al. (2021b) attributed the rapid expansion of C. furcoides to its capacity to rapidly shift its natural climatic niche after introduced into new areas.

C. furcoides is a large-sized phytoplankton species (162–322 μm lineal dimension), K-selected, stress-tolerant, with a slow growth rate, low surface/volume ratio, high nutrient storage capacity and high resistance to herbivory (Bustamante Gil et al. 2012; Lürling et al. 2021; Olrik 1994; Pollingher 1988; Reynolds 2006; Weithoff et al. 2001). C. furcoides shares morphological characteristics with Ceratium hirundinella (O.F. Müller 1773) Dujard 1841, which is a common species in Uruguay (Fabre et al. 2010; Goyenola et al. 2014) and the distinction between the two species can be difficult. The overall shape and size of these two species are similar, and both have an apical horn on the epitheca and a variable hypotheca with two or three antiapical horns (Huber-Pestalozzi 1950; Hickel 1988; Popovsky & Pfister 1990). The main morphological differences occur in the epitheca, where the apical horn of C. furcoides is slightly thicker and cone-shaped than that of C. hirundinella, whose plate 4’ is shorter and does not reach the apex of the apical horn (Fig. 1) (Calado & Larsen 1997; Popovsky & Pfister 1990; Santos-Wisniewski et al. 2007). C. furcoides can be mistakenly identified as C. hirundinella (Bustamante Gil et al. 2012; Calado & Larsen 1997; Cavalcante et al. 2013) both because of the morphological similarity but also because of a high overlap in terms of ecological requirements. The genus Ceratium (Schrank) forms blooms in lakes and reservoirs during the warmer months in the pantropical region (Bustamante Gil et al. 2012; Cavalcante et al. 2016; Silva et al. 2018). Although some species of the genus have been registered at oligotrophic conditions (Bucka & Zurek 1994; Padišák 1985) they are typically found in eutrophic-hypereutrophic systems (Claps & Ardoihan 2007; Hart & Wragg 2009; Whittington et al. 2000) often co-occurring with cyanobacteria (Lund 1965). Species within the Ceratium genus are highly mobile and may control their position in the water column to perform diurnal vertical migration to areas with high availability of light and nutrients, particularly in deep or stratified ecosystems (Heany & Talling 1980; Reynolds 2006). Both species may coexist in the same ecosystems (Goldyn & Kowalczewska-Madura 2008; Hickel...
but C. furcoides often become dominant (Boltovskoy et al. 2013; Meichtry de Zaburlín et al. 2016; Salusso & Moraña 2014) and eventually, this may lead to the exclusion of C. hirundinella (Salusso & Moraña 2014). The competitive ability C. furcoides and its potential to form rapid cumulative blooms has been attributed to its ability to produce cysts during unfavourable environmental conditions or in response to density-dependent processes (Bustamante Gil et al. 2012). These cysts are deposited in surface sediments and can germinate during periods of mixing when environmental conditions become favourable again thereby constituting an important inoculum that provides the potential for high population densities throughout the year (Bustamante Gil et al. 2012; Cavalcante et al. 2016).

The expansion of C. furcoides has adverse consequences on water quality and ecosystem functioning. Blooms of C. furcoides often promote oxygen depletion, brown coloration, taste, odour, and may cause filter saturation in water treatment plants (Matsumura-Tundisi et al. 2010; Morales 2016; Taylor et al. 1995). While fish kill events due to C. hirundinella have been recorded (Bazán et al. 2007; Nicholls et al. 1980), there is little evidence of the mechanisms behind fish kills associated with blooms of C. furcoides. Similarly than for other Ceratium species, these may link oxygen depletion because of high biomass accumulations and the clogging or even damage of the gills causing the fish death by asphyxia (Bazán et al. 2007; Campanelli et al. 2017; Matsumura-Tundisi et al. 2010; Morales 2016; Nicholls et al. 1980).

We here describe two extreme events related to the expansion of C. furcoides distribution: (1) the first appearance and bloom of C. furcoides in 2012 in a subtropical eutrophic shallow lake in Uruguay (Lake Blanca), where we analyse the main environmental drivers associated with its bloom. (2) The register of a fish kill event of Prochilodus lineatus (Valenciennes, 1837) occurred during a bloom of C. furcoides in the deep eutrophic Lake Puente de las Americas in southern Uruguay in 2016.

Methods

Study area

Lake Blanca is a subtropical shallow lake \((Z_{max} = 3.2 \text{ m}, \text{ fetch} = 1.3 \text{ km})\) located at the southeastern coast of Uruguay \((34^\circ \text{ S; } 54^\circ 83' \text{ W, Area: } 5.4 \text{ km}^2)\), used for tap water provision (Kruk et al. 2009; Pacheco et al. 2010). It is a polymictic, eutrophic lake with low plant coverage during the
study period, although it often has extensive coverage of submerged plants (Mazzeo et al. 2003). The lake has experienced several episodes of persistent cyanobacterial blooms of Microcystis aeruginosa (Kützing 1846) and Raphidiopsis raciborskii (Woloszynska) Aguilerá, Berrendero Gómez, Kas-tovksy, Echenique & Salerno 2018 (formerly Cylindropermopsis raciborskii (Woloszynska) Seenayya & Subba Raju 1972), limiting its exploitation as a tap water source (Pacheco et al. 2010).

Lake Puente de las Americas (34° 87' S; 56° 03' W, Area: 0.13 km²), is a relatively deep mine pit lake with a short fetch (Zmax = 7.5, fetch = 0.66 km) located in a periurban area in southern Uruguay. It originated from sand mining in the 1960’s and is described as a eutrophic to hypereutrophic lake with recurrent stratification and anoxia in the hypolimnion, especially during summer. The lake has recently undergone drastic ecosystem alterations due to the relocation of sediments at the lakeshore (Goyenola et al. 2014, 2018). Lake Puente de las Americas is located nearby the strongly eutrophicated Carrasco stream, and can have sporadic water connection with the lake depending on the hydrological conditions (Goyenola et al. 2014), though not during the study period. At least since 2010, the lake has had intensive phytoplankton blooms, with high turbidity and the frequent presence of cyanobacterial blooms of Planktothrix agardhii (Gomont) Anagnostidis & Komárek 1988 and Raphidiopsis raciborskii. The previous presence of Ceratium in this lake was restricted to C. hirundinella registered in June 2013 (Goyenola et al. 2014) while C. furcoides had not previously been recorded.

Physical, chemical and biological methods

Within the framework of different research programs, we monthly sampled phytoplankton, zooplankton and environmental variables in Lake Blanca from May 2011 (July 2010 for phytoplankton) to October 2013, with a fortnightly sampling frequency during the warmest months (November to May). We sampled physical and chemical variables (in situ parameters, chlorophyll-a and nutrients), phytoplankton and zooplankton at three sampling points along a pelagic mid-lake transect. At each of these sampling points, we measured in situ: temperature (°C), pH, conductivity (µS.cm⁻¹), turbidity (NTU) and dissolved oxygen (µg.L⁻¹ and %) at mid-depth using an YSI 650 MDS multiprobe. At the same points, we collected water integrating the entire water column by using a tube sampler (10 cm diameter). From this depth-integrated water, we directly collected samples for nutrient, chlorophyll-a determinations and phytoplankton. Then, we collected the zooplankton samples by filtering 10 L of this depth-integrated water through a 50-µm mesh net. Phytoplankton and zooplankton samples were preserved with acidified lugol’s iodine solution to 5%. For pelagic chlorophyll-a (Chl_a) samples were collected from the depth-integrated water and filtered in situ on GF/C fiberglass filters, followed by extraction in 95% cold ethanol and spectrophotometric measures (absorbance 665–750 nm) in the laboratory, following Nusch (1980) and ISO10260 (1992). Total nitrogen (TN) and phosphorus (TP) concentrations were determined according to Valderrama (1981), and nitrate (NO₃⁻), ammonia (NH₄⁺) and orthophosphate (PO₄³⁻) were determined according to APHA (2005) (all the concentrations expressed in µg.L⁻¹).

We examined the potential role of extreme wind events as a trigger promoting C. furcoides bloom in Lake Blanca. Historical data series on the maximum wind speed (sustained at least for 3 h) were obtained from a nearby meteorological station for the period 2010–2013 (Laguna del Sauce WMO N°86,586 INUMET). Furthermore, due to the use of Lake Blanca for drinking water provision, we analysed the presence of C. furcoides in tap water after the purification process in the drinking water treatment plant and in a distribution tank, located 2 km away from the drinking water treatment plant (El Chorro, Maldonado 34° 54’02” S; 54° 48’54” W), using qualitative samples taken with a 20-µm mesh plankton net.

Plankton identification and counting

Phytoplankton was counted according to Utermöhl (1958) by the settling technique in random fields, at 100 to 400X magnification using an Olympus CKX 41 inverted microscope. Counting lasted until reaching at least 100 individuals of the most frequent phytoplankton species (Lund et al. 1958). We identified the phytoplankton to species level and we calculated the species volume by measuring at least 30 organisms of each species according to Hillebrand et al. (1999). We did not consider picoplankton (smaller than 2 µm).
We treated the cells with NaClO 20% to separate cell wall plates and perform dinoflagellates identification based on Popovsky´ & Pfiester (1990) and Steidinger & Tanger (1997). *C. furcoides* individuals were first differentiated from the almost similar *C. hirundinella* by its shape and then identified based on the position of the apical plate 4' that does not reach the apex (Fig. 1) (Cavalcante et al. 2013; Hickel et al. 1988; Meichtry de Zaburlı´n et al. 2014; Moreira et al. 2015).

Zooplankton was identified and counted in the laboratory according to Paggi & de Paggi (1974). We calculated the ratio mesozooplankton (calanoid copepods and cladocerans) to microzooplankton (copepod nauplii and rotifers) (Meso:micr) from abundance data (ind.L$^{-1}$) as a proxy of zooplankton grazing potential on phytoplankton (Pacheco et al., 2010).

Data analysis

The environmental and biological variables explaining the phytoplankton composition in Lake Blanca were analysed by canonical correspondence analysis (CCA) to constrain the composition variance. We first performed a detrended correspondence analysis to determine which constrained method to use, and as the longest axis was longer than three standard deviations, we selected the unimodal-based method (CCA) (ter Braak & Verdonschot 1995). We selected the environmental and biological explanatory variables to incorporate in the CCA model by stepwise selection, comparing R$^2$ with the full model and checking the significance of each variable and model by Monte-Carlo permutation test. We inspected the variance inflation factor (VIF) of the variables to identify collinearity, excluding variables with VIF > 10 or VIF = 0 (ter Braak & Verdonschot 1995).

We analysed the environmental and biological variables associated with the bloom of *C. furcoides* in Lake Blanca by partial least-squares regressions (PLS), cross-validating the model by permutation test and selecting the variables best explaining the high abundances of *C. furcoides*.

We z-scored standardised environmental data and log (x + 1) transformed the phytoplankton biovolume data, excluding rare species with a lower contribution than 1% to the total phytoplankton biomass from the analysis, to avoid bias in the sensitive methods. All the statistical analyses were performed in R 3.6.2 (R Core Team 2019) using the ‘vegan’ package (Oksanen et al. 2013).

Fish kill register methods

As part of a research program in the Lake Puente de las Americas, we performed three monthly sampling campaigns in 19 June, 29 August and 22 September 2016. We measured Secchi disk depth (m), dissolved oxygen (mg.L$^{-1}$ and %) and turbidity (NTU) and collected depth-integrated chlorophyll a (µg.L$^{-1}$) and phytoplankton samples following the same analytical methods as for the Lake Blanca samples. The sampling campaign included the fish kill of *Prochilodus lineatus* (Valenciennes, 1837) occurring the 29 August 2016 concomitant with a bloom of *C. furcoides*. *Prochilodus lineatus* (Characiformes) is a large-sized (aprox. 80 cm in total length and 7 kg of fresh biomass) migratory fish from the Rı´tio de la Plata basin (Castro & Vari 2003; Zaniboni et al., 2004). It feeds mainly on organic matter from the sediment (detritivore) also consuming periphyton and phytoplankton, and therefore has a fundamental role in freshwater food webs and ecosystem functioning (Flecker 1996; Benedito et al. 2018). Dead fish were manually collected at the lakeshore, where they were abundant (hundreds) and kept in cold until laboratory processing. In the laboratory, we analysed in microscope the material accumulated in the gills. We compared the general conditions of the gills, the amount of material accumulated on the filaments, and the phytoplankton from this accumulated material from the dead fish collected during the bloom of *C. furcoides* (29 August 2016) with the gills from fish collected in the subsequent sampling campaign (22 September 2016) without *C. furcoides* bloom.

Results

The environmental characteristics were highly variable in Lake Blanca during the period 2011–2013 (Table 1, Fig. 2). Turbidity was at its historical maximum during the *C. furcoides* bloom, coinciding with the lowest transparency (Secchi Disk depth) (Fig. 2). The levels of nutrients, chlorophyll-a and transparency corresponded to mesotrophic-eutrophic conditions (Carlson 1977). Nitrogen concentrations varied considerably, with a TN peak during the initial
cyanobacterial bloom in 2011, while \( \text{NH}_4^+ \) was low throughout the period except for a peak during the second half of 2012; \( \text{NO}_3^- \) had the highest concentrations in 2013 during the \textit{C. furcoides} bloom (Fig. 2, Table 1). Phosphorus varied considerably as well, with low \( \text{PO}_4^{3-} \) concentrations during 2013 (Fig. 2), and similarly to TN, TP rapidly declined at the end of the study period (Oct 2013, Fig. 2).

The phytoplankton community showed substantial variations during 2010–2013, with alternating periods of high and low biomass and marked taxa replacements (Fig. 3). From 4 July 2010 to 27 July 2011, cyanobacteria dominated the phytoplankton community in Lake Blanca, with extremely high biomasses (c.a. \( 60 \text{ mm}^3 \cdot \text{ L}^{-1} \)) and a persistent bloom of \textit{Raphidiopsis raciborskii} (formerly \textit{Cylindrospermopsis raciborskii}). This was followed by a period of relatively low phytoplankton biomass and taxa replacement from desmids (mostly \textit{Closterium acciculare T.West 1860 and Staurastrum leptocladium Nordstedt 1870}) to chlorophytes (\textit{Coelastrum sp., Pediastrum sp. and Botryococcus sp.}) (July 2011 to December 2012), followed by the bloom of \textit{C. furcoides}. An abrupt change in phytoplankton composition occurred just before the bloom of \textit{C. furcoides} with a low phytoplankton biomass, mainly represented by tychoplanktonic diatoms and euglenoids, but dinoflagellate cysts and suspended sediment also appeared in the samples. This period from July to December 2012, coincided with the most extreme wind events, with wind speeds above \( 100 \text{ km. h}^{-1} \) for more than 3 h (Fig. 3).

The \textit{C. furcoides} bloom was characterised by rapid growth from 2 December 2012 (Fig. 3) and this species constituted more than \( 96\% \) of the total phytoplankton biovolume, and, hence, the drastic reduction of other groups, particularly dinoflagellates (Fig. 4) from December 2012 to September 2013. Before the consolidation of the \textit{C. furcoides} bloom, dinoflagellates were mainly represented by \textit{Peridinium spp.} and low biomasses of \textit{C. hirundinella} (Fig. 4). After the \textit{C. furcoides} bloom, both the \textit{Peridinium spp.} and the \textit{C. hirundinella} populations reached low biomasses (\textit{Peridinium spp.} maximum = \( 1.97 \text{ mm}^3 \cdot \text{L}^{-1} \), \textit{C. hirundinella} maximum = \( 0.72 \text{ mm}^3 \cdot \text{L}^{-1} \)) relative to \textit{C. furcoides} (\( 25.76 \text{ mm}^3 \cdot \text{L}^{-1} \)) (Fig. 4). The zooplankton in Lake Blanca was largely dominated by small-sized rotifers such as \textit{Keratella spp., Filinia spp. (microzooplankton) and small-bodied cladocerans (mesozooplankton) such as Bosmina spp.} (Table 2).

According to the CCA, phytoplankton composition in Lake Blanca was largely explained by turbidity (Turb), the ratio of mesozooplankton to microzooplankton (Meso:micro), total phosphorus (TP) and ammonium (\( \text{NH}_4^+ \)) concentrations (CCA: \( F = 11.78, p = 0.008 \); Fig. 5), with the first two axes explaining 59.8% over 69.9% of the total constrained variance. \textit{C. furcoides} biomass was positively correlated with turbidity and the Meso:micro ratio and negatively with the \( \text{NH}_4^+ \) concentration. Similarly, the PLS analysis also identified turbidity and the Meso:micro ratio as positive factors and zooplankton biomass, \( \text{NH}_4^+ \) and TP as factors negatively correlated with \textit{C. furcoides} based on the eight selected components, explaining 86.9% of the total variance.

At the end of the study period, during the biomass peak of \textit{C. furcoides}, we observed cells in process of cyst formation and the presence of cysts in the water column although we did not count these cysts since it was not possible to differentiate from the cyst of \textit{C. hirundinella}. These cysts passed the water purification process and were found in the tap water. Furthermore, in January 2013 we observed adult \textit{C. furcoides} in one
of the tap water distribution tanks, with deformities in the apical and antiapical horns (Fig. 6).
Although in this study we did not analyse the fish community in Lake Blanca, we did not record fish kills in Laguna Blanca during the study period.

Fish kill event

On 29 August 2016, a massive fish kill of *Prochilodus lineatus* was registered in Lake Puente de las Americas during a bloom of *C. furcoides*. Before the bloom (19 June 2016), the lake exhibited intermediate phytoplankton biomass (Chl_a = 50 µg.L⁻¹) in the surface water, the transparency (SD = 1.0 m) was intermediate and the turbidity (Turb = 5 NTU) low, while intermediate levels of dissolved oxygen in the surface water prevailed (OD = 73–86%). The phytoplankton was dominated by cyanobacteria, mostly *Dolichospermum circinale* (Rabenhorst ex Bornet & Flahault) P. Wacklin, L. Hoffmann & J. Komárek 2009 and *Aphanocapsa elachista* West & G.S.West 1894, up to 5000 org.mL⁻¹. At the sampling event on 29 August 2016, we registered the bloom of *C. furcoides* in Lake Puente de las Americas. As in Blanca Lake, the bloom of *C. furcoides* in this lake was characterised by a drastic increase in phytoplankton biomass (Chl_a = 170.4 µg.L⁻¹) with 99% consisting of *C. furcoides*, high turbidity (Turb = 18.2 NTU) and low transparency (SD = 0.6 m). Furthermore, the bloom increased the surface oxygen to oversaturation (81.6–115.9%). On the subsequent sampling event (22 September 2016), the phytoplankton biomass was markedly lower (16.8–19.5 µg.L⁻¹) the bloom of *C. furcoides* had collapsed and high amounts of *C. furcoides* cysts but not adult organisms were recorded. Dissolved oxygen and saturation depth profiles showed hypoxia or anoxia at depths of more than 2 m, coinciding with the beginning of the bloom of *C. furcoides* in late August (Fig. 7). Turbidity also decreased (Turb = 13 NTU), while surface saturation of dissolved oxygen remained high, 104–107%. At this time, the phytoplankton included various groups such as diatoms, mainly *Aulacoseira distans* (Ehrenberg) Simonsen 1979 and *Cyclotella meneghiniana* (Kützing 1844), euglenoids (*Trachelomonas* spp.), *Chlorophyta* (*Scenedesmus* spp.), *Charophyta* (*Staurastrum* spp.) and *Plagioselmis nannoplanctica* (Skuja) G. Novarino, I. A. N. Lucas & Morrall 1994.

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Table 2 Zooplankton main group abundance by seasons in Lake Blanca during the period May 2011 to October 2013

|               | Cladocera | Calanoids | Cyclopoids | Nauplii | Rotifera | Meso:Micro | Total   |
|---------------|-----------|-----------|------------|---------|----------|------------|---------|
| Spring        | 149.8     | 24.1      | 12.3       | 163.9   | 611.1    | 0.6        | 961.3   |
| Min           | 27.7      | 5.3       | 0          | 84.0    | 18.7     | 0.1        | 234.4   |
| Max           | 389.0     | 83.3      | 26.7       | 286.7   | 3166.7   | 2.0        | 3572.0  |
| Summer        | 269.8     | 17.1      | 49.5       | 156.5   | 1307.3   | 0.4        | 1800.1  |
| Min           | 46.7      | 0         | 4.0        | 87.0    | 96.0     | 0.1        | 374.1   |
| Max           | 624.0     | 104.0     | 136.0      | 290.7   | 4834.7   | 1.2        | 5214.6  |
| Autumn        | 226.7     | 8.0       | 87.3       | 166.7   | 2331.3   | 0.2        | 2820.0  |
| Min           | 90.7      | 1.3       | 53.3       | 90.7    | 761.3    | 0.1        | 1294.7  |
| Max           | 368.0     | 16.0      | 161.3      | 244.0   | 4640.0   | 0.5        | 5357.3  |
| Winter        | 333.6     | 10.1      | 39.9       | 123.5   | 730.6    | 0.5        | 1237.7  |
| Min           | 95.6      | 1.3       | 0          | 20.0    | 376.0    | 0.1        | 597.3   |
| Max           | 685.3     | 26.6      | 96.0       | 237.3   | 1588.9   | 1.0        | 1797.8  |

Fig. 5 Biplot of the canonical correspondence analysis for phytoplankton composition in Lake Blanca. Environmental variables best explaining phytoplankton composition in Lake Blanca: turbidity (Turb), ratio mesozooplankton to microzooplankton (Meso:micro), total phosphorus (TP) and ammonium (NH₄⁺). Monte Carlo: F = 11.78, p = 0.008. Total variance explained: 69.9% λ₁ = 45.3%, λ₂ = 14.5% (59.8%)
In the initial visual inspection of the dead fish, the cause of the fish kill could not be determined. Although it was not possible to record the number of dead fish in the shoreline, the high density of hundreds of dead fish observed largely exceeded the

![Image of Ceratium furcoides](image)

**Fig. 6** *Ceratium furcoides* during the bloom in Lake Blanca in 2012–2013. Top panel: normal appearance of adult *C. furcoides* (left) and with condensed material during previous to the cyst formation (right). Lower panel: Adult organisms of *C. furcoides* from one of the tap water distribution tanks in El Chorro, Maldonado. All organisms presented deformities in their apical horns (a, b) or lack of one of their antapicals (c, d)

![Graphs showing dissolved oxygen concentration and oxygen saturation in-depth in Lake Puente de las Americas, Uruguay from June to September 2016](image)

**Fig. 7** Dissolved oxygen concentration and oxygen saturation in-depth in Lake Puente de las Americas, Uruguay from June to September 2016.
limit to define a fish kill for lakes of 25 ind.km² (La & Cook 2011). This indicated that the event was not an incidental mortality restricted to few organisms, but a massive mortality caused by extended environmental stress in the lake. In the microscopic analysis, we found dense accumulations of C. furcoides in all gill filaments (Fig. 8). In contrast, we did not observe accumulations of C. furcoides in the gills of specimens of P. lineatus collected after the bloom on 22 September 2016 (Supplementary material 1). Instead, we registered a few phytoplankton individuals of Aulacoseira granulata (Ehrenberg) Simonsen 1979, Cyclotella meneghiniana and Staurastrum sp., but in very low amounts.

Discussion

In this study, we recorded a C. furcoides bloom at Lake Blanca, occurring after a state of cyanobacterial dominance, and potentially facilitated by extreme wind events that increased cyst resuspension from the sediments. This bloom started in spring 2012 and maintained its increase throughout the year, favoured by the high nutrient availability and low grazing. The bloom of C. furcoides displaced other dinoflagellate species previously existing in the system. At Lake Puente de las Américas we recorded the fish kill of P. lineatus during a C. furcoides bloom. We hypothesised that the oxygen depletion in the hypolimnion promoted by the high biomasses of C. furcoides together with the accumulation of C. furcoides in the gills could have induced the fish kill of P. lineatus as previously suggested. This study constitutes to our knowledge the earliest register of the presence and bloom of Ceratium furcoides in Uruguay (December 2012) as well as the first record for the country of a fish kill during its bloom.

Invasive C. furcoides has expanded its distribution to southern Uruguay, an area previously indicated as having high invasion potential (Macêdo et al. 2021b; Meichtry de Zaburlín et al. 2016). Lake Blanca basin is not connected to the Salto Grande reservoir, 500 km north in the large river Uruguay which is the geographically closest record of this species. C. furcoides is widely distributed in northern Argentina and Brazil (Macêdo et al. 2021a; Meichtry de Zaburlín et al. 2016) from were probably colonized Salto Grande, while C. furcoides likely arrived in Lake Blanca from south Brazil (State of Rio Grande do Sul) which is geographically closer and where C. furcoides has also been recorded (Cavalcante et al. 2013; Cassol et al. 2014). The distribution patterns of C. furcoides are complex, and it seems that this species frequently colonizes freshwaters from basins that are geographically close but unconnected implying that their spread cannot be attributed to connectivity alone (Moreira et al. 2015; Silva et al. 2018). Instead, the transport of cells or cysts by migratory birds and boats (Kristiansen 1996; Padisák et al. 2016; Silva et al. 2018) may play an important role in dispersal which can furthermore be facilitated by the presence of reservoirs in large rivers, that confer suitable environmental conditions for blooms of C. furcoides (Meichtry de Zaburlin et al. 2014; Silva et al. 2018).

![Fig. 8](image_url) Prochilodus lineatus (Valenciennes, 1837) gills during the bloom of Ceratium furcoides (Levander) Langhans 1925 in Puente de las Americas Lake, Uruguay, on 29 August 2016. Left: general appearance of the gills with dark accumulations of C. furcoides in the gill filaments. Center: zoom to the C. furcoides accumulations. Scale bar = 50 μm.
The finding of the adult organisms in the drinking water distribution tank further evidences the dispersal potential of *C. furcoides*. The adult *C. furcoides* are typically retained during the purification process in the drinking water plant because of their large size (160 μm average linear dimension) and their sensitivity to chlorination (required during the water purification process) (De Almeida et al. 2016; Van der Walt 2011). A possible feasible explanation is that these adult organisms of *C. furcoides* germinated from cysts that were not retained in the purification process because of their small-sized and higher resistance to chlorination (De Almeida et al. 2016; Van der Walt 2011).

The occurrence of *C. furcoides* bloom after a cyanobacteria dominance, as seen in Lake Blanca (with *R. raciborskii* and *Microcystis aeruginosa*) has been described previously (Bustamante Gil et al. 2012; Cavalcante et al. 2016; Matsumura-Tundisi et al. 2010). Crossetti et al. (2019) proposed that disruption of steady dominance of cyanobacteria might open a window of opportunity for the rapid development of *C. furcoides* blooms. Thus, *C. furcoides* share ecological behaviour with large sized cyanobacteria, as their ability for luxury consumption and high nutrient storage as well as low sinking and grazing susceptibility, which may explain their alternation or even co-dominance in freshwaters (Crossetti et al. 2019; Kruk et al. 2021; Reynolds 2006).

Lake Blanca experienced a period of high transparency with low phytoplankton biomass just before the bloom of *C. furcoides*. The rapid bloom of *C. furcoides* indicates that *C. furcoides* was already present in Lake Blanca before this study although it was not registered in pelagic samples but instead it might have colonized from cysts in the sediments (Bustamante Gil et al. 2012; Hansson et al. 1994; Reynolds & Walby 1975). The extreme wind events before the bloom, likely facilitated resuspension of the cysts from the sediments, as described elsewhere (Bustamante Gil et al. 2012; Matsumura-Tundisi et al. 2010). Other cyst-forming species, such as *Peridinium spp.* and *C. hirundinella*, also increased their biomass in this period but rapidly disappeared. This pattern has been attributed to the competitive exclusion by *C. furcoides* (Moreira et al. 2015; Rengefors et al. 2004; Reynolds 2006). Thus, Kruk et al. (2021) found that *C. furcoides* exhibit a high competitive fitness, which explains its rapid dominance and exclusion of other previously resident dinoflagellate species. The high biomass of *C. furcoides* bloom led to high turbidity and a decline in the concentration of dissolved nutrients due to the rapid nutrient uptake and storage in the cells, which is also coinciding with previous findings (Matsumura-Tundisi et al. 2010; Bustamante Gil et al. 2012). *C. furcoides* require high nutrient availability and resuspension of its cysts from the sediments to start the bloom (Almanza et al. 2016; Bustamante Gil et al. 2012; Chapman et al. 1982; Claps & Ardohain 2007; Hart & Wragg 2009; Matsumura-Tundisi et al. 2010; Whittington et al. 2000). Consequently, a high nutrient uptake-and storage capacity, as well as the ability to swim, which give access both to light on the surface and benthic nutrients (Reynolds 2006) may provide this species with a high competitive ability under eutrophic conditions.

We found that the bloom of *C. furcoides* in Lake Blanca began just before summer with warm temperatures and lasted throughout the following year, continuing even during cold months, indicating that high temperatures may have triggered the bloom but that low temperatures did not hinder its persistence. This finding coincides with previous studies reporting high temperatures to be important during the initial stages of a bloom but also that these are not necessary to maintain the bloom (Meichtry de Zaburlı´n et al. 2016; Cavalcante et al. 2016). Once established, the bloom of *C. furcoides* may persist due to its large size, providing the species with a low grazing susceptibility (Lürling 2021; Olrik 1994; Pollingher 1988) which is typically even lower in subtropical freshwaters due to the dominance of small-sized zooplankton (Bustamante Gil et al. 2012; Cavalcante et al. 2016; Crossetti et al. 2019; Meehroff et al. 2007; Morales 2016). In accordance, the zooplankton in Lake Blanca consisted mostly of small taxa (Table 2), such as small cladocerans and rotifers (*Bosmina, Keratella, and Filinia*) as also reported in previous studies (Iglesias et al. 2007; Pacheco et al. 2010) and consequently, they did not control *C. furcoides* by grazing (Bustamante Gil et al. 2012; Lürling 2021; Reynolds 2006).

Although we did not evidence fish kills in Lake Blanca, where we recorded a bloom of *C. furcoides*, we observed the fish kill of *P. lineatus* in Lake Puente de las Americas, during a *C. furcoides* bloom. We did not observe unusual activities in the urban catchment such as chemical or mechanical alterations,
connection with the stream, sediment removal, disposal of industrial effluents, or any other potential influx of pollutants to the lake during the period of fish kills. However, we found massive accumulations of *C. furcoides* in the gills of the dead *P. lineatus*, in comparison to what we found in gills from fish collected when the bloom had already disappeared from the system. According to the effects previously described for other species of *Ceratium* and proposed for *C. furcoides*, such accumulations can saturate or even damage the gills, thereby affecting the respiratory capacity of the fish (Bazán et al. 2007; Mahoney & Steimle 1979; Nicholls et al. 1980; Onoue 1990). Furthermore, clogged gills with excess mucus production and edema in secondary lamellae caused by *Ceratium* facilitate fish death by asphyxia (Onoue 1990). The massive accumulation of *C. furcoides* in the gills may have accentuated the sensitivity of *P. lineatus* to anoxia in the hypolimnion promoted by the bloom of *C. furcoides* in Lake Puente de las Americas, and therefore facilitated the mass mortality by asphyxia of *P. lineatus*. The risk of fish kills is higher in deep stratified lakes where the phytoplankton blooms may cause anoxia in the hypolimnion, particularly at night. Oxygen depletion is not common in shallow lakes exposed to the mixing by the wind and this may explain why we did not register fish kills in the shallow Lake Blanca.

The expansion of *C. furcoides* has accelerated in recent years in the subtropical region of South America (Meichtry de Zaburlín et al. 2016) as well as in Uruguay. In addition to our observations in Lake Blanca and Lake Puente de las Americas, *C. furcoides* was recently found in shallow lakes: Lake Escondida in 2014 (34° 82’ S; 54°62’ W) (JP Pacheco unpubl. data), Lake Sauce in 2016 (34°82’ S; 55°06’ W) (González-Madina et al. 2019), in the river Santa Lucia in 2015 (34° 30’ S; 56° 23’ W) and the reservoir San Francisco in 2015 (34° 39’ S; 55° 21’ W) (Meerhoff et al. 2017). The rapid spread of *C. furcoides*, is facilitated by eutrophic conditions and likely by global warming (Crossetti et al. 2019; Macêdo et al. 2021b; Kruk et al. 2021). Thus, recent studies have shown that *C. furcoides* can adapt its climatic niche and that its optimum temperature is higher than that of other related species implying that global warming may therefore favour the invasion and dominance of *C. furcoides* (Kruk et al. 2021; Macêdo et al. 2021b). The rapid spread of *C. furcoides* may entail the risk of its negative impact on ecosystem structure and function including its potential to promote fish kills. The spread of *C. furcoides* in Uruguay may have been a silent invasion due to difficulties in distinguishing this species from *C. hirundinella*. Given the rapid expansion and impacts of *C. furcoides* in South American freshwater ecosystems, it is necessary to increase the surveillance capacity in phytoplankton biomonitoring programs, beyond the more widespread focus on cyanobacteria, including also invasive species as these may otherwise spread unnoticed.

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**Authors contributions** JPP conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft, CI investigation, writing—review & editing, GG funding acquisition, investigation, writing—review & editing, FTM investigation, writing—review & editing, CF: investigation, writing—review & editing, ABP: writing—review & editing, supervision MM funding acquisition, investigation, writing—review & editing, EG: writing—review & editing, supervision EM funding acquisition, investigation, writing—review & editing, EJ funding acquisition, writing—review & editing, supervision.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Code availability** Not applicable.
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Declarations

Conflicts of interest  The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approvals  Not applicable.

Consent to participate  Not applicable.

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