Invasion of Ceratium furcoides in subtropical lakes in Uruguay: environmental drivers and first fish kill record

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Research Article

Keywords: Phytoplankton, dinoflagellate bloom, Prochilodus lineatus, eutrophication, massive fish mortality

DOI: https://doi.org/10.21203/rs.3.rs-210795/v1

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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 blooms. We here report two events related to *C. furcoides* distribution expansion in Uruguay: 1) the first appearance and main environmental drivers (physico-chemical variables, extreme wind events and zooplankton composition) of the bloom of *C. furcoides* in 2012 in a subtropical eutrophic shallow lake (Lake Blanca, Uruguay), and 2) the fish kill event of *Prochilodus lineatus* likely caused by *C. furcoides* in 2016 in a deep eutrophic lake (Puente de las Americas, Uruguay), which is the first fish kill attributable to *C. furcoides* registered in the world.

The bloom of *C. furcoides* in Lake Blanca started in spring 2012 (October) during a clear water period with high phytoplankton species replacement after a cyanobacterial bloom of *Raphidiopsis raciborskii*. Extreme wind events during this period resuspended cysts from the sediments, which likely started the *C. furcoides* bloom. High nutrient availability and low zooplankton grazing, allowed the bloom to expand and reach 96% of the phytoplankton biomass. Our results further indicate that the fish kill of *Prochilodus lineatus* in Lake Puente de las Americas was likely promoted by the high biomass of *C. furcoides* bloom, causing gill damage and clogging together with oxygen depletion in the benthic zone. Our study is the earliest record of *C. furcoides* in Uruguay and it shows the drastic consequences of *C. furcoides* bloom in freshwaters and its potential of inducing massive fish kills.

Introduction

*Ceratium furcoides* (Levander) Langhans 1925 is a freshwater dinoflagellate species which has recently expanded its geographic distribution range to southern South America (Meichtry de Zaburlín et al. 2016) and is currently considered invasive in this region (Boltovskoy et al. 2013).

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 (Cassol et al. 2014; Cavalcante et al. 2013, 2016; Jati et al. 2014; 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 invasion has been described as high for the littoral W-NW of Uruguay (Meichtry de Zaburlín et al. 2016).

*Ceratium 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; 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 is 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; Popovský & Pfeifer 1990). The main morphological differences between the two species 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; Popovský & Pfeifer 1990; Santos-Wisniewski et al. 2007). *C. furcoides* is often 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 (Carty 2003; O’Sullivan & Reynolds 2004; Pollinger 1988). Although some species of the genus have been registered at oligotrophic conditions (Bucka & Zurek 1994; Padisák 1985) they are typically found in eutrophic-hypereutrophic systems (Claps & Ardohain 2007; Hart 2007; 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). Consequently, both species may coexist in the same ecosystems (Goldyn & Kowalczewska-Madura 2007; Hickel 1985; Stefaniac et al. 2007) 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 rapidly form cumulative blooms has been attributed to the ability to produce cysts. Under unfavourable environmental conditions or in response to density-dependent processes, *C. furcoides* can produce cysts for resistance and dispersion (Bustamante Gil et al. 2012). These cysts, deposited in surface sediments, can germinate during periods of mixing when environmental conditions are favourable, thereby constituting an important inoculum that may maintain 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. Accumulative 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 had been no clear evidence of a fish kill caused by *C. furcoides*, although some authors have mentioned its potential to cause fish kills (Campanelli et al. 2017; Matsumura-Tundisi et al. 2010; Morales 2016).

We report here two extreme events related to the expansion of *C. furcoides* distribution: 1) the earliest appearance and bloom of *C. furcoides* for Uruguay in 2012 in Lake Blanca, a subtropical eutrophic shallow lake, where we analyse in detail the environmental factors associated with its bloom. 2) As an extreme environmental impact derived from the bloom of *C. furcoides*, we register the fish kill event of *Prochilodus lineatus* (Valenciennes, 1837) associated with the bloom of *C. furcoides* in the deep eutrophic Lake Puente de las Americas in southern Uruguay in 2016, likely the first fish kill attributable to *C. furcoides* registered in the world.

**Methods**

**Study area**

Lake Blanca is a subtropical shallow lake (Zmax= 3.2 m, fetch=1.3 km) located at the south-eastern coast of Uruguay (34°89’ S; 54°83’ W, Area: 5.4 km²), used for tap water provision (Kruk et al. 2009; Pacheco et al. 2010). It is polymictic, eutrophic lake with low plant coverage during the study period, although it is often covered by submerged plants (Mazzeo et al. 2003). The lake has experienced several episodes of persistent cyanobacterial blooms of *Microcystis aeruginosa* and *Raphidiopsis raciborskii* (formerly *Cylindrospermopsis raciborskii*), 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= 0.66km) located in a periurban area in south Uruguay. It originated from sand mining 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; Goyenola et al. 2018). Lake Puente de las Americas is located nearby the strongly eutrophicated Carrasco stream, having sporadic water connection depending on the hydrological conditions (Goyenola
et al. 2014). At least since 2010, the lake has had intensive phytoplankton blooms, with high turbidity and frequent presence of cyanobacterial blooms of *Planktothrix agardhii* 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.

**Physico-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). The samples were taken at three sampling points along a pelagic mid-lake transect. At each sampling point, we measured: temperature, pH, conductivity, turbidity and dissolved oxygen at mid-depth using a YSI 650 MDS multiprobe. We collected depth-integrated samples with a tube sampler (10 cm diameter) integrating the entire water column. From the integrated water samples, we collected sub-samples for physico-chemical, phytoplankton and zooplankton analyses. Zooplankton samples were collected by filtering 10 L of the column-integrated water sample through a 50-µm mesh net. Zooplankton and phytoplankton samples were preserved with acidified lugol's iodine solution to 5%. Pelagic chlorophyll-a (Chl-a) samples were collected and filtered *in situ* through GF/C glass fiber filters, followed by extraction in 95% cold ethanol and spectrophotometrical 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 (PO₄) were determined according to APHA (2005).

We examined the potential role of extreme wind events as trigger promoting *C. furcoides* bloom in Lake Blanca. Historical data series on the maximum wind speed (sustained at least for 3 hours) were obtained from a nearby meteorological station for the period 2010-2013 (Laguna del Sauce WMO N°86586 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 potabilization process in the water treatment plant and in a distribution tank using qualitative samples taken with a 20-µm mesh plankton net.

**Plankton identification and counting**

Phytoplankton was identified to species level and counted in random fields at 100 to 400X magnification using an Olympus CKX 41 inverted microscope (Utermöhl 1958). Counting lasted until at least 100 individuals of the most frequent phytoplankton species (Lund *et al.* 1958), considering the organism (cell, colony or filament) as the unit and calculating the biovolume according to Hillebrand *et al.* (1999). We did not consider picoplankton (smaller than 2 µm) or tychoplankton (periphytic resuspended organisms). We treated the cells with NaClO 20% to separate cell wall plates and perform dinoflagellates identification based on Popovský & Pfiester (1990) and Steidinger & Tanger (1997). *Ceratium 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).

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:micro) 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 during June to September 2016. We measured Secchi disk depth, dissolved oxygen and turbidity and collected depth-integrated chlorophyll a and phytoplankton samples following the same analytical methods as for the Lake Blanca samples. The sampling campaign included the day of the fish kill, 29 August 2016. *Prochilodus lineatus* (Valenciennes, 1837) is a large-sized (aprox. 80 cm in total length and 7 kg of fresh biomass) migratory fish from the Río 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 and frozen 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 with the gills and material from healthy fish obtained in the subsequent sampling campaign (September 2016).

Results

The environmental characteristics were highly variable in Lake Blanca during the period 2011-2013 (Table I, 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 widely, with a TN peak during the initial cyanobacterial
bloom in 2011, while NH$_4$ was low throughout the period except for a peak during the second half of 2012; NO$_3$ had the highest concentrations in 2013 during the *C. furcoides* bloom (Fig. 2, Table I). Phosphorus varied widely as well, with low PO$_4$ 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 July 2010 to July 2011, cyanobacteria dominated the phytoplankton community in Lake Blanca, with extremely high biomasses (c.a. 60 mm$^3$.L$^{-1}$) and a persistent bloom of *Raphidiopsis raciborskii* (formerly *Cylindrospermopsis raciborskii*). This was followed by a period of relatively low phytoplankton biomass and taxa replacement from desmids (mostly *Closterium acicularis* and *Staurastrum leptocladum*) to chlorophytes (*Coelastrum sp.*, *Pediastrum spp.* and *Botryococcus sp.*), followed by the bloom of *C. furcoides*. An abrupt change in phytoplankton composition occurred just before *C. furcoides* bloom. This period was characterised by low phytoplankton biomass, mainly represented by tychoplanktonic diatoms and Euglenoids, while also dinoflagellate cysts and resuspended sediment appeared in the samples. The period coincided with the most extreme wind events, with wind speeds above 100 km. h$^{-1}$ for more than 3 hours (Fig. 3).

The *C. furcoides* bloom was characterised by rapid growth (Fig. 3) thus, it constituted more than 96% of the total phytoplankton biovolume, and led to collapse of other groups, particularly dinoflagellates (Fig. 4). Before the consolidation of the *C. furcoides* bloom, dinoflagellates were mainly represented by *Peridinium spp.* and low biomasses of *C. hirundinella* (Fig. 4). After the *C. furcoides* bloom, both the *Peridinium spp.* and the *C. hirundinella* populations reached low biomasses (*Peridinium spp.* maximum= 1.97 mm$^3$.L$^{-1}$) relative to *C. furcoides* (25.76 mm$^3$.L$^{-1}$) (Fig 4). The zooplankton in Lake Blanca was largely dominated by small-sized rotifers such as *Keratella spp.*, *Filinia spp.* (microzooplankton) and the small-bodied cladoceran *Bosmina spp.* (mesozooplankton).

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 (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. *C. furcoides* biomass was positively correlated with turbidity and the Meso: micro ratio and negatively with the NH$_4$ concentration. Similarly, the PLS analysis also identified turbidity and the Meso: micro ratio as positive factors and zooplankton biomass, NH$_4$ and TP as factors negatively correlated with *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 *C. furcoides*, we observed cells with cyst formation (Fig. 6) and the presence of cysts in the water column. These cysts passed the water purification process and were found in the tap water. Furthermore, we observed both cysts and adult organisms of *C. furcoides* in one of the tap water distribution tanks, located 2 km away from the potabilization plant (El Chorro, Maldonado 34°54'02" S; 54°48'54" W); the adults with deformities in the apical and antiapical horns (Fig. 6).

Although in this study we did not analyze 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* (Characiformes) was registered in Lake Puente de las Americas during a *C. furcoides* bloom. Before the bloom (19 June), the lake exhibited intermediate phytoplankton conditions.
biomass (Chl_a = 50µg.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 circinalis* and *Aphanocapsa elachista* up to 5000 org.mL^{-1}). On the sampling event on 30 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 = 0.6m). 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 (16.8-19.5µg.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 2m, coinciding with the beginning of the bloom of *C. furcoides* in late August (Fig. 8). 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* and *Cyclotella meneghiniana*), euglenoids (*Trachelomonas* spp.), Chlorophyta (*Scenedesmus* spp.), Charophyta (*Staurastrum* spp.) and *Plagioselmis nannoplanctica*.

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 dead fish observed were clearly much higher than the limit to define a fish kill for lakes of 25 ind.km^{-2} (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, clogging the filaments and even stuck into the gill tissue (Fig. 8). Contrary, the specimens of *P. lineatus* collected after the bloom on 22 September 2016 had normal gill tissue (Fig. 9), without phytoplankton accumulations and the presence of only a few *Aulacoseira granulata*, *Cyclotella meneghiniana* and *Staurastrum* sp.individuals.

**Discussion**

This study constitutes the earliest record of *Ceratium furcoides* in Uruguay (October 2012) and likely the first record worldwide of a fish kill attributable to its bloom.

Invasive *C. furcoides* has expanded its distribution to Uruguay, an area previously indicated as having high invasion potential (Meichtry de Zaburlín *et al.* 2016). Lake Blanca basin is not connected to the geographically closest record of this species, the Salto Grande reservoir, 500 km north in the large river Uruguay. Therefore, although *C. furcoides* probably colonized Salto Grande from northern Argentina or Brasil, where it has been extensively recorded (Meichtry de Zaburlín *et al.* 2016) *C. furcoides* likely arrived in Laguna Blanca from south Brazil (State of Rio Grande do Sul) geographically closer and where *C. furcoides* has also been recorded (Cassol *et al.* 2014).

The recording of cysts and adult organisms in the drinking water distribution tank further evidences the dispersal potential of *C. furcoides*. Even though the adult organisms of *C. furcoides* were retained during the potabilization because of their large size (160 µm average linear dimension) and their sensitivity to chlorination, the small-sized (22 µm linear dimension) and more resistant cysts can go through the water purification process and germinate somewhere else. However, all these adult organisms developed from cysts presented deformities, possibly because of their sensitivity to chlorination.
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). *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; Claps & Ardohain 2007; Hart 2007; 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 *et al.* 2006) may provide this species with a high competitive ability under eutrophic conditions. This further indicates that eutrophication promotes suitable conditions to facilitate the invasion of *C. furcoides* in freshwater ecosystems.

Lake Blanca experienced a period of high transparency with low phytoplankton biomass just before the bloom of *C. furcoides* started. The rapid bloom and dominance of *C. furcoides* can be explained by the colonization from the cyst bank in the sediments (Bustamante Gil *et al.* 2012; Hansson *et al.* 1994; Reynolds & Walby 1975), indicating that *C. furcoides* was already present in Lake Blanca before this study although not been registered in pelagic samples. 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, likely due to competitive exclusion by *C. furcoides* (Moreira *et al.* 2015; Rengefors *et al.* 2004; Reynolds 2006). 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, coinciding with previous findings (Matsumura-Tundisi *et al.* 2010; Bustamante Gil *et al.* 2012).

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 low temperatures did not affect its persistence. This finding coincides with previous studies reporting that high temperatures are important during the initial stages to trigger the bloom but are not necessary to maintain the bloom (Meichtry de Zaburlín *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 (Pollingher 1988, Olrik 1994) 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; Meerhoff *et al.* 2007; Morales 2016). In accordance, the zooplankton in Lake Blanca consisted mostly of small taxa, 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; Reynolds 2006).

The bloom of *C. furcoides* can cause different environmental impacts, and fish kills is one of the most drastic consequences. Although we did not evidence fish kills at Lake Blanca, where we recorded the process of emergence and bloom of *C. furcoides*, we observed the fish kill of *P. lineatus* in Lake Puente de las Americas, during the bloom of *C. furcoides*. We found that the gills of *P. lineatus* were affected both by clogging and histopathological lesions due to accumulations of *C. furcoides*. The affectation of the gills may have accentuated the sensitivity of *P. lineatus* to anoxia in the benthic zone promoted by the bloom of *C. furcoides* likely caused the mass mortality by asphyxia of *P. lineatus*. Furthermore, fish death by asphyxia is facilitated by clogged gills with excess mucus production and edema in secondary lamellae caused by **Ceratium** (Onoue 1990) and add to explain mass mortality of aquatic organisms due to anoxic conditions promoted by the genus **Ceratium** (Bazán *et al.* 2007; Mahoney & Steimle 1979; Nicholls *et al.* 1980; Onoue 1990).
The expansion of *C. furcoides* in the subtropical region of South America has accelerated in recent years (Meichtry de Zaburlín *et al.* 2016) and in Uruguay, besides the record in Lake Blanca and Lake Puente de las Americas reported here, *C. furcoides* was recently found in shallow lakes Lake Escondida in 2014 (34°82’ S; 54°62’ W), Lake Sauce in 2016 (34°82’ S; 55°06’ W), in the river Santa Lucia in 2015 (34°30’ S; 56°23’ W) (JP Pacheco unpubl. Data) and the reservoir San Francisco in 2015 (34°39’ S; 55°21’ W) (Meerhoff *et al.* 2017). The rapid spread of *C. furcoides*, facilitated by eutrophic conditions, may entail fish kill as reported for Lake Puente de las Americas in this study. 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 could explain why we did not register fish kills in the shallow Lake Blanca.

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. This is particularly needed for genera holding invasive species as these may otherwise spread unnoticed. The spread of *C. furcoides* in Uruguay may have been a silent invasion due to difficulties in distinguishing this species from *C. hirundinella*. Improving phytoplankton biomonitoring programs allows to act proactively and avoid environmental consequences of the blooms as the massive fish kill reported in this study.

**Declarations**

**Acknowledgments**: This study was supported by Aarhus University, Sino-Danish Center, the University of the Chinese Academy of Sciences and the University of the Republic, Uruguay. E.J. is also supported by the TÜBITAK, BIDEB 2232 program (118C250). The research leading to the results of Lake Blanca received funding from the project ANII-FCE (2009-2749) and of Lake Puente de las Americas from PEDCA – CURE program, Canelones Commune. We thank Dr. Anne Mette Poulsen for manuscript editing, and to Nicolás Vidal, Anahí López Rodríguez, Lucía Gaucher and Paula Levrini for their valuable field assistance.

**Funding**: This study was supported by Aarhus University, Sino-Danish Center, the University of the Chinese Academy of Sciences and the University of the Republic, Uruguay. E.J. is also supported by the TÜBITAK, BIDEB 2232 program (118C250). The research leading to the results of Lake Blanca received funding from the project ANII-FCE (2009-2749) and of Lake Puente de las Americas from PEDCA – CURE program, Canelones Commune.

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

**Availability of data and material**: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

**Code availability**: not applicable

**Authors contributions**: Juan Pablo Pacheco: conceptualization, methodology, formal analysis, investigation, data curation, writing - original draft, Carlos Iglesias: investigation, writing - review & editing, Guillermo Goyenola: funding acquisition, investigation, writing - review & editing, Franco Teixeira de Mello: investigation, writing - review & editing, Claudia Fosalba: investigation, writing - review & editing, Annette Baattrup-Pedersen: writing - review & editing, supervision Mariana Meerhoff: funding acquisition, investigation, writing - review & editing, Erik Jeppesen: funding acquisition, writing - review & editing, supervision.

**Ethics approvals**: not applicable

**Consent to participate**: not applicable
Consent for publication: not applicable

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**Table**

**Table I.** Main physico-chemical characteristics of Lake Blanca during the period May 2011 to October 2013. Temp: water temperature (ºC), Cond: conductivity (µS.cm⁻¹), SD: Secchi disk depth (m), Turb: turbidity (NTU), pH, Alk: alkalinity (mEq.CaCO₃⁻².L⁻¹), DO: dissolved oxygen (mg.L⁻¹), DO %: percentage of dissolved oxygen, Chl_a: chlorophyll a (µg.L⁻¹), TN: total nitrogen (µg.L⁻¹), NO₃: nitrate (µg.L⁻¹), NH₄: ammonia (µg.L⁻¹), TP: total phosphorus (µg.L⁻¹), PO₄: orthophosphate (µg.L⁻¹).

|       | Temp | Cond  | SD  | Turb | pH  | Alk | DO  | DO % | Chl_a | TN   | NO₃ | NH₄ | TP  | PO₄ |
|-------|------|-------|-----|------|-----|-----|-----|------|-------|------|-----|-----|-----|-----|
| Mean  | 18.0 | 338.2 | 0.9 | 7.0  | 8.0 | 91.0| 9.1 | 94.3 | 1.84  | 1078 | 112 | 24  | 52  | 15  |
| Max   | 28.4 | 380.0 | 1.7 | 20.1 | 9.0 | 140 | 11.5| 141.5| 6.17  | 3015 | 348 | 133 | 77  | 39  |
| Min   | 8.7  | 286.0 | 0.2 | 2.4  | 7.4 | 64  | 5.6 | 67.0 | 0.17  | 644  | 26  | 5   | 19  | 1   |

**Figures**

**Figure 1**

Ceratium furcoides from Lake Blanca, Uruguay in 2012. Ventral views before (left) and after (right) being treated with NaClO 20% to separate the cell wall plates. Arrows indicate the 4’ plate not reaching the apex of the apical horn.
Figure 2

Light and nutrients in Lake Blanca for the period May 2011 – October 2013. Turbidity and transparency as Secchi disk depth (upper panel) total nitrogen (TN), nitrate (NO3) and ammonia (NH4) (central panel), total phosphorus and orthophosphate (lower panel).
Figure 3

Temporal dynamics of phytoplankton groups as biovolume, total chlorophyll-a (blue area) (upper panel) and maximum maintained wind speed (> 3 hours) (lower panel) in Lake Blanca for the period July 2010 – October 2013. Note that dinoflagellates (Dinophyceae) in the upper plot, correspond almost exclusively to C. furcoides. The blue horizontal line in the lower panel represents the average maximum wind speed and the dashed red line represents the 99% upper quartile of extreme wind events.
Figure 4

Temporal variation of dinoflagellates C. furcoides, C. hirundinella and Peridinium sp. biovolume before and during the bloom of C. furcoides in Lake Blanca. Note the biovolume data in the x-axis is expressed in Log of biomass (µm3.L-1) to represent together the extremely different values among species.
Figure 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% \( \lambda_1 = 45.3\% \), \( \lambda_2 = 14.5\% \) (59.8%).

Figure 6

Ceratium furcoides during the bloom in Lake Blanca in 2012-2013. Top panel: normal appearance of C. furcoides (left) and one organism with the cyst formed inside the cell wall (black arrow). 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 antiapicals (c, d).
Figure 7

Dissolved oxygen concentration and oxygen saturation in-depth in Puente de las Americas Lake, Uruguay from June to September 2016.

Figure 8

Prochilodus lineatus (Valenciennes, 1837) gills during the bloom of Ceratium furcoides (Levander) Langhans 1925 in Puente de las Americas Lake, Uruguay, on August 29th, 2016. Left: general appearance of the gills with dark accumulations of C. furcoides clogging the gill filaments. Center: zoom to the C. furcoides accumulations. Right: C. furcoides cell stuck in the gill tissue. Scale bar= 50µm.

Figure 9

Gills of P. lineatus after the collapse of the bloom of C. furcoides in Puente de las Americas Lake, Uruguay, on September 22th, 2016. Upper panels: general view of the gills at 3 and 8 X. Lower panels: sediments and phytoplankton found in the gills at 40 X.