


## Spreading of the invasive dinoflagellate *Ceratium furcoides* (Levander) Langhans throughout the Paraíba do Sul ecoregion, South America, Brazil

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### ABSTRACT

#### Spreading of the invasive dinoflagellate *Ceratium furcoides* (Levander) Langhans across Paraíba do Sul ecoregion, South America, Brazil: reservoirs on warning

The proliferation of the freshwater dinoflagellate *Ceratium furcoides* (Levander) continues to escalate within South America. Early detection and the subsequent monitoring of this non-indigenous species are essential mitigation policies in the basins at potential risk. A combination of these policies with a better understanding of the dinoflagellate's environmental habitat would thus, assist in reducing possible impacts on the highly diverse aquatic biodiversity of this region. The invasive dinoflagellate can now be found in the tropical reservoirs of three hydroelectric power plants, which extends its presence over a distance of ~500 km along the Paraíba do Sul eco-region in southeastern Brazil. Less than favorable water management strategies between river basins have probably accelerated this expansion. Water residence time has also most likely influenced the presence and abundance of *C. furcoides*. The smallest recorded size of *C. furcoides* reported in the literature (51-68 µm length, 14-16 µm width) was detected in the reservoir with the lowest water residence time, this indicates a probable adaptation of this invader to water current. The variety of environmental conditions in which *C. furcoides* was found reinforces the assumption that it is a highly eurytopic species. Despite there being no evidence of blooms, the invasiveness of *C. furcoides* suggests that other nearby aquatic systems throughout Paraíba do Sul and Guandu river basins may indeed already harbor populations of *C. furcoides*. This scenario heightens the urgency to formulate a monitoring program with an integrated and predictive approach on a regional scale as millions of people depend economically upon these river systems and importantly, for water supply.

**Key words:** aquatic invasion, dinoflagellate, reservoirs, plasticity, water residence time

### RESUMO

#### Expansão do dinoflagelado invasor *Ceratium furcoides* (Levander) Langhans sobre a ecorregião Paraíba do Sul, América do Sul, Brasil: reservatórios em alerta

A distribuição não nativa de *Ceratium furcoides* está se expandindo na América do Sul. A detecção precoce e o rastreamento desse dinoflagelado bem como o aprimoramento do conhecimento sobre seus requisitos ambientais são essenciais estratégias de

mitigação em bacias potencialmente ameaçadas. Tais ações de mitigação, combinadas ao conhecimento dos requisitos ambientais desse dinoflagelado, podem auxiliar na redução de possíveis impactos à biodiversidade aquática, altamente diversificada, desta região. Este dinoflagelado invasor alcançou três reservatórios tropicais, estendendo sua ocorrência por mais de 500 km ao longo da ecorregião Paraíba do Sul, no sudeste do Brasil. O gerenciamento artificial entre bacias hidrográficas pode ter acelerado a expansão da distribuição na região. O tempo de residência da água provavelmente exerce um importante papel influenciando a presença e a abundância de *C. furcoides*. O menor comprimento de *C. furcoides* relatado na literatura (51-68 µm e 14-16 µm, respectivamente para comprimento e largura) foi detectado no reservatório com o menor tempo de residência, indicando uma provável adaptação desse invasor à ambientes mais lóticos. A variedade de condições ambientais em que *C. furcoides* foi encontrado o reforça como uma espécie altamente euritópica. Apesar de não haver evidências de florações, a capacidade de dispersão de *C. furcoides* permitem prever que outros sistemas aquáticos nas proximidades das bacias dos rios Paraíba do Sul e Guandu já possam abrigar populações de *C. furcoides*. Esse cenário suscita preocupação em escala regional, uma vez que diversas atividades econômicas e abastecimento de água para milhões de pessoas dependem desse sistema de rios.

**Palavras chave:** *invasão aquática, dinoflagelados, reservatórios, plasticidade, tempo de residência*

## INTRODUCTION

Invasive species pose a continued threat to freshwater biodiversity especially in those dedicated human modified ecosystems, such as reservoirs (Johnson *et al.*, 2008). These artificial systems prove to be more prone to biological invasion and often act as “stepping-stones” for the proliferation of invasive species (Havel *et al.*, 2005a). In particular, the structure of plankton assemblages in recently impounded waterways indicate strong shifts favored by an increase in water retention time, temperature and transparency (Branco *et al.*, 2019). Furthermore, several planktonic species could quickly invade new habitats (Shurin, 2000) by responding to high ecological plasticity due to features such as high rates of reproduction and adaptability (Litvinchuk *et al.*, 2001), asexual reproduction; thus resulting in colonization from either a single or a few individuals (Dodson & Frey, 2001) and further to this, under propagule pressure, as resting eggs and cysts permit planktonic organisms to exploit a number of potential dispersal vectors (Havel & Shurin, 2004; Genitsaris *et al.*, 2011).

Moreover, the number of established non-native species is much higher in the tropics than in temperate zones (Sax, 2001) which has now also increased emerging threats to freshwater biodiversity (Reid *et al.*, 2019). In tropical regions such as Latin America and the Caribbean, those freshwater ecosystems that harbor a rich and unique biodiversity must currently contend with severe multiple

threats of widespread damming, mining, agriculture, overfishing, contamination, aquaculture, climate change and the introduction of alien species (UNEP, 2010). As man-made infrastructure, water impoundments are constructed for multiple purposes such as water supply and hydropower generation. This also produces a flow-on effect thus influencing ecohydrological dynamics such as fish migration, river flow, riverine habitats, and the proliferation of alien species along river basins (Freeman *et al.*, 2002; Liermann *et al.*, 2012; Xiong *et al.*, 2018). The sum of such various threats could indeed magnify a series of negative effects on aquatic ecosystems. Contained within this list of prospective threats is the rise in number of dams projected for construction in the near future (Anderson *et al.*, 2018; Pereira *et al.*, 2017).

Surprisingly, microorganisms are seldom recorded as invasive, in comparison to macroscopic organism, this due to difficulties in detection and accurate identification (Lebret *et al.*, 2013). In relation to small planktonic species, to detect novel populations does require considerable numerical density; as such, their detection suggests some effective dispersal or colonization. Among freshwater phytoplankton, the diatom *Didymosphenia geminate* Lyngbye, the cyanobacteria *Raphidiopsis (Cylindrospermopsis) raciborskii* Woloszynska and *Aphanizomenon (Chrysochlorum) ovalisporum* Forti, and the dinoflagellate *Ceratium furcoides* Levander are recognized as key examples of invasive species (Costa *et al.*, 2017; Crossetti *et al.*, 2019).

Several authors have documented (Mac Donagh *et al.*, 2005; Boltovskoy *et al.*, 2013; Cavalcante *et al.*, 2013; Crossetti *et al.*, 2019; Roriz *et al.*, 2019), the recent invasion by species of the genus *Ceratium* into South America. Originally recorded in European lakes, *Ceratium furcoides* Levander (Langhans 1925) is now acknowledged as a global invasive species over a broad-spectrum of latitudinal and longitudinal range, from England down to New Zealand and from Korea across to Canada (Meichtry-de-Zaburlin *et al.*, 2016; Silva *et al.*, 2012; Silva *et al.*, 2018). During the last decade *C. furcoides* has been spreading rapidly across the South American continent: Argentina (Meichtry-de-Zaburlin *et al.*, 2014), Bolivia (Morales, 2016), Colombia (Ramírez-R *et al.*, 2005; Bustamante Gil *et al.*, 2012), Chile (Almanza *et al.*, 2016), Paraguay (Meichtry-de-Zaburlin *et al.*, 2014), Uruguay (Meichtry-de-Zaburlin *et al.*, 2016;), and Brazil (Santos-Wisniewski *et al.*, 2007; Cavalcante *et al.*, 2013; Cassol *et al.*, 2014; Moreira *et al.*, 2015; Roriz *et al.*, 2019; this study). All of the above countries were considered to be equally susceptible to invasion by *C. furcoides* (Meichtry-de-Zaburlin *et al.*, 2016).

Whilst non toxic, *Ceratium* spp. can impair water quality (Matsumura-Tundisi *et al.*, 2010) and produce difficulties for water treatment, reducing coagulation, sedimentation and increase clogging (Van Ginkel *et al.*, 2001; Ewerts *et al.*, 2014). A bloom of *C. furcoides* has recently been associated to a mass fish kill in a Bolivian reservoir (Morales, 2016). According to the author, the fish kill was caused by the reduction of available oxygen either associated to a decomposition of the biomass after *C. furcoides*' population collapse or due to night breathing by a large number of this dinoflagellate. Thus, it becomes essential to detect and better understand the distribution patterns of *C. furcoides* within South America with much more awareness of its ecology and environment requirements in order to mitigate any possible impact on this continent's highly diverse aquatic biodiversity.

Provided herein are new occurrences of *Ceratium furcoides* in a suite of connected reservoirs of different limnological features across the Paraíba do Sul ecoregion. The major morphologi-

cal features related to species taxonomic identification and plasticity are briefly addressed.

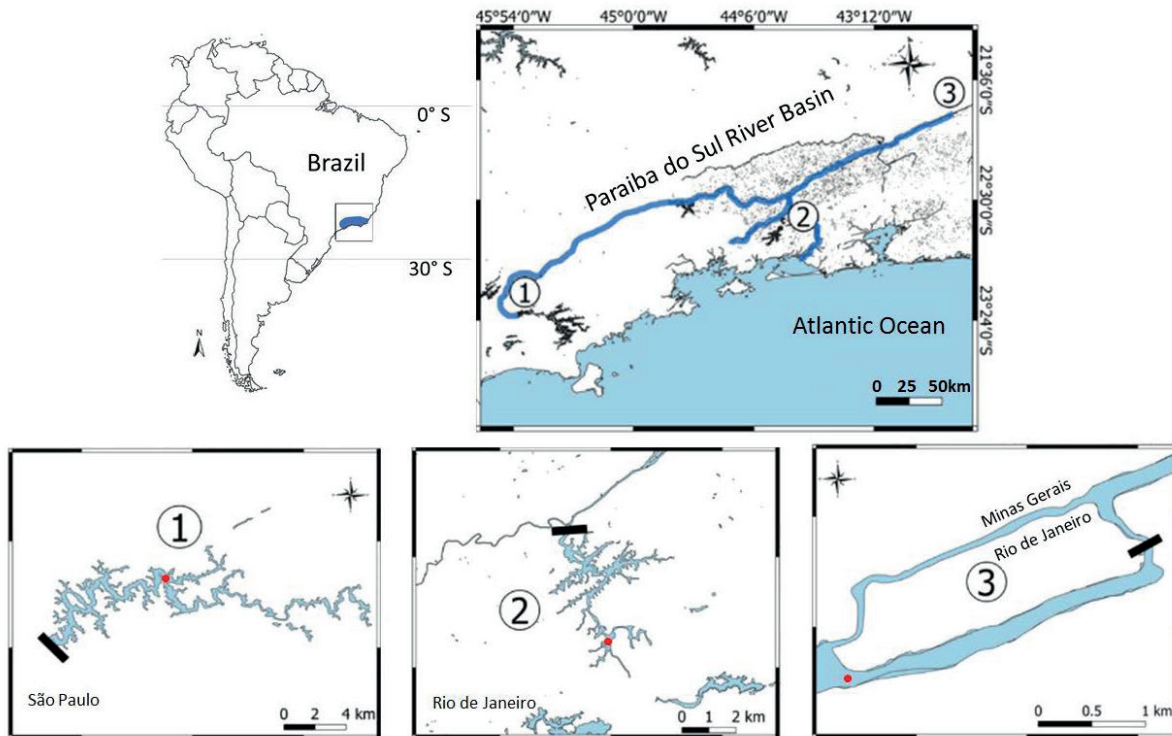
## MATERIAL AND METHODS

### Study area

This study was conducted in three reservoirs of the Paraíba do Sul River Basin, which encompasses portions of the states of Minas Gerais, São Paulo and Rio de Janeiro, totaling an area of 57 000 km<sup>2</sup>. Paraíba do Sul is the principal river in the Southeast Atlantic Hydrographic province and is largely dammed along its course. Section of its waterflow has been diverted through a set of pumped-storage reservoirs to increase water provision of the Guandu River basin, which services agricultural and industrial activity, hydropower generation, as well as domestic supply for a population of 14.2 million people (CEIVAP, 2020), including the second largest metropolitan region of Brazil (Rio de Janeiro). Santa Branca Reservoir (SBR) is in the upper stretch of the Paraíba do Sul River, very near to the Paraibuna Reservoir, being the upstream and largest dam within this river. Ilha dos Pombos Reservoir (IPO) is situated between the middle-lower and lower reaches of Paraíba do Sul River, after the water diversion to the Guandu River. Despite sharing the same river, the SBR and IPO reservoirs are approximately 450 km apart. Vigário (VIG), being the third reservoir in our study, receives water diverted from the Paraíba do Sul River, which connects this last river to the Guandu River Basin (Fig. 1). VIG Reservoir as such is, geographically located between the SBR (~218 km apart) and the IPO (~159 km) reservoirs. The SBR Reservoir presents the largest surface area (27.2 km<sup>2</sup>) and water retention time (62 days). Both the VIG and the IPO reservoir are smaller and with lower retention time, being, 3.3 and 4.26 km<sup>2</sup>, and 2.0 and 0.2 days, respectively.

### Sampling and laboratory analysis

Quantitative plankton samples and environmental variables were collected from surface layers at the three reservoirs during summer (December)



**Figure 1.** Map showing the Paraíba do Sul River Basin in southeast Brazil and the studied reservoirs from the upstream Santa Branca, the middle-positioned Vigário Reservoir that receives diverted waters and the downstream Ilha dos Pombos Reservoir. Red dots depict sampling sites where *C. furcoides* were found. Black lines represent dams. Coordinates where *C. furcoides* were found: (1) SBR 23° 20' 03" S, 45° 47' 48" W; (2) VIG 22° 40' 13" S, 43° 52' 51" W and (3) IPO 21° 51' 16.4" S, 42° 36' 23.6" W. *Mapa mostrando a Bacia do Rio Paraíba do Sul no sudeste brasileiro e cada reservatório, de mais a montante (Santa Branca), o intermediário Vigário que recebe águas transpostas, e o mais a jusante Ilha dos Pombos. Em vermelho, os pontos onde Ceratium furcoides foi encontrado. Barras pretas representam as barragens dos reservatórios. Pontos vermelhos representam locais onde C. furcoides foi encontrado: (1) SBR 23° 20' 03" S, 45° 47' 48" O; (2) VIG 22° 40' 13" S, 43° 52' 51" O and (3) IPO 21° 51' 16.4" S, 42° 36' 23.6" O.*

and winter (July), from 2011 to 2014. In addition, qualitative plankton samples were taken by vertical hauls along the euphotic layer using a plankton net of 68  $\mu\text{m}$  mesh and 20 cm diameter. The euphotic layer depth was estimated as Secchi depth multiplied by 2.7 in accordance with Esteves (2011). The number of sampling stations varied according to area size of reservoir being four from the SBR Reservoir, three from VIG and two from IPO. Physical and chemical variables (water temperature, dissolved oxygen, electrical conductivity and pH) were measured *in situ* with a YSI®85 multiparameter probe. Chlorophyll-*a* was determined by extraction in heated (70-75 °C) 90 % ethanol - following Nusch & Palme (1975). Water transparency was measured by the Secchi

disk depth and turbidity by the INSTRUTHERM TD300 turbidimeter. Collected water samples were filtered through Whatman GF/C filters and then frozen for total alkalinity and dissolved nutrient concentrations analysis in accordance with APHA (2005). Plankton samples were immediately fixed with Lugol-acetic acid. Phytoplankton species counts conformed to Utermöhl (1958) by applying an inverted microscope Axiovert 10 (Zeiss Oberkochen) with 400 $\times$  magnification. Cells were enumerated, for at least 100 specimens of the most frequent taxa (Lund *et al.*, 1958). Biomass was estimated by employing specific biovolume calculations in line with Rocha & Duncan (1985). Specific biovolume was estimated from the product of abundance and

each species mean cell volume. The population carbon content was estimated by multiplying the population density and the mean carbon content of *C. furcoides*.

**Data analysis**

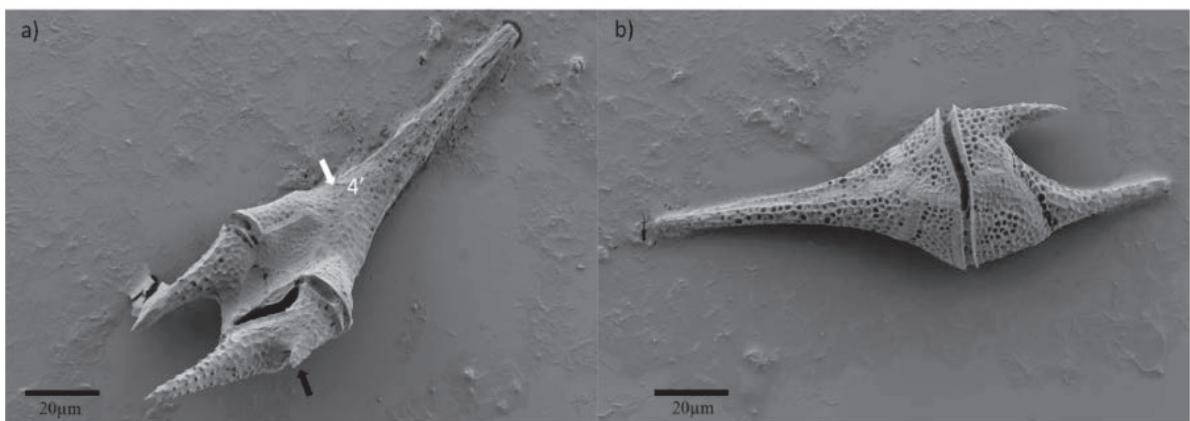
Morphological measurements of *C. furcoides* were taken from qualitative samples. Cell length and width were expressed as total mean, minimum and maximum values (N = 21) and compared between reservoirs via analysis of variance (ANOVA). *Ceratium* specimens were photographed under a Scanning Electron Microscopy AURIGA 40 - ZEISS (Work distance = 4.4 mm and 1.55 K $\times$  magnification) to avoid misidentification. Toledo's (1983) Trophic State Index (TSI) was applied to estimate the degree of eutrophication within each reservoir. Water temperature, dissolved oxygen (DO), alkalinity (Alk), turbidity, electric conductivity (Cond), nitrite, total phosphorus (TP), chlorophyll-*a* and pH were included in this analysis.

**RESULTS**

Populations of *Ceratium furcoides* were found for the first time in winter samples, concurrently in the three reservoirs of the Paraíba do Sul River.

Electron microscopic photographs (Fig. 2) confirmed the identification of *Ceratium furcoides*, as plate 4'' never extends to the apex in this species (Hickel, 1988; Moestrup & Calado, 2018), being the main morphological distinctiveness between this species and *C. hirundinella*. In the SBR Reservoir, the invader was also detected in the winters of 2011 and 2013 and in the summer of 2014 in a single sampling point while in VIG and IPO it was only discovered in 2011 and then went undetected in subsequent years.

Populations of *Ceratium furcoides* inhabit across a broad range of water temperature, dissolved oxygen, pH, turbidity, nitrate and total phosphorus (Table 1). In all reservoirs *C. furcoides* were detected in sites afar from the dam and displaying low densities (from 26 to 63 ind/mL). Although no blooms of this dinoflagellate were uncovered during the study period, a significant variation of *C. furcoides* contribution to total phytoplankton biomass - along a duration of time - was noted in the SBR Reservoir. The contribution of *C. furcoides* to the total phytoplankton biomass in this reservoir varied from 8.9 % in the winter of 2011 to 81.9 % within the same season in 2012. In the VIG Reservoir, *C. furcoides* accounted for 1.5 % of total phytoplankton biomass, whereas in the IPO, *C. furcoides* constituted 19.6 % of total biomass.



**Figure 2.** Electromicrography (SEM) of *Ceratium furcoides* from Santa Branca Reservoir: a) Ventral view showing Plate 4' (white arrow), with the third antapical horn (black arrow) - phenotypic plasticity; b) Dorsal view. Scale bars = 20  $\mu$ m. *Eletromicrografia (MEV) do Ceratium furcoides coletado no Reservatório de Santa Branca: a) Vista ventral mostrando a 4ª placa (seta branca), com o terceiro chifre anti-apical (seta preta) – suposta plasticidade fenotípica; b) Vista dorsal. Barra de escala = 20 $\mu$ m.*

**Table 1.** Mean values of limnological variables and trophic state of the sites where *C. furcoides* was found. Trophic state classifications according to Toledo *et al.* (1983): Oligotrophic  $24 < TSI \leq 44$ , Mesotrophic  $44 < TSI \leq 54$ , Eutrophic  $54 < TSI \leq 74$ , and Hypereutrophic  $TSI > 74$ . Relative biomass  $\mu\text{g C/l}$  (%) by major phytoplankton systematic groups and total density for the sampling sites and year where *Ceratium furcoides* were found. *Valores médios das variáveis limnológicas e estado trófico dos pontos onde Ceratium furcoides foi amostrado. Classificação trófica segundo Toledo et al. (1983): Oligotrófico  $24 < TSI \leq 44$ , Mesotrófico  $44 < TSI \leq 54$ , Eutrófico  $54 < TSI \leq 74$ , e Hipereutrófico  $TSI > 74$ . Biomassa relativa  $\mu\text{g C/l}$  (%) por grandes grupos sistemáticos do fitoplâncton e densidade total por ponto e ano onde Ceratium furcoides foi encontrado.*

Variables	SBR (2011)	SBR (2013)	SBR (2014)	VIG (2011)	IPO (2011)
	winter	winter	summer	winter	winter
Temperature (°C)	19.6	20.8	30.24	21.5	20.3
Dissolved oxygen (mg/l)	6.89	5.43	8.55	3.2	6.83
Conductivity ( $\mu\text{S/cm}$ )	29.2	31.5	45	81.5	57
Turbidity (NTU)	2.2	1.56	2.2	6.92	8.96
Water transparency (m)	2.75	3.30	1.60	1.25	1.5
pH	5.6	6.79	8.99	6.5	7.9
Orthophosphate (mg/l)	0.02	0	0.01	0.04	0.04
Total phosphorus (mg/l)	0.03	0.03	0.02	0.07	0.08
Ammonium (mg/l)	0.01	0	0.02	0.13	0.01
Nitrite (mg/l)	0.02	0	0.03	0.12	0.1
Nitrate (mg/l)	0.17	0.89	0.35	4.37	6.47
Chlorophyll- <i>a</i> ( $\mu\text{g/l}$ )	1.48	0.65	1.6	0.74	0.74
Trophic State Index	40.39	30.95	40.31	51.65	52.28
Mean euphotic zone (m)	8.1	8.9	4.3	2.02	3.4
Relative biomass $\mu\text{gC/l}$ (%)	8.9	81.9	38	1.5	19.5
Density (ind/ml)	63	52	30	26	36

Whilst downstream from the SBR, we found a gradient of increasing turbidity and high concentrations of nitrate and total phosphorus. As a result, samples from the VIG and IPO reservoirs mostly correlated to high values of turbidity, and nutrient concentrations. Samples in which cells had been detected also corresponded with a wide range of pH and dissolved oxygen. The SBR Reservoir was mostly associated to the greatest multiple variation, which also presented separate samples from different seasons and years. These findings revealed the large environmental variability among the conditions in which this species inhabited.

Increases in turbidity and nutrient content in the VIG and IPO reservoirs confirmed the gradient of eutrophication from upstream to downstream Paraíba do Sul River, to include the Trophic State Index (TSI). Nitrogen content recorded more significant degree of difference from upstream reservoir to downstream. According to the TSI, the SBR Reservoir was recognized

as being oligotrophic while the two other reservoirs were mesotrophic.

Cell length and width differed significantly among reservoirs ( $df = 20$ ,  $F = 35.99$ ,  $p = 0.0004$ ;  $df = 20$ ,  $F = 17.79$ ,  $p = 0.003$ ) decreasing from the SBR and VIG reservoirs to the IPO Reservoir (Table 2).

## DISCUSSION

The pervasiveness of *C. furcoides* from the Paraná River basin (linked to the Del Plata basin) to Paraíba do Sul River follows the species expected route north, as detailed by Meichtry-de-Zaburlín *et al.* (2016) and Silva *et al.* (2018). However, water management strategies that link systems and river basins may exacerbate and further accelerate this species proliferation. We detected the dinoflagellate possibly migrating downstream from one river basin (Paraíba do Sul River) to another (Guandu River) via artificial water diversion, which can easily

**Table 2.** *Ceratium furcoides* measurements of body length and width, expressed as total mean, minimum and maximum values for Santa Branca (SBR), Vigário (VIG) and Ilha dos Pombos (IPO) reservoirs. N = 30, 21 and 21, respectively. *Medidas de comprimento e largura corporal de Ceratium furcoides expressas pelos valores médio, mínimo e máximo para os reservatórios de Santa Branca (SBR), Vigário (VIG) e Ilha dos Pombos (IPO). N = 30, 21 e 21, respectivamente.*

Length (µm)	mean	minimum	maximum
SBR	178	149	208
VIG	197	174	214
IPO	62	51	68
Width (µm)	mean	minimum	maximum
SBR	50	44	57
VIG	43	33	55
IPO	16	14	18

facilitate the spread of non-native species by the connecting hydrographic basins (Anderson *et al.*, 2006; Zhan *et al.*, 2015; Daga *et al.*, 2020). Likewise, Nishimura *et al.* (2015) previously reported the migration of *C. furcoides* from one reservoir to another (Billings to Guarapiranga Reservoir, Paraná River Basin) as a result of the artificial management of water for domestic supply. Moreno-Ostos *et al.* (2007) also reported the downstream transfer of *C. hirundinella* by way of a system of reservoirs. The most extensive invasion of *C. furcoides* resulting from water transfers was recently reported in northeastern Brazil where water from the São Francisco Basin was diverted to a northern river basin. *Ceratium furcoides* drifted via water transposition along the total stretch of waterway and then coursed into associated reservoirs (Mendes *et al.*, 2018).

By herein updating new records of this pervasive dinoflagellate within tropical freshwaters (Silva *et al.*, 2018; Roriz *et al.*, 2019), we provided a snapshot of simultaneous occurrence in three long-distant interconnected reservoirs. Within the present study, *C. furcoides* proved to be more prevalent in the SBR Reservoir, being ever present in the winter months of 2011 and 2013 and, again in the summer of 2014. It was not the case that *C. furcoides* spread throughout this entire system, being only recorded afar from the

dam (Fig. 1), thus, in agreement with the studies of Cassol *et al.* (2014) and Silva *et al.* (2012) who discovered that in other tropical reservoirs, the highest cell concentrations were located as distance increased from the dam. Spatial variability in nutrient distribution within reservoirs appear to be related to the presence and abundance of *Ceratium*. Meichtry-de-Zaburlín *et al.* (2014) in Yacyretá Reservoir (Argentina-Paraguay) and Roriz *et al.* (2019) in Paranoá Reservoir (Midwest Brazil) verified a greater abundance of *C. furcoides* nearer to tributaries, feeding off nutrient inputs from human activities such as urbanization, agriculture and industry. The low densities and no evidence of blooms (Table 1) were comparable to the results of Nishimura *et al.* (2015) in the Billings Reservoir.

The unique occurrence of *C. furcoides* in the winter of 2011 in the VIG and IPO suggests the nomadic nature of this species in such systems that provide favorable mesotrophic conditions but a low water retention time. By right, typical large-celled organisms such as *Ceratium* with a long cell cycle and low rate of cell division (Bellingier & Sigee, 2010), should not find suitability in environments with low water retention time. The influence of this hydrological variable on *C. furcoides* was reported by Cassol *et al.* (2017) in the Itaúba Reservoir in southern Brazil. According to the authors, an increase in retention time favored the proliferation of this species.

Despite the possible limitations as mentioned above, the low mean abundance (26-63 ind/mL) found in the three reservoirs (Table 1) were comparable to those previously reported in other South American tropical mesotrophic reservoirs. In the first record from the Furnas Reservoir, as reported by Santos-Wisniewski *et al.* (2007), the species attained a maximum mean density of 12 ind/mL and following up some years after, within the very same reservoir Silva *et al.* (2012) recorded mean density up to 28 ind/mL. In the Paranoá Reservoir, Roriz *et al.* (2019) documented abundances between 6 and 45 ind/mL. Greater abundances (between 62-103 ind/mL) were reported by Bustamante-Gil *et al.* (2012) in the reservoir Riogrande II, Colombia, and by Silva *et al.* (2018) (39-137 ind/mL) in the João Leite Reservoir, Midwest Brazil. Conditions of bloom

(>1000 ind/mL) was reported by Matsumura-Tundisi *et al.* (2010) in the Billings Reservoir during the winter (21 455 ind/mL), and by Silva *et al.* (2018) in the Corumbá Reservoir (up to 2050 ind/mL). Blooms were also discovered in South-American sub-tropical reservoirs such as in the eutrophic Maestra Reservoir (2680 ind/mL) and in the meso-eutrophic Faxinal Reservoir (2819 ind/mL) by Cavalcante *et al.* (2016), and in the Itaúba Reservoir (up to 2036 ind/mL) by Cassol *et al.* (2014).

Spreading of *C. furcoides* in South American reservoirs have been linked to several factors. Proliferation of *C. furcoides* have been broadly associated to: the increase of nutrient content (Silva *et al.*, 2012; Bustamante-Gil *et al.*, 2012; Meichtry-de-Zaburlin *et al.*, 2014; Morales, 2016; Crossetti *et al.*, 2019), water column stability (Bustamante-Gil *et al.*, 2012; Meichtry-de-Zaburlin *et al.*, 2014;), a combination of optimal conditions of temperature (up to 25 °C), organic matter, and pH (Cavalcante *et al.*, 2016; Cassol *et al.*, 2017), high dissolved oxygen (Roriz *et al.*, 2019). The eurytopic features were again evident by the presence of warm water in the SBR Reservoir (30.2 °C), and by the wide ranging variability in environmental conditions in which this species appeared to thrive within the three reservoirs (Table 1).

Whilst possessing vertical migration ability, which is an important adaptive behavior for nutrient intake through varying layers of the water column, *C. furcoides* presents several features that go somehow in explaining its proliferation. The cyst formation (Pollinger, 1988), which is a result of sexual reproduction (Hickel, 1988) also increases dispersion rates of *Ceratium* (Donagh *et al.*, 2005). Phagotrophic ability and mixotrophic nutrition, plus the development of horns (proposed defensive structures) all contribute to lowering grazing pressure by zooplankton (Ginkel *et al.*, 2005). Furthermore, morphological plasticity can likewise be related to eurytopic features. Variation in size of *C. furcoides* over periods of time have already been detected in South American reservoirs, this such as seasonal cell-size variation (Cavalcante *et al.*, 2018; Roriz *et al.*, 2019) and smaller individuals (length between 118-315 µm) during blooms (Almanza *et al.*,

2016). The broad morphometric variation in *Ceratium* has been considered an adaptive trait for environmental filtering, especially when dealing with changes in water temperature (Lindström, 1992; Cavalcante *et al.*, 2016), but also the case with biotic pressures (e.g. herbivory) and resistance to mechanical damage (Bertolo *et al.*, 2010). In addition to variation in size, *C. furcoides* morphological plasticity can also be related to variation in the number of horns (the third atypical horn identified as being in the first stages in figure 2), this generally associated to seasonal environmental changes and abundance of the population (Lindström, 1992; Almanza *et al.*, 2016).

Size and form selection are perhaps the strongest driving forces shaping phytoplankton assemblages under variable environmental conditions (Morabito *et al.*, 2007). Dynamic aquatic environments support a large diversity of different sizes and shapes of species either present in the assemblages or as propagules “ready to develop” as the environmental template changes (Padisák, 1992). The difference in *C. furcoides* cell size across the reservoirs reported in this study might be related to adaptation to water current, as smaller individuals were found in the IPO Reservoir. This more hydrodynamic and eutrophic system presented the smaller cell sizes (length between 51-68 µm), not only comparable to the SBR and VIG reservoirs but overall in similar data available within the literature of Brazilian freshwaters (Oliveira *et al.*, 2011; Cassol *et al.*, 2014; Moreira *et al.*, 2015). Considering the short retention time of the IPO reservoir (0.2 days), it can be suggested that the dinoflagellate population primarily venture from the Paraíba do Sul River. Being of small size, in tandem with an adaptation to mechanical damage due to water current, could well be a resource-saving strategy to population maintenance and propagule density increase until arriving at a more favorable environment (Hutchinson, 1967; Raven, 1998; Cavalcante *et al.*, 2016; Sharma & Rai, 2011). Moreover, under a river-flowing condition, size may not prove an important factor in avoiding predation.

Blooms of *Ceratium* species have been directly related to multiple negative effects ranging from fish-kill through gill clogging and oxygen



depletion in the water column (Smayda, 1997; Matsumura-Tundisi *et al.*, 2010) to foul-tasting and odor in drinking waters (Ewerts *et al.*, 2013). This scenario requires concern on a regional scale as both economic activity and the domestic water supply for millions of people depend on these river systems. The extensive monitoring of eutrophic reservoirs within this system, e.g. the Funil Reservoir in Paraíba do Sul mainstream, must have non-detection status upgraded and currently revised, this should include an improvement in sampling techniques by deep sampling resulting from *Ceratium* ability to migrate into the water column. Furthermore, within this context of effective monitoring, fluctuations in trophic and hydrological conditions or, in retention time due to expected rainfall variation - the result of climate change - presents a possible “window of opportunity” for populations of *C. furcoides* to further proliferate (Matsumura-Tundisi *et al.*, 2010; Crossetti *et al.*, 2019). In view of the fact that these reservoirs are included in monitoring programs overseen by environmental control agencies, in the recognition of multi-purpose priority of these waters (CETESB, 2020; INEA, 2020), this presents as a recent invasion. However, up until this point in time, there is no occurrence of *Ceratium* bloom.

## CONCLUSION

Herein, more than solely documenting for the first time the expansion of the dinoflagellate *Ceratium furcoides* within two economically important river basins in Brazil's Paraíba do Sul ecoregion, our study additionally highlights the importance of monitoring tropical systems greatly impacted by human activity from which can further enhance the risk of biological invasion (Johnson *et al.*, 2008). From scrutinizing the eurytopic features and dispersal ability of *C. furcoides*, we can forecast that other nearby systems throughout Paraíba do Sul and Guandu river basins, including reservoirs and small lakes are potential grounds for the proliferation of *C. furcoides*. Future studies are recommended to focus on the relationships among *C. furcoides* populations features in Brazilian reservoirs, in order to understand the expansion success of this species.

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