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Biological Invasion in Rio Grande Do Sul:
Monitoring *Ceratium furcoides* (Levander) Langhans, its drivers, and Ecological interactions in a high-altitude subtropical reservoir in Brazil.

Dissertação no âmbito do Mestrado em Ecologia,
orientada pelo Professor Doutor Leonel Pereira dos Reis Tomás Pereira
e pela Professora Doutora Luciana Cardoso,
apresentada ao Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia
da Universidade de Coimbra.

Setembro de 2019

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ABSTRACT

Ceratium furcoides (Levander) Langhans is a phytoplankton species invasive in Brazilian freshwaters, associated with ecological impacts affecting the water quality and local aquatic community. This study explored the interactions between phytoplankton species during the invasion of *Ceratium furcoides* and the drivers (meteorological, physical, and chemical variables) contributing to its dominance and blooms in a subtropical high-altitude reservoir (Marrecas, Southern Brazil). The monitoring program was implemented weekly to monthly since 2014 (n=116), depending on the cyanobacteria density. Descriptive, hypothesis tests, correlations, and multivariate statistics (PCA and CCA) were employed to understand the temporal (seasonal and interannual) distribution patterns of the phytoplankton community and the environmental variables. During the study, *Ceratium furcoides* (Miozoa) avoided summers and preferred springs (southern hemisphere), displaying in October of 2014 the highest density ever reported (15,865 ind.mL^{-1}). It showed positive correlation with iron, manganese, and turbidity evidencing its dependency on the mixing period which resuspends its cysts from the bottom, activating them with the light and high temperatures of the epilimnion/surface (optimal temperature for the species during spring). *Chroomonas*, *Cryptomonas* (Cryptophyta), *Discostella* (Bacillariophyta), and after 2016 also *Chlamydomonas* (Chlorophyta) were the only taxa present during *Ceratium furcoides* peaks. *Chroomonas*, *Cryptomonas*, and *Aulacoseira* (Bacillariophyta), which inhabit turbulent waters, correlated positively with the invader while, Chlorophyta (*Sphaerocystis*, *Schroederia,* and *Monoraphidium*) and Bacillariophyta (*Urosolenia, Rhizosolenia,* and *Discostella)* that preferred summer and fall, Cyanobacteria (*Pseudanabaena*) that preferred winter and fall, Ochrophyta (*Mallomonas*) that avoided spring, and *Chlamydomonas* with no seasonality, all showed negative correlations with the invader. *Ceratium furcoides* peaks were associated with higher dissolved oxygen levels and lower species richness. Throughout time, *Ceratium furcoides* and the rest of the phytoplankton density peaks decreased considerably showing, although not conclusively, evidence of stable coexistence.

***Key words**: Phytoplankton dynamics, Ecology, Dinophyceae, Dinophyta, Artificial lake.*

RESUMO

Ceratium furcoides (Levander) Langhans é uma espécie invasora de fitoplâncton para as águas doces brasileiras, associada a impactos ecológicos que afetam a qualidade da água e a comunidade aquática local. Este estudo explorou as interações entre espécies fitoplanctónicas durante a invasão de *Ceratium furcoides* e os vetores (variáveis meteorológicas, físicas e químicas), contribuindo para sua dominância e florescimento numa barragem subtropical de altitude (Marrecas, Sul do Brasil). O programa de monitorização foi implementado semanalmente a mensal desde 2014 (n = 116), dependendo da densidade das cianobactérias. Testes descritivos, de hipóteses, correlações e estatística multivariada (PCA e CCA) foram utilizados para compreender os padrões de distribuição temporal (sazonal e interanual) da comunidade fitoplanctónica e as variáveis ambientais. Durante o estudo, *Ceratium furcoides* (Miozoa) evitou os verões e preferiu as primaveras, exibindo em outubro de 2014 a maior densidade reportada (15.865 ind.mL^{-1}). Apresentou uma correlação positiva com a presença de ferro, manganês e turbidez, evidenciando a sua dependência do período de mistura que re-suspende os seus cistos do fundo, ativando-os com a luz e as altas temperaturas do "epilimnion" (camada superior da coluna de água num lago estratificado) (temperatura ótima para a espécie durante a primavera). *Chroomonas*, *Cryptomonas* (Cryptophyta), *Discostella* (Bacillariophyta), e depois de 2016 também *Chlamydomonas* (Chlorophyta) foram os únicos taxa presentes durante os picos de *Ceratium furcoides*. *Chroomonas*, *Cryptomonas* e *Aulacoseira* (Bacillariophyta), que habitam águas turbulentas, correlacionaram-se positivamente com o invasor, enquanto as Chlorophyta (*Sphaerocystis*, *Schroederia* e *Monoraphidium*) e as Bacillariophyta (*Urosolenia*, *Rhizosolenia* e *Discostella*) que preferiram o verão e o outono, Cyanobacteria (*Pseudanabaena*) que preferiram o inverno e o outono, Ochrophyta (*Mallomonas*) que evitavam a primavera e *Chlamydomonas* sem sazonalidade, todos apresentaram correlações negativas com o invasor. Os picos de *Ceratium furcoides* foram associados a maiores níveis de oxigénio dissolvido e menor riqueza de espécies. Ao longo do tempo, *Ceratium furcoides* e o resto dos picos de densidade do fitoplâncton diminuíram consideravelmente mostrando, embora não conclusivamente, evidências de coexistência estável.

Palavras-chave: Dinâmica do fitoplâncton, Ecologia, Dinophyceae, Dinophyta, Lago artificial.

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INTRODUCTION

Biological Invasion

Biological invasion is defined as the entry, establishment, spreading and rapidly dominance of a non-native species in an ecological system (Kernan, 2015). The introduction of the invader is usually directly or indirectly anthropogenic, and its dominance frequently generates effects on the biotic elements and the environment of the system (Alpert et al., 2000; Kernan, 2015). Biological invasions have commonly been associated with alterations in the structure and functioning of ecosystems such as changes in the species composition, community dominance, primary productivity, and biodiversity (Gurevitch & Padilla, 2004; Mooney & Cleland, 2001). All of the above, might result in further and profound ecological, evolutionary, and economic impacts (Epanchin-Niell & Wilen, 2012; Kernan, 2015). Therefore, biological invasions have been key subjects for the management and conservation of natural and semi-natural landscapes and their resources.

Freshwater systems are particularly susceptible to biological invasions, especially by microorganisms, as their establishment is typically unnoticed and favored by water flow (Padisák et al., 2016). Various species of microalgae are expanding their geographic distribution range very fast (Blanco & Ector, 2009; Lilly et al., 2007; Sukenik et al., 2012). The dispersion of these microalgae is often intensified by anthropogenic activities (Nagai et al., 2007). Moreover, several studies indicate that human-altered ecosystems, especially water reservoirs and dams, promote the spreading and growth of invasive species´ population (Johnson et al., 2008; Kirkwood et al., 2009). Therefore, the study of these environments is necessary to unveil the processes, dynamics, drivers, and consequences regarding invasive species colonization, establishment, and blooms.

The invasive genus *Ceratium* Schrank *and Ceratium furcoides* (Levander) Langhans

Throughout the world, members of the genus *Ceratium* Schrank have invaded continental aquatic systems (Meichtry de Zaburlín et al., 2016) and in many cases have produced plankton blooms (Van Ginkel et al., 2004). Although *Ceratium* populations lack toxicity, their blooms can produce filter clogging and can cause an unpleasant taste and a fetid odor on the hydric resource, affecting the industry of drinking water and of water treatment (Matsumura-Tundisi et al., 2010; Van Ginkel et al., 2007). Furthermore, they can represent important threats to the ichthyofauna, zooplankton, and the macroinvertebrates of a system, due to oxygen depletion as a result of bacterial consumption of the invader collapsed cells after the formation of blooms (Hart & Wragg, 2009; Matsumura-Tundisi et al., 2010; Smayda, 1997; Wehr & Sheath, 2003). In some cases, they have also been associated with disruption

Fig. 1 *Ceratium furcoides*. Photography by Oscar Rojas, 2019.

of the planktonic community affecting the cyanobacterial dominance and influencing interactions among different species (Crossetti et al., 2018).

Ceratium. furcoides (Levander) Langhans is original from the northern hemisphere (Carty & Parrow, 2015). However, at present, it has been reported as exotic or invasive in systems around the world as in Australia (Ling & Tyler, 2000), New Zealand (Simmonds et al., 2015; Thomasson, 1974), Egypt (El-Otify et al., 2003), Turkey (Çelekli, Obali, & Külköylüoğlu, 2007), China (Chu et al., 2008), India (Keshri et al., 2013; Khondker et al., 2009), Iran (Darki, 2014), Korea (Li et al., 2015), Taiwan (Wu & Chou, 1998), Cuba (Comas, 2009), and since 2000 in South-America, reaching countries such as Colombia (Ramírez-R, Gutiérrez, & Vargas, 2005), Argentina, Paraguay (Meichtry de Zaburlin et al., 2014), Bolivia (Morales, 2016), and Brazil (Boltovskoy et al., 2013).

Ceratium furcoides in Brazil

In Brazil, *Ceratium furcoides'* invasions have been preceded by disturbance events (including drought and macrophyte removal) that modify the availability of resources disrupting the general cyanobacterial dominance and allowing the recruiting of other species including the dinoflagellate (Crossetti et al., 2018). *Ceratium furcoides* is mixotrophic, skillful swimmer, shows low herbivory pressure due to its morphology (Fig. 1), has the capacity to form cysts, and is capable of an effective dispersal due to its ability to form dense blooms, making it the perfect organism to outcompete the local phytoplankton in Brazilian water bodies (Cavalcante et al., 2016). As a consequence, the invader has established in rivers and reservoirs from the southeastern (Matsumura-Tundisi et al., 2010; Santos-Wisniewski et al., 2007), northeastern (Oliveira et al., 2011), and southern regions of the country (Cavalcante et al., 2013; Jati et al., 2014). When established, the invader increased its abundance dominating the ecosystem and producing blooms that are dependent on the cyst bank in the bottom (Crossetti et al., 2018). Its abundance has been associated primarily, with a combination of optimal conditions of temperature, organic matter, and pH, and secondarily, with availability of nutrient such as phosphorus and nitrates (Cavalcante et al., 2016). But despite all the research carried out on the topic, a lot is needed to understand the invader dynamics, drivers, and especially the ecological interactions in Brazilian freshwater systems.

Aim of the research

Phytoplankton's invasions are poorly documented, one of the reasons being the lack of reliable historical data (Padisák et al., 2016). Consequently, studies assessing the ecological interactions within the phytoplankton communities during an invasion process are scarce. The present study explored the biotic (interactions among phytoplankton species and population dynamics based on densities and dominance) and environmental variables (physical, chemical and meteorological) shortly after an invasion process by *Ceratium furcoides* in a high-altitude subtropical reservoir (Marrecas in Caxias do Sul, Rio Grande do Sul, Brazil), which has been monitored weekly to monthly since 2014 after the first occurrence of the invader within the system in 2013 (Almeida et al., 2013).

METHODOLOGY

Study area:

The present study was conducted in Marrecas system (29° 2'S, 50°58'W) located in Caxias do Sul region, Rio Grande do Sul, Southern Brazil (Fig. 2), 25 km northeast from the city of Caxias do Sul, within the Taquari-Antas Hydrographic basin (SAMAE, 2016; Schneider et al., 2014). This is one of the main sub-basins of the Patos Lagoon basin which presents high fish diversity and it is recognized as a freshwater ecoregion by Abell et al. (2008) that drains into the Atlantic Ocean (Becker et al., 2013). Marrecas system is a provisioning water reservoir, filled in 2013, with the expectations of supplying with drinking water a total of 250 000 people in the city of Caxias do Sul for a period of 20 years (SAMAE, 2015). It has a storage capacity of over 33 billion liters of water, and an initial flow of 900 liters of running water per second (Pionero, n.d.; SAMAE, 2015). The reservoir is in a subtropical environment, characterized by a temperate regional climate and lacking a dry season (Cfa; Köppen, 1936). The annual mean temperature during the study period (2014-2018) was 17.5 ºC, and the total annual precipitation ranged between 1972 mm (2017) and 2257 mm (2015), with a mean annual precipitation of 2065 mm (2014-2018) (INMET- Instituto Nacional de Meteorologia, 2019).

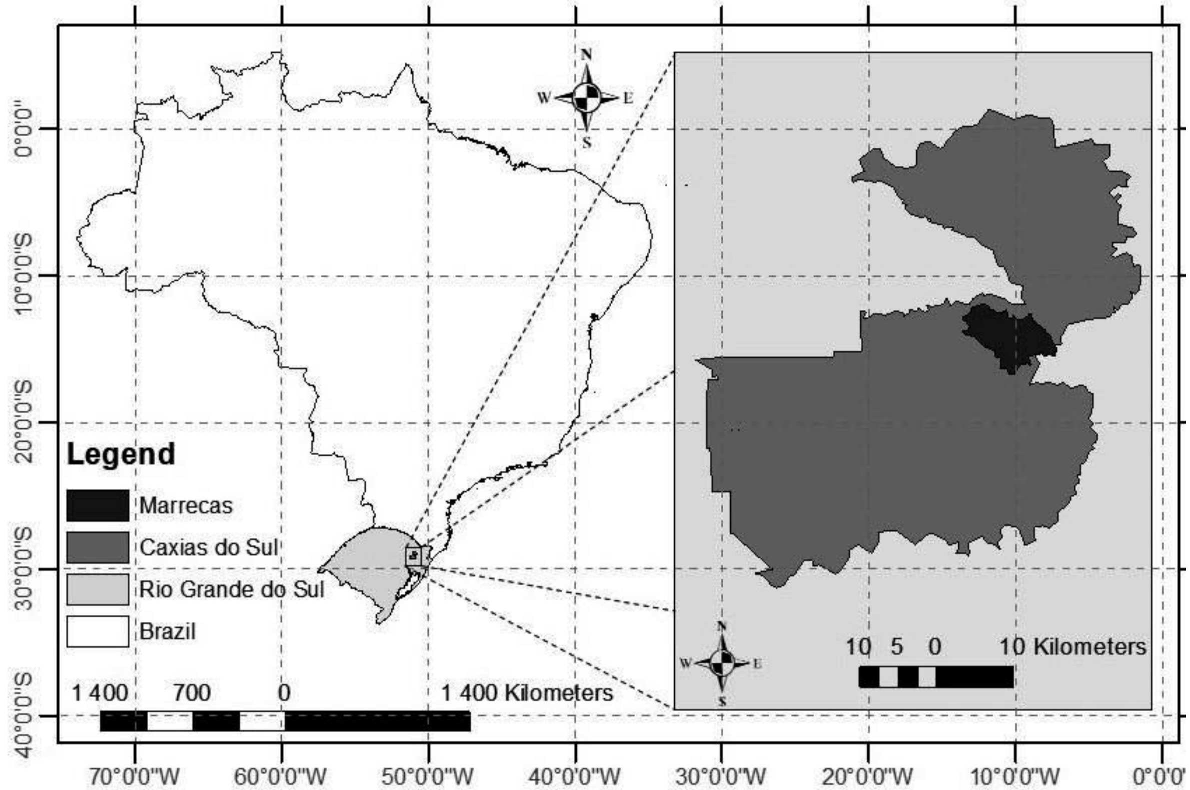


Fig. 2. Marrecas reservoir map.

Map showing the location of Rio Grande do Sul in Brazil (light gray), the region of Caxias do Sul (dark gray) and Marrecas reservoir (black). Country and Region maps obtained from (GADM, n.d.); and Marrecas reservoir map from SAMAE (2015).

In 2013, the reservoir presented for the first time the invasive species *Ceratium furcoides* (Almeida et al., 2013) which, has shown detrimental effects in the water and ecology of different reservoirs in South America (Meichtry de Zaburlín et al., 2016; Morales, 2016; Santos-Wisniewski et al., 2007). Consequently, The Municipal Autonomous Service of Water and Sewer (SAMAE, by its initials in Portuguese) initiated a monitoring program addressing the phytoplankton community (including the invader), and the water quality (physical and chemical variables) of the reservoir. The monitoring program has continued ever since.

Physical, chemical, biological, and meteorological variables

Sampling was conducted by the team of SAMAE weekly to monthly depending on the cyanobacteria density (weekly during algae blooms) from January 2014 to December 2018 at the point of water intake of the reservoir (Fig. 2). Water samples were collected with plastic bottles of 500 mL on the surface of the reservoir for physical and chemical analysis at the SAMAE quality control laboratory and with glass bottles of 250 mL for phytoplankton counting. Water temperature, pH, dissolved oxygen, and conductivity were measured in the field using a model U-10 Horiba probe, while turbidity employing a turbidimeter HACH 2100P. CO_2 was estimated by the titration method with sodium carbonate, organic matter by the titration method with potassium permanganate, ammonium (NH_4^+), phosphates (PO_4), nitrate (NO_3^-), iron (Fe), and manganese (Mn) were assessed through concentration analyses employing the photometer NOVA 60 Merck with the respective colorimetric test kits in the SAMAE quality control laboratory. The surface water samples for phytoplankton community analysis were preserved with Lugol´s iodine. Phytoplankton quantification followed Utermöhl (1958) in 10 mL settling chambers in an inverted microscope; and species were sorted into genus and phylum. Additionally, daily meteorological data (daily precipitation, weekly precipitation, air temperature, relative humidity, and wind velocity) from January 2014 to December 2018 was obtained from Caxias do Sul Meteorological Station (INMET- Instituto Nacional de Meteorologia, 2019).

Data analysis

The phytoplankton dataset was organized and selected including only the genera occurring in more than 10% of the total phytoplankton in at least one sample, eliminating the rest to avoid noise. The datasets (meteorological, physical, chemical, and biological variables) were explored using descriptive analyses in STATISTICA 7 software (StatSoft, 2004) to find temporal patterns (seasonal and interannual), which were supported with hypothesis tests (Kruskal-Wallis) and post-hoc Dunn test in RStudio (RStudio Team, 2016). Additionally, a combination of multivariate analysis employing PC-Ord 6 (McCune & Mefford, 2011) were performed to: detect general trends of the environmental variables including meteorological, physical and chemical variables (Principal Components Analysis PCA, using variance/covariance); identify a linear or unimodal response of the phytoplankton community (Detrended Correspondence Analysis DCA); and find interactions between the environmental variables and phytoplankton community (Canonical Correspondence Analysis CCA). Prior to the PCA and CCA analysis, the data was transformed by log x+1 (except pH). Subsequently, two-way cluster analyses (Sørensen as distance measure) in PC-Ord 6 (McCune & Mefford, 2011) were ran based on the phytoplankton densities to identify seasonality of the genera as well as co-occurrence throughout the period of study. All these analyses were supported by correlation analysis based on Spearman index employing PAST 3.25 (Hammer & Harper, 2008).

RESULTS

Meteorological data

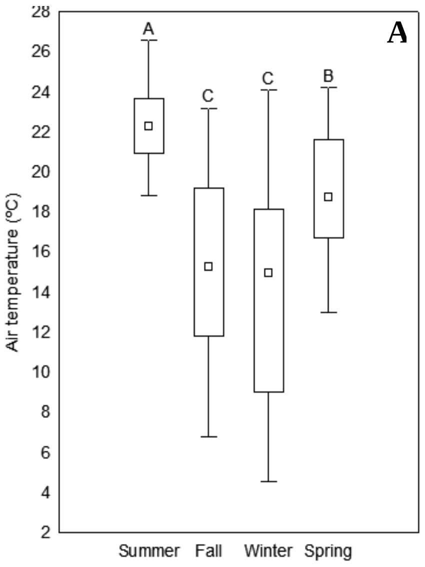
Throughout the study only air temperature showed significant difference between seasons [Kruskal-Wallis (KW), chi-squared (X^2) = 51.071, degrees of freedom (df) = 3, p-value (p) <0.001] and no meteorological variable showed significant difference interannually (Figs. 3 and 4). The air temperatures were characteristic of a subtropical region, with higher values during summer (median: 22.28 ºC) and spring (median: 18.76 ºC) and lower values during winter (median: 15.14 ºC) and fall (median: 15 ºC); all seasons differed significantly in temperature except fall from winter (Fig. 3A). The hottest temperatures occurred in 2014 and 2015 and the coldest in 2016 and 2017 (Fig. 4A). Precipitation showed values between 0 mm and 69.8 mm (median of 0 mm) along the period of study, winter showed the highest volume and the fall the highest peaks (Fig. 3B). Interannually, the highest peaks occurred in 2017 and 2015 (Fig. 4B). Weekly precipitation (total rain volume during the week) ranged from 0 mm to 197.7 mm (median of 32.1 mm) along the period of study. It showed higher peaks in winter and spring and a higher median in summer (Fig. 3C). Throughout time it showed a decrease in the intensity of the peaks during 2017 and 2018 (Fig. 4C). The wind velocity showed higher peaks during winter and fall (Fig. 3D) and throughout the years in 2014, 2017, and 2018 (Fig. 4D) (View Tables 1 and 2).

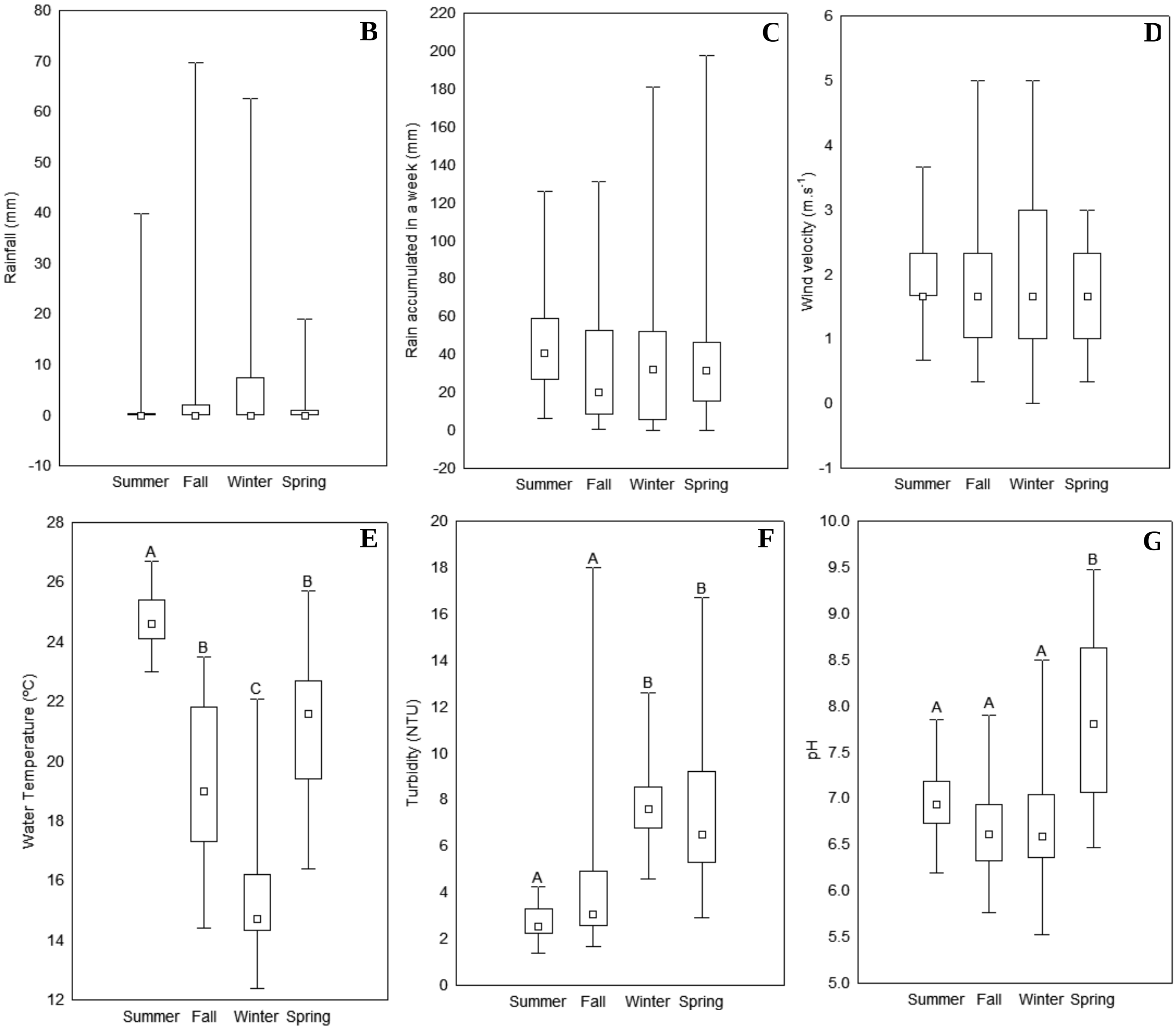
Fig. 3 Boxplots: Seasonality of the meteorological, physical, and chemical variables, including: air temperature (**A**), daily precipitation (**B**), weekly precipitation (**C**), wind velocity (**D**), water temperature (**E**), turbidity (**F**), pH (**G**), dissolved oxygen (**H**), organic matter (**I**), ammonium (**J**), nitrate (**K**), phosphate (**L**), iron (**M**), manganese (**N**), carbon dioxide (**O**), and conductivity (**P**).

Legend:

-□- Median
□ 25%-75%
⊥ Min-Max

Distinct letters (A to D) above boxes indicate significant differences according to Kruskal-Wallis and post-hoc Dunn test.





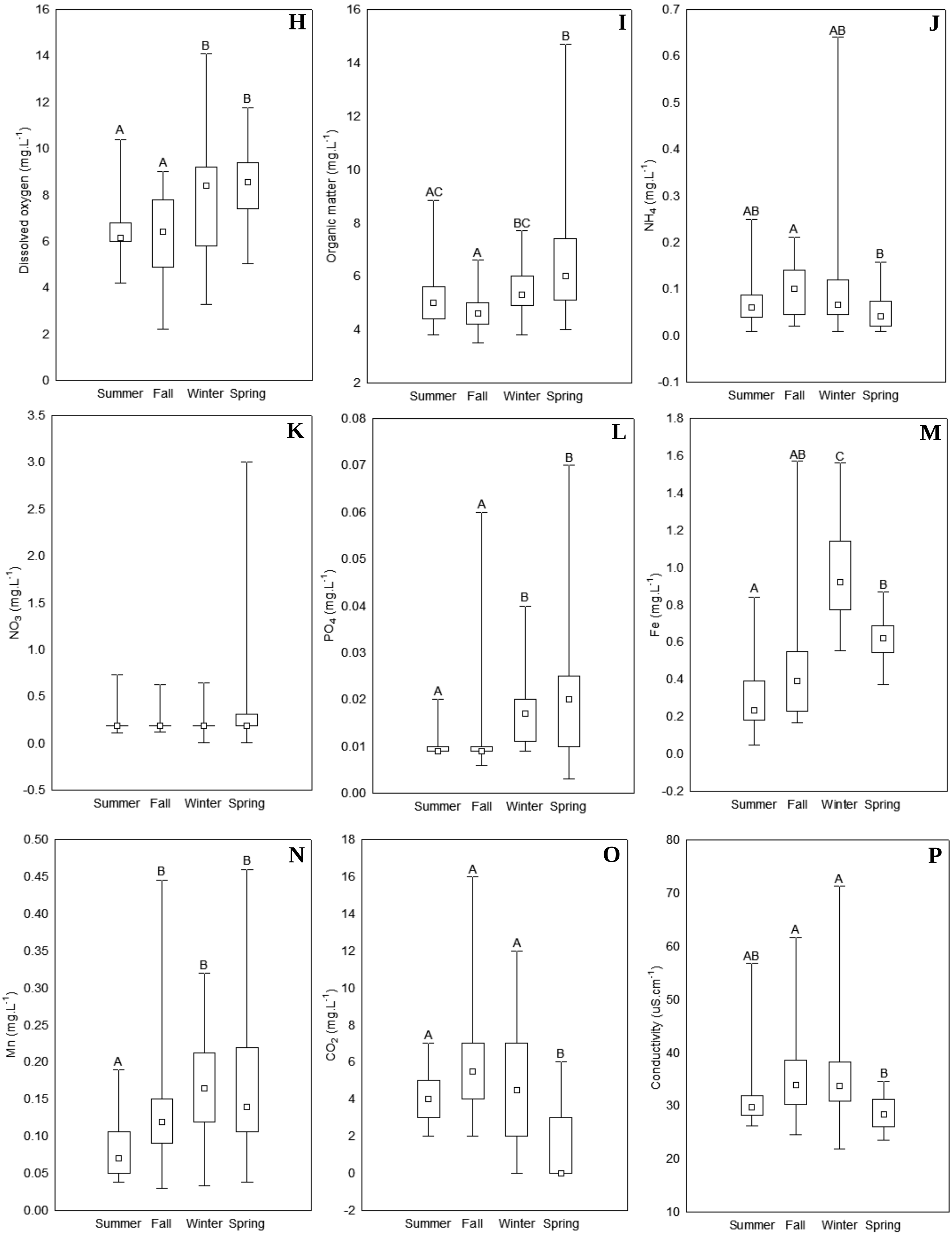
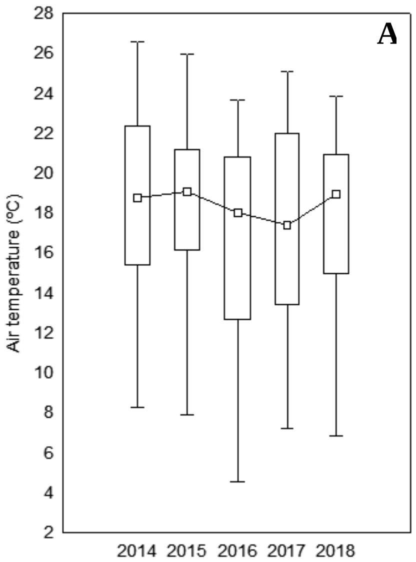

H
Dissolved oxygen (mg.L-1)
0 2 4 6 8 10 12 14 16
A A B B
Summer Fall Winter Spring
I
Organic matter (mg.L-1)
2 4 6 8 10 12 14 16
AC A BC B
Summer Fall Winter Spring
J
NH4 (mg.L-1)
-0.1 0.0 0.1 0.2 0.3 0.4 0.5 0.6 0.7
AB A AB B
Summer Fall Winter Spring
K
NO3 (mg.L-1)
-0.5 0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
Summer Fall Winter Spring
L
PO4 (mg.L-1)
0.00 0.01 0.02 0.03 0.04 0.05 0.06 0.07 0.08
A A B B
Summer Fall Winter Spring
M
Fe (mg.L-1)
-0.2 0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8
A AB C B
Summer Fall Winter Spring
N
Mn (mg.L-1)
0.00 0.05 0.10 0.15 0.20 0.25 0.30 0.35 0.40 0.45 0.50
A B B B
Summer Fall Winter Spring
O
CO2 (mg.L-1)
-2 0 2 4 6 8 10 12 14 16 18
A A A B
Summer Fall Winter Spring
P
Conductivity (uS.cm-1)
10 20 30 40 50 60 70 80
AB A A B
Summer Fall Winter Spring

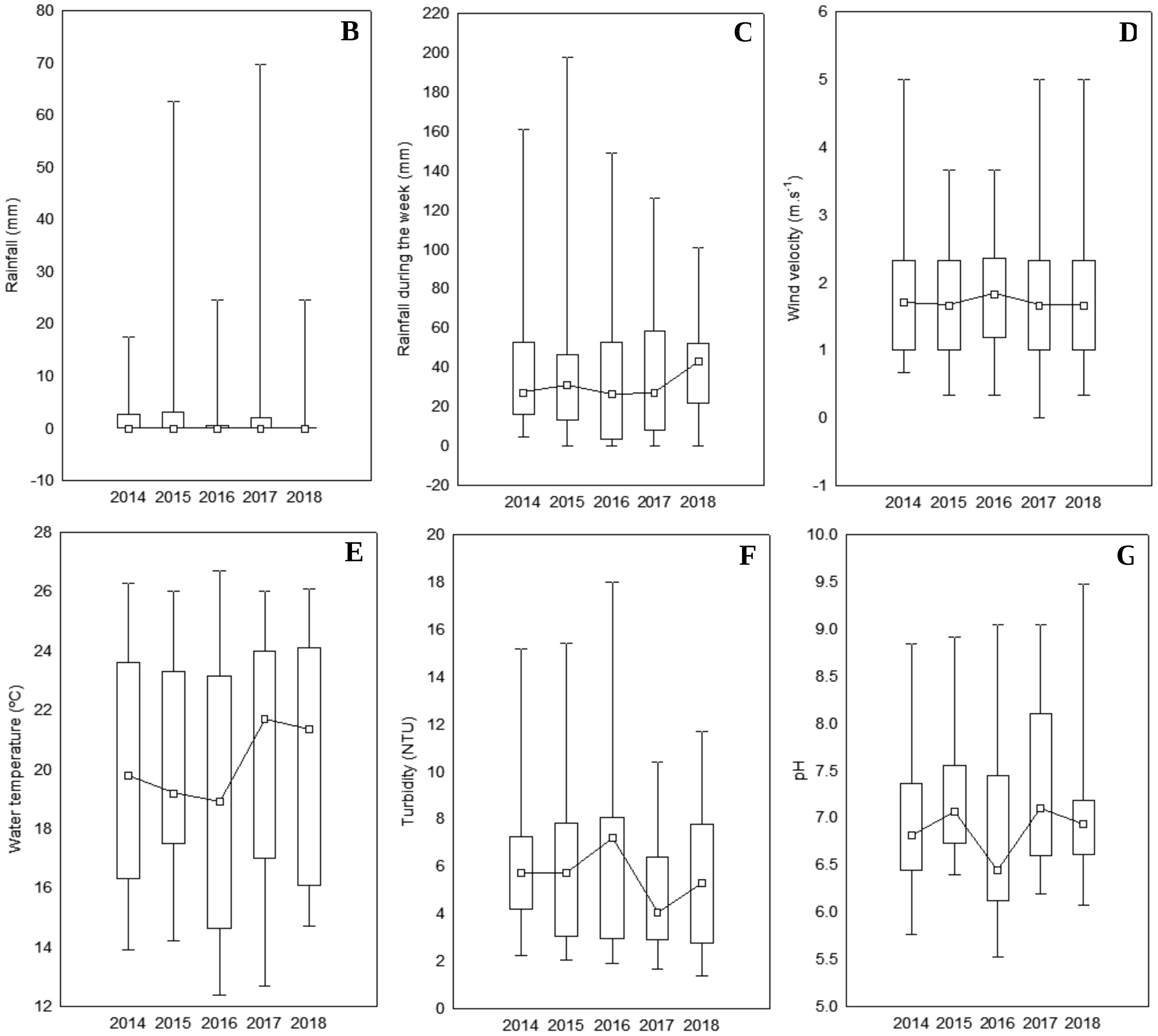
Fig. 4 Boxplots: Changes of the meteorological, physical, and chemical variables throughout time. Including: air temperature (**A**), daily precipitation (**B**), weekly precipitation (**C**), wind velocity (**D**), water temperature (**E**), turbidity (**F**), pH (**G**), dissolved oxygen (**H**), organic matter (**I**), ammonium (**J**), nitrate (**K**), phosphate (**L**), iron (**M**), manganese (**N**), carbon dioxide (**O**), and conductivity (**P**).

Legend:

-□- Median
□ 25%-75%
⊥ Min-Max

Distinct letters (A to D) above boxes indicate significant differences according to Kruskal-Wallis and post-hoc Dunn test.





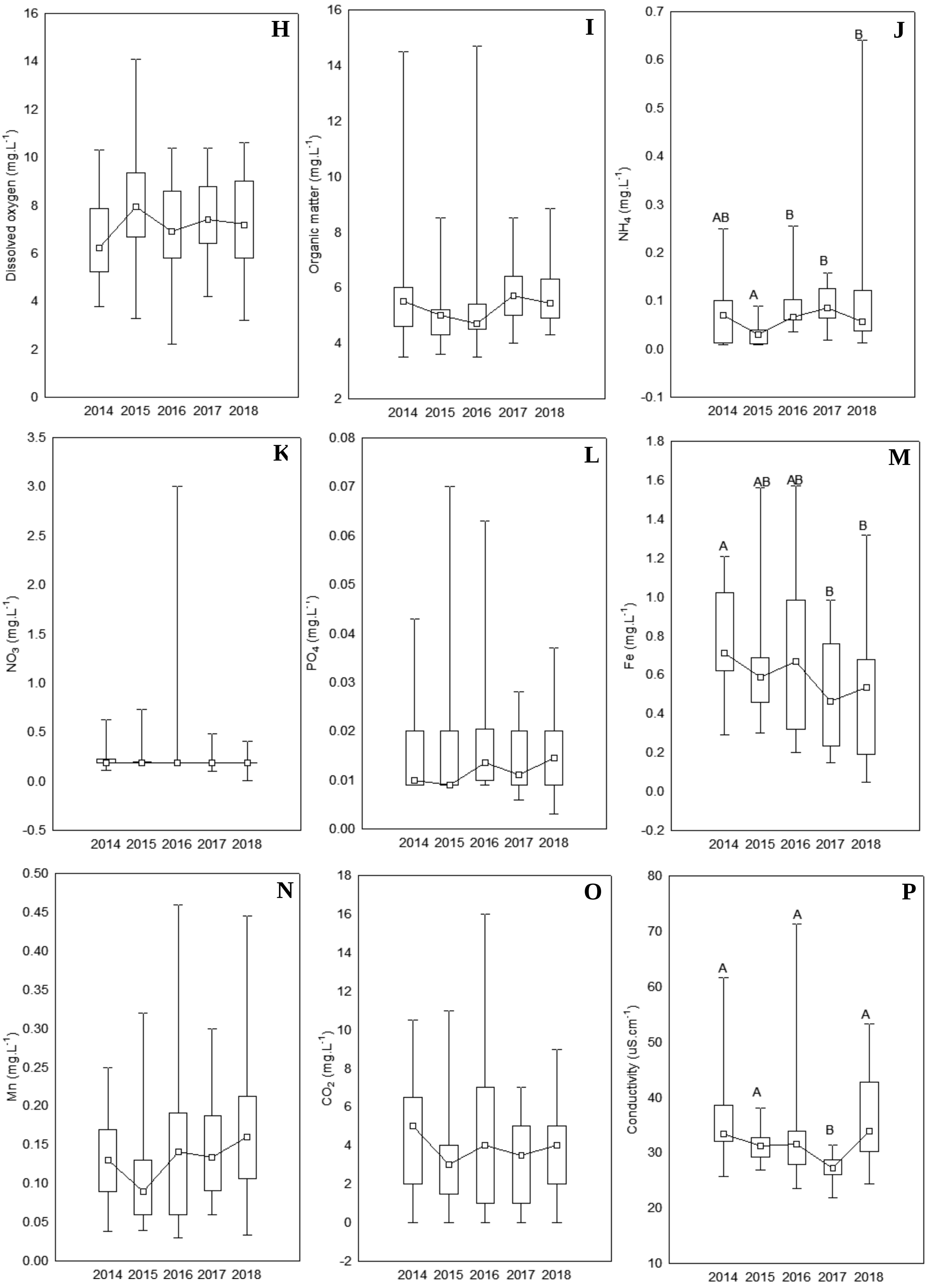

H
Dissolved oxygen (mg.L^{-1})
0
2
4
6
8
10
12
14
16
2014 2015 2016 2017 2018
I
Organic matter (mg.L^{-1})
2
4
6
8
10
12
14
16
2014 2015 2016 2017 2018
J
NH$_4$ (mg.L^{-1})
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
AB
A
B
B
B
2014 2015 2016 2017 2018
K
NO$_3$ (mg.L^{-1})
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
2014 2015 2016 2017 2018
L
PO$_4$ (mg.L^{-1})
0.00
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
2014 2015 2016 2017 2018
M
Fe (mg.L^{-1})
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
A
AB
AB
B
B
2014 2015 2016 2017 2018
N
Mn (mg.L^{-1})
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
0.50
2014 2015 2016 2017 2018
O
CO$_2$ (mg.L^{-1})
-2
0
2
4
6
8
10
12
14
16
18
2014 2015 2016 2017 2018
P
Conductivity (uS.cm^{-1})
10
20
30
40
50
60
70
80
A
A
A
B
A
2014 2015 2016 2017 2018

Table 1. Range (Max= maximum, Min= minimum), mean, and standard deviation (SD) of meteorological, physical, and chemical variables of Marrecas reservoir throughout the season (summer, fall, winter, and spring) during the period of study.

	Summer				**Fall**				**Winter**				**Spring**			
	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD
Temp °C	22.34	26.56	18.8	2.02	15.14	23.16	6.76	4.63	14.25	24.08	4.52	4.85	18.95	24.24	13	2.97
Temp Max °C	28.28	33.6	24.6	2.42	20.25	29.6	11.2	4.62	19.91	30.2	9.8	5.3	24.47	30.8	18.4	3.8
Temp Min °C	18.06	22.8	13.8	2.3	12.04	18.2	3.6	4.82	10.41	18.6	1.4	4.89	14.75	21	7.2	3.5
Rain mm	2.6	39.8	0	8.17	5.06	69.8	0	14.37	6.36	62.6	0	14.2	1.94	19.1	0	4.72
Rain (7 days) mm	47.16	126.2	6.3	33.23	37.86	131.1	0.4	36.88	38.44	181.1	0	44.51	42.13	197.7	0	43.56
Wind $m.s^{-1}$	1.88	3.67	0.67	0.84	1.76	5	0.33	0.96	2.23	5	0	1.3	1.65	3	0.33	0.81
Wind (2 days) $m.s^{-1}$	1.83	2.67	1	0.53	1.56	3.33	0.5	0.61	2.12	4.67	0.67	0.99	1.84	3	0.83	0.63
Water Temp °C	24.81	26.7	23	0.95	19.25	23.5	14.4	2.91	15.27	22.1	12.4	1.96	21.15	25.7	16.4	2.26
Turbidity NTU	2.77	4.26	1.37	0.72	4.5	18	1.66	3.41	7.79	12.6	5.29	1.51	7.67	16.7	2.91	3.55
pH	6.98	7.85	6.2	0.44	6.65	7.9	5.76	0.51	6.72	8.5	5.52	0.64	7.9	9.47	6.47	0.9
DO $mg.L^{-1}$	6.46	10.4	4.2	1.16	6.27	9	2.2	1.72	7.97	14.08	3.3	2.72	8.35	11.75	5.05	1.55
Org. $mg.L^{-1}$	5.39	8.86	3.8	1.38	4.64	6.6	3.5	0.71	5.41	7.7	3.8	0.89	6.76	14.7	4	2.71
NH_4 $mg.L^{-1}$	0.07	0.25	0.01	0.05	0.1	0.21	0.02	0.05	0.11	0.64	0.01	0.12	0.05	0.16	0.01	0.04
NO_3 $mg.L^{-1}$	0.23	0.73	0.11	0.13	0.22	0.63	0.12	0.11	0.23	0.65	0.01	0.12	0.33	3	0.01	0.5
PO_4 $mg.L^{-1}$	0.01	0.02	0.01	0	0.01	0.06	0.01	0.01	0.02	0.04	0.01	0.01	0.02	0.07	0	0.02
Fe $mg.L^{-1}$	0.3	0.84	0.05	0.19	0.5	1.57	0.17	0.37	0.94	1.56	0.56	0.25	0.62	0.87	0.37	0.12
Mn $mg.L^{-1}$	0.08	0.19	0.04	0.04	0.14	0.45	0.03	0.09	0.17	0.32	0.03	0.07	0.16	0.46	0.04	0.09
CO_2 $mg.L^{-1}$	3.86	7	2	1.37	6.13	16	2	3.22	4.6	12	0	2.97	1.46	6	0	1.8
Cond. $uS.cm^{-1}$	31.21	56.8	26.3	5.92	36.29	61.6	24.54	8.96	35.02	71.4	21.9	9.27	28.57	34.5	23.5	3.03

Table 2. Range (Max= maximum, Min= minimum), mean, and standard deviation (SD) of meteorological, physical, and chemical variables of Marrecas reservoir throughout the season (summer, fall, winter, and spring) during the period of study.

	2014				**2015**				**2016**				**2017**				**2018**			
	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD	Mean	Max	Min	SD
Temp °C	18.20	26.56	8.28	5.14	18.09	25.96	7.88	4.59	16.47	23.68	4.52	5.49	17.72	25.08	7.20	4.82	17.74	23.84	6.84	4.66
Temp Max °C	24.01	33.60	13.20	5.71	23.76	33.40	11.40	5.21	21.94	31.00	9.80	5.83	23.11	31.20	15.80	5.18	23.32	29.60	12.80	4.97
Temp Min °C	14.13	22.80	5.20	5.26	14.42	21.00	5.40	4.48	13.08	20.00	2.00	5.55	13.69	21.20	1.40	4.85	13.49	18.20	4.00	4.64
Rain mm	2.57	17.60	0.00	4.91	5.75	62.60	0.00	14.88	2.98	24.60	0.00	6.44	6.16	69.80	0.00	15.60	1.60	24.60	0.00	5.15
Rain (7 days) mm	42.47	161	4.6	42.9	46.05	197.7	0	50.9	39.23	149.2	0	44.1	36.51	126.2	0	35.4	42.77	101	0	27.3
Wind m.s^{-1}	1.95	5.00	0.67	1.28	1.73	3.67	0.33	0.78	1.95	3.67	0.33	0.92	1.96	5.00	0.00	1.19	1.82	5.00	0.33	0.98
Wind (2 days) m.s^{-1}	2.07	3.33	0.67	0.75	1.71	3.33	0.50	0.68	1.97	4.00	1.00	0.71	1.83	4.67	0.67	0.82	1.75	3.50	0.83	0.72
Water Temp °C	19.81	26.30	13.90	4.09	20.00	26.00	14.20	3.65	19.06	26.70	12.40	4.54	20.39	26.00	12.70	3.88	20.54	26.10	14.70	3.96
Turbidity NTU	6.19	15.20	2.24	2.99	6.18	15.40	2.07	3.70	7.11	18.00	1.93	4.31	4.88	10.40	1.66	2.47	5.52	11.70	1.37	2.88
pH	7.07	8.84	5.76	0.91	7.20	8.92	6.40	0.61	6.80	9.05	5.52	0.93	7.34	9.04	6.20	0.89	7.13	9.47	6.07	0.87
DO mg.L^{-1}	6.64	10.33	3.78	1.77	8.20	14.08	3.30	2.68	7.10	10.40	2.20	2.12	7.45	10.40	4.20	1.41	7.20	10.60	3.20	2.02
Org. mg.L^{-1}	6.07	14.50	3.50	2.61	4.97	8.50	3.60	1.05	5.80	14.70	3.50	2.87	5.79	8.50	4.00	1.27	5.73	8.86	4.30	1.18
NH_4 mg.L^{-1}	0.07	0.25	0.01	0.07	0.03	0.09	0.01	0.02	0.10	0.26	0.04	0.06	0.09	0.16	0.02	0.04	0.10	0.64	0.01	0.13
NO_3 mg.L^{-1}	0.22	0.63	0.11	0.12	0.26	0.73	0.19	0.14	0.39	3.00	0.19	0.60	0.23	0.48	0.10	0.10	0.19	0.41	0.01	0.09
PO_4 mg.L^{-1}	0.01	0.04	0.01	0.01	0.02	0.07	0.01	0.02	0.02	0.06	0.01	0.01	0.01	0.03	0.01	0.01	0.02	0.04	0.00	0.01
Fe mg.L^{-1}	0.77	1.21	0.29	0.26	0.65	1.56	0.30	0.31	0.72	1.57	0.20	0.40	0.49	0.98	0.15	0.25	0.49	1.32	0.05	0.31
Mn mg.L^{-1}	0.13	0.25	0.04	0.06	0.11	0.32	0.04	0.07	0.15	0.46	0.03	0.10	0.15	0.30	0.06	0.07	0.17	0.45	0.03	0.09
CO_2 mg.L^{-1}	4.53	10.50	0.00	3.08	3.28	11.00	0.00	2.57	4.38	16.00	0.00	4.21	3.38	7.00	0.00	2.32	3.92	9.00	0.00	2.54
Cond. uS.cm^{-1}	36.74	61.60	25.80	9.73	31.68	38.10	26.90	3.10	32.62	71.40	23.50	9.39	27.25	31.38	21.90	2.07	36.15	53.25	24.30	8.39

Physical and chemical variables

Seasonally, all the physical and chemical variables except nitrate differed significantly ($p<0.05$). However, interannually, only ammonium ($p > 0.0001$), iron ($p = 0.011$), and conductivity ($p > 0.0001$) differed significantly (Figs. 3 and 4).

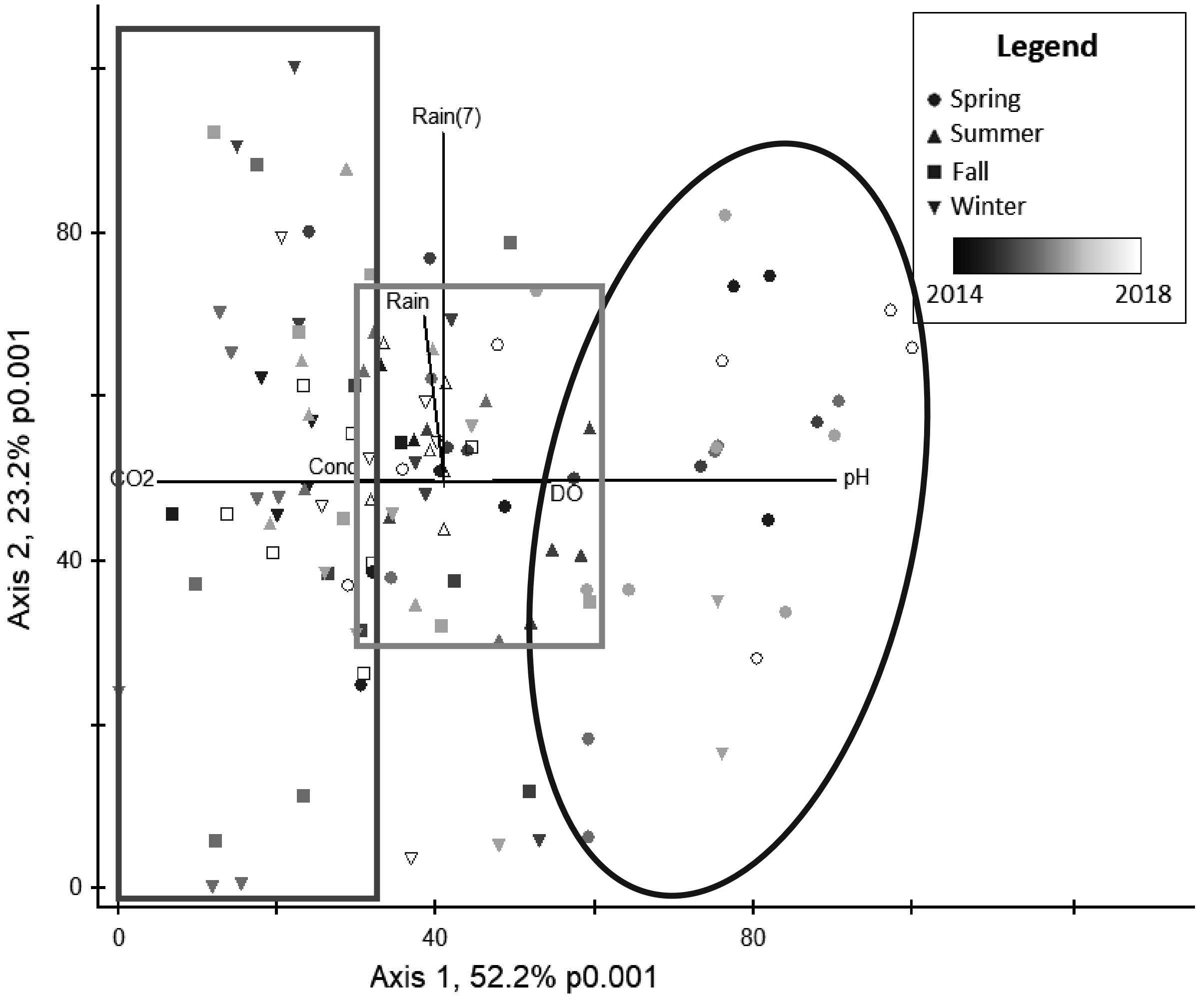
The water temperature showed values between 12.4 ºC-26.7 ºC (median: 20.55 ºC) along the period of study, showing the characteristic subtropical pattern with higher temperatures during summer (median: 24.6 ºC) and spring (median: 21.6 ºC) and lower during fall (median: 18.75 ºC) and winter (median: 14.7 ºC), all, except fall from spring, differed significantly ($p = 4.725e-11$) (Fig. 3E). Interannually, 2016 showed the lowest median and the maximum and the minimum extreme values of water temperature, while 2017 and 2018 showed slightly higher medians than the rest of the seasons (Fig. 4E). Turbidity showed a range between 1.37-18 NTU (median 5.73 NTU) with significantly higher values ($p = 5.429e-14$) in winter (median: 7.7 NTU) and spring (median: 6.48 NTU) when compared with fall (median: 3.09 NTU) and summer (median: 2.52 NTU) (Fig. 3F); 2017 and 2018 showed lower medians (although not significantly different) and lower peaks (<10 NTU, only one of 11.5 in 2018) when compared with the rest (>12 NTU, at least once per year) (Fig. 4F). The pH showed values between 5.52 and 9.47 (median of 6.93, neutral) along the period of study, with significantly higher values ($p<0.001$) in spring (median: 7.8, slightly basic) when compared with the rest (<7 neutral to slightly acid) (Fig. 3G); interannually, 2016 showed the lowest values (Fig. 4G). Dissolved oxygen showed values between 2.2 - 14.08 mg.L^{-1} (median: 7.2 mg.L^{-1}) along the period of study, with significantly higher values ($p <0.001$) in spring (median: 8.55 mg.L^{-1}), and winter (median: 8.5 mg.L^{-1}), when compared with fall (median: 6.4 mg.L^{-1}) and summer (median: 6.14 mg.L^{-1}) (Fig. 3H). During the study, 2014 showed lower medians and 2015 the highest (although not significantly different), and only one level of anoxia (<2 mg.L^{-1}) was detected during fall in 2016 (Fig. 4H). Organic matter showed a range between 3.5-14.7 mg.L^{-1} (median: 5.1 mg.L^{-1}) along the period of study, with significantly higher values ($p<0.001$) during spring (median: 6 mg.L^{-1}) when compared with the rest (medians <5.3mg.L^{-1}) (Fig. 3I). Interannually, 2015, 2017 and 2018 showed less pronounced peaks (<8.5, only one above in 2018 during spring), when compared with 2014 and 2016 (peaks >14) and higher (although not significantly different) medians in 2017 and 2014 (Fig. 4I).

Ammonium showed a range between 0.009-0.64 mg.L^{-1} (median: 0.061 mg.L^{-1}) along the study. Seasonally, fall (median: 0.10 mg.L^{-1}) and winter (median: 0.0.066 mg.L^{-1}), that also showed the highest peaks (>0.24 mg.L^{-1}), showed significantly higher values ($p = 0.003747$) when compared with summer (median: 0.06 mg.L^{-1}) and spring (median: 0.042 mg.L^{-1}) (Fig. 3J). Interannually, 2015 (median: 0.03 mg.L^{-1}) showed significantly lower values ($p = 0.000008174$) and the highest peaks occurred in 2018 (>0.6 mg.L^{-1}), 2014 (>0.25 mg.L^{-1}), and 2016 (>0.2 mg.L^{-1}) (Fig. 4J). Nitrate showed a range between 0.01- 3 mg.L^{-1} (median 0.19 mg.L^{-1}) along the study, without any significant seasonal nor interannually difference, however, the highest peaks were observed during spring of 2016 (Figs. 3K and 4K). Phosphate showed a range between 0.003-0.07 mg.L^{-1} (median: 0.0125 mg.L^{-1}) along the period of study. Seasonally, spring (median: 0.02 mg.L^{-1}) and winter (median: 0.018 mg.L^{-1}) showed significant higher values ($p<0.001$) when compared with fall (median: 0.009 mg.L^{-1}) and summer (median: 0.009 mg.L^{-1}) (Fig. 3L); and, although not significantly, 2015 and 2016 showed the highest peaks (>0.045 mg.L^{-1}) and 2014 and 2015 the lowest medians (Fig. 4L). Iron showed a range between 0.05 and 1.57 mg.L^{-1} (median: 0.61 mg.L^{-1}) during the study. Seasonally, winter (median: 0.9 mg.L^{-1}) showed significantly higher values (p = 9.769e-14) followed by spring and fall (medians: 0.62 mg.L^{-1} and 0.4 mg.L^{-1}, respectively) and summer showed significantly lower (median:0.23 mg.L^{-1}) (Fig. 3M). Interannually, 2017 (median: 0.46 mg.L^{-1}) and 2018 (median: 0.54 mg.L^{-1}) showed significantly lower values (p = 0.01148) when compared with the highest in 2014 (median: 0.71 mg.L^{-1}) and the highest peaks were observed in 2015 and 2016 (Fig. 4M).

Manganese showed a range between 0.03 and 0.46 mg.L^{-1} (median: 0.13 mg.L^{-1}) during the period of study. Seasonally, summer (median: 0.07 mg.L^{-1}) showed significantly lower values ($p<0.0001$) when compared with the rest (median >0.12 mg.L^{-1}) (Fig. 3N). Interannually, 2015 showed the lowest median, and the highest peaks were observed in 2016 and 2018 (Fig. 4N). Carbon dioxide showed a range between 0 and 16 mg.L^{-1} (median of 4 mg.L^{-1}) during the study, with significantly lower values ($p<0.001$) in spring (median: 0 mg.L^{-1}) when compared with the rest (medians >4 mg.L^{-1}) (Fig. 3O). Interannually, 2016 showed the highest peak (16 mg.L^{-1}) and 2014 the highest median, although not significantly different from the rest (Fig. 4O). Conductivity showed a range between 21.9 uS.cm^{-1} and 71.4 uS.cm^{-1} (median: 31.28 uS.cm^{-1}) during the period of study, with significantly higher values ($p<0.001$) in fall and winter (medians: 34.1 uS.cm^{-1} and 33.55 uS.cm^{-1}, respectively) when compared with summer and spring (medians: 29.68 uS.cm^{-1} and 28.41 uS.cm^{-1}, respectively) (Fig. 3P), and significantly lower values (p = 0.0000001699) in 2017 (median: 27.27 uS.cm^{-1}) when compared with the rest (medians>31.3 uS.cm^{-1}) (Fig. 4P) (View Tables 1 and 2).

The PCA ordination for 16 abiotic variables explained a total of 75.4% of data variability in the first two axes (Fig. 5); from the abiotic variables, only seven were plotted: pH (r = 0.994), CO_2 (r = -0.85), DO (r = 0.52), Water temperature (r = 0.43) and conductivity (r = -0.47) were the principal variables in the composition of the first axis (52.2%); while accumulated rain during the week/Rain 7 (r = 0.92) and Rain (r = 0.64) were the most important for the composition of the second (23.2%). The PCA's diagram showed most of the samples of spring in the right quadrants (isolated from the rest) with higher pH and dissolved oxygen, summer overlapping with some samples from fall and winter in the center, and winter and fall in the left quadrants with higher CO_2.

Fig. 5 Principal component analysis var/covar (PCA) of meteorological, physical and chemical variables in seasonal scale. DO: dissolved oxygen, Cond: conductivity, Rain: daily precipitation, Rain (7): weekly precipitation. The dark gray circle contains principally samples taken during spring, the light gray small square samples taken in summer, and the dark gray rectangle samples in winter and fall.



Phytoplankton community

In the present study, there were reported 71 genera belonging to eight different phyla: Bacillariophyta (7 genera), Chlorophyta (28 genera), Cryptophyta (3 genera), Ochrophyta (6 genera), Cyanobacteria (12 genera), Miozoa (3 genera), Euglenozoa (4 genera), Charophyta (8 genera). From these, 25 genera from seven different phyla showed a representation above 10% of the total density in at least one sample. These were: *Aulacoseira, Discostella, Nitzschia, Rhizosolenia, Thalassiosira,* and *Urosolenia* from Bacillariophyta; *Elakatothrix* from Charophyta; *Chlamydomonas, Coelastrum, Eutetramorus, Schroederia, Korshikoviella, Monoraphidium, Scenedesmus, Sphaerocystis,* and a non-identified genus from Chlorophyta; *Chroomonas* and *Cryptomonas* from Cryptophyta; *Dinobryon, Epipyxis, Mallomonas, Synura,* and *Gonyostomum* from Ochrophyta; *Pseudanabaena,* and *Synechococcus* from

Cyanobacteria; *Ceratium* from Miozoa. Throughout the study, the most representative taxa were Miozoa (27.4%): *Ceratium* (27.4%), Cryptophyta (22.8%): *Chroomonas* (12.7%) and *Cryptomonas* (10.1%), Bacillariophyta (19.9%): *Discostella* (11.5%) and Chlorophyta (18.1%): *Monoraphidium* (9.8%). The rest of the phyla showed a low representation (<12% of the total phytoplankton density).

During the period of study (2014-2018), *Ceratium furcoides* showed a decrease in the intensity of its density peaks (Figs. 6A and 7B). Initiating in the spring of 2014 with the highest density peak ever reported (15865 ind.mL^{-1}), then decreasing almost half of its density in spring of 2015 oscillating in the fall of 2016 and then decreasing throughout 2017 (peaks in winter and spring) until barely reaching a density peak of 1000 ind.mL^{-1} in the spring of 2018 (Fig. 6A and 7B). Its density showed significant differences ($p<0.001$) when comparing 2014 and 2015 (1818 and 1041 ind.mL^{-1}, respectively) with 2016 (806 ind.mL^{-1}), and 2014 with 2018 (244 ind.mL^{-1}); furthermore, the density median decreased through the years (Fig. 7B). Regarding dominance, *Ceratium furcoides* showed periods of high dominance (above 50%) during winter and spring (2014, 2015, 2017), late fall and spring (2016), and early summer and spring (2018). The invader dominance experienced a decrease from 2014 (mean 50.4%, median 57.12%) to 2016 (mean 22.7%, median 1.91%), significantly lower values ($p<0.01$) but then increased again in 2017 (mean 30.7%, median 34.1%) and 2018 (mean 23.6%, median 16.7%) (Fig. 6B and 7D). *Ceratium furcoides* showed a seasonal preference towards spring (Figs. 6A, 6B, 7A, and 7C) with significantly higher densities ($p<0.001$) when compared with the rest of the seasons (Fig. 7A) and most of the peaks (densities above 1000ind./mL and proportions above 30%) (Fig 6B). Regarding the other phytoplankton groups, Cyanobacteria emerged in 2016, it avoided summers and increased its density during falls and winters (and spring only in 2018) always avoiding the periods with *Ceratium furcoides* dominance. Chlorophyta showed all its peaks in summer, but in 2015 showed its peaks also in late spring and Bacillariophyta showed its peaks in summer and fall (the highest in 2015) avoiding *Ceratium furcoides* peaks. Cryptophyta appeared to be more dominant during winter and spring, and occasionally in fall, but during 2015 and 2016 it showed high dominance in summer as well. Ochrophyta preferred summer and fall, avoided spring and it seemed to avoid *Ceratium furcoides* peaks and its dominance as well (Fig. 6B).

Ceratium furcoides co-occurred principally with *Cryptomonas, Chroomonas, Discostella,* (2014, 2015, 2016, 2017, 2018), *Nitzschia* (2014), *Aulacoseira* (2015) and *Chlamydomonas* (2017 and 2018) (Fig. 8). Although it was clustered independently in 2016, when analyzing the figures 8C it co-occurs in spring with *Chroomonas*, *Cryptomonas* and *Nitzschia*, in part of the winter with *Chlamydomonas* and *Mallomonas* besides the ones mentioned (Fig. 8C). Some of the phytoplankton genera showed relatively high densities principally during the periods of low *Ceratium furcoides´* densities including *Monoraphidium* in 2014, 2015, 2016, 2018; *Rhizosolenia* and *Coelastrum* in 2014; *Pseudanaeba* in 2016, 2017, and 2018; *Schroederia* and *Mallomonas* in 2016, 2017 (Fig. 8).

Fig. 6 Phyla of the phytoplankton community throughout the study period (2014-2018), phyla densities (A) and dominance /percentages (B). Legend: S = summer, F = fall, W = winter, SP = spring

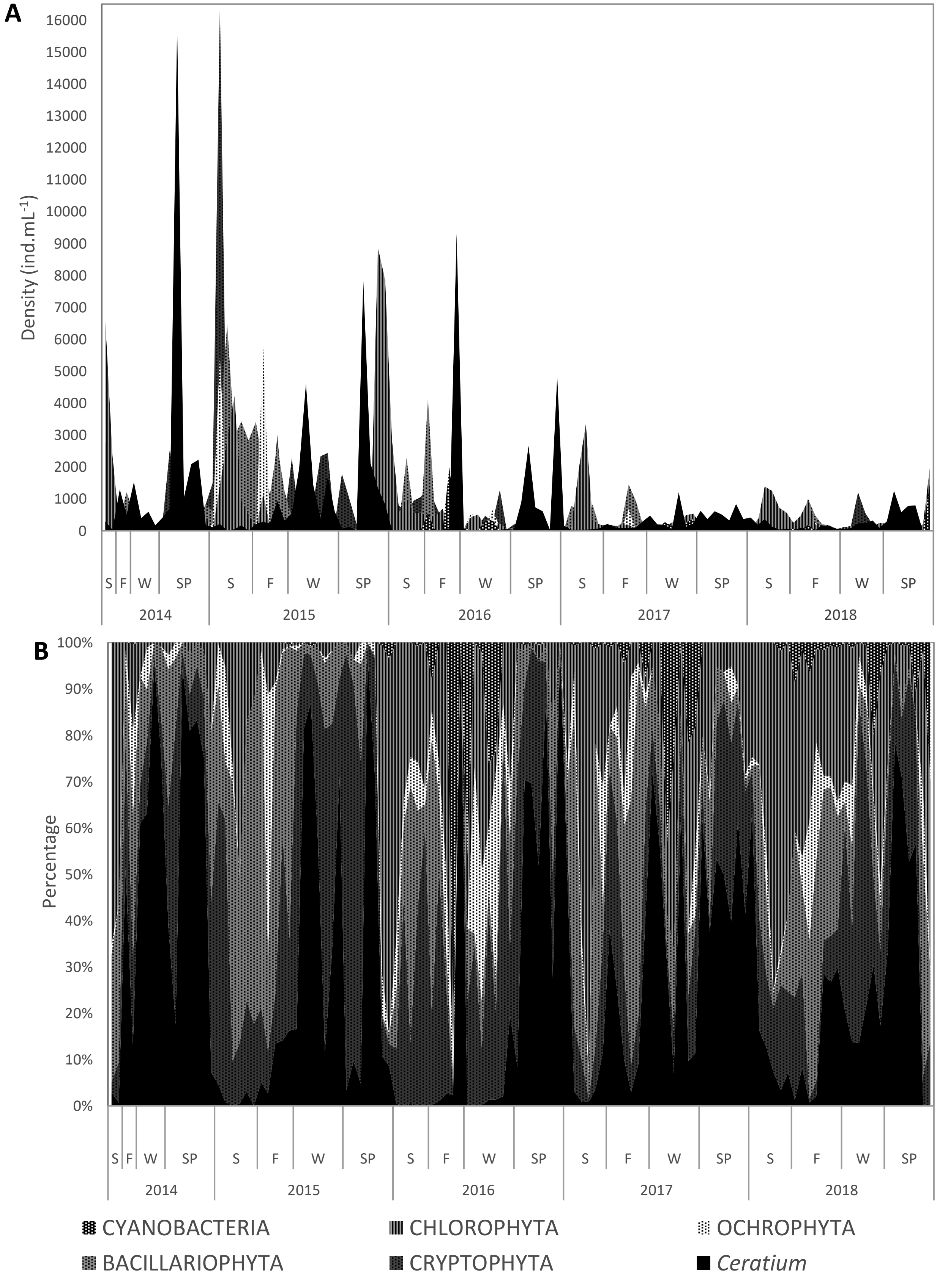
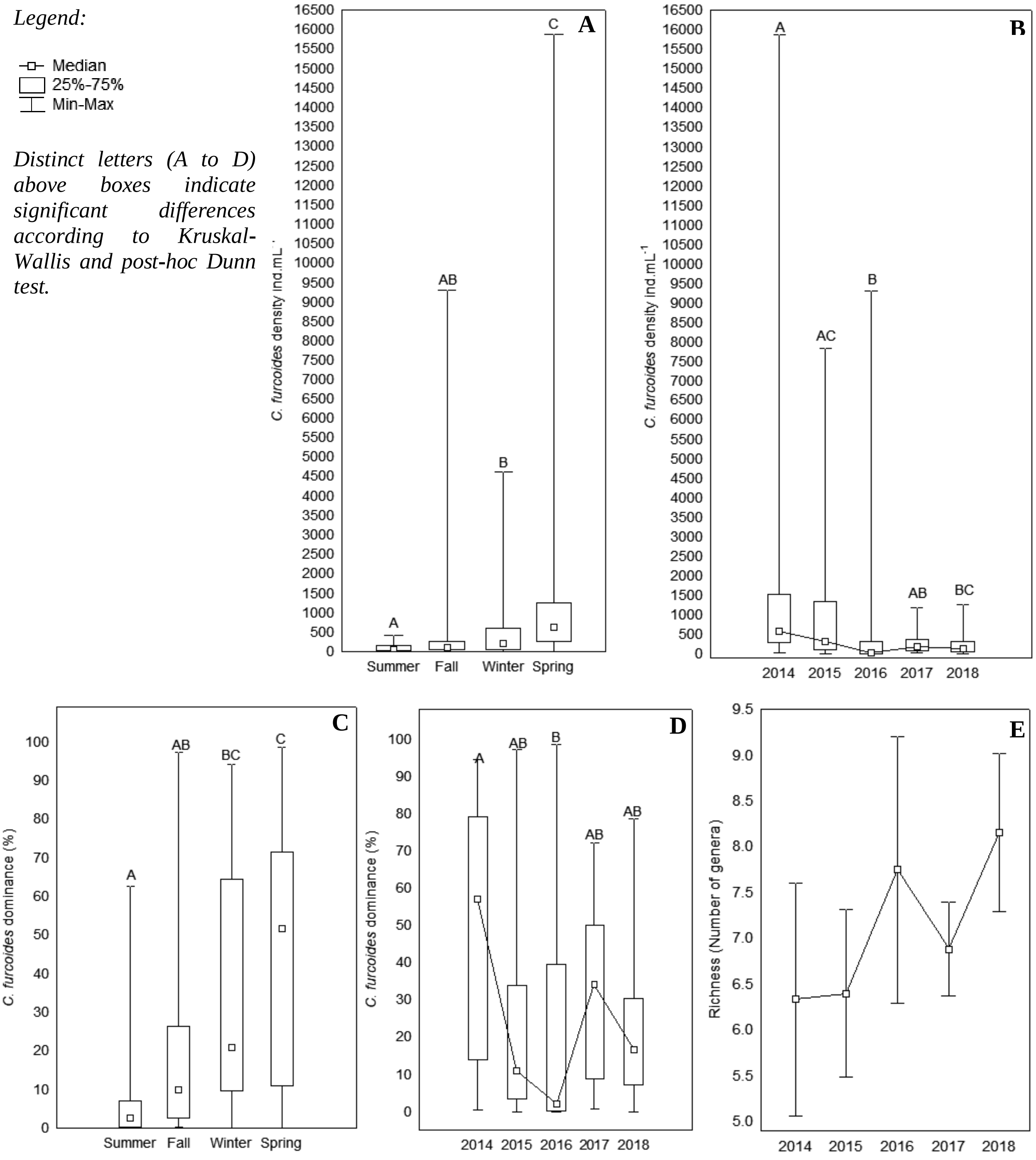
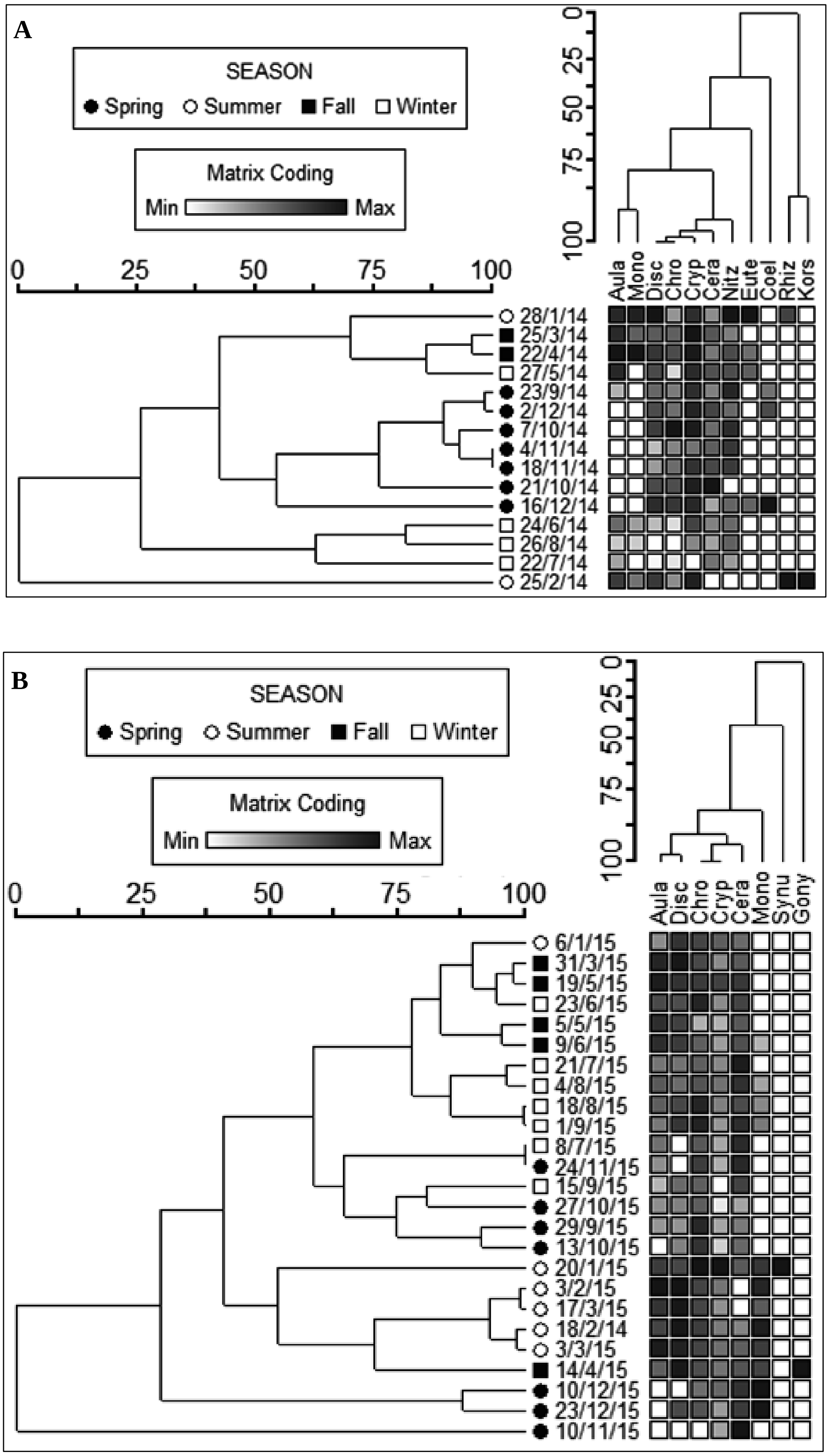


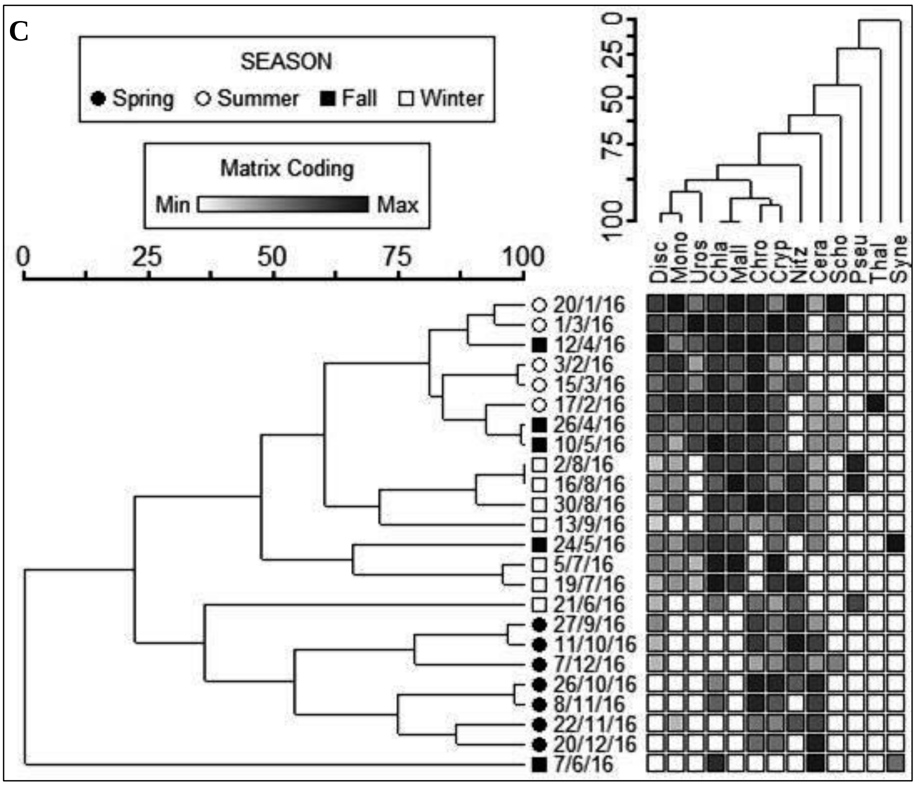
Fig. 7 Boxplot of *Ceratium furcoides'* density along the seasons (**A**) and throughout the years (**B**); *Ceratium furcoides* dominance along the seasons (**C**) and throughout the years (**D**); and plot of means of the richness (number of genera) throughout the years (**E**).



Distinct letters (A to D) above boxes indicate significant differences according to Kruskal-Wallis and post-hoc Dunn test.

Fig. 8 Two-way dendrogram based on the phytoplankton density in 2014 (**A**), 2015 (**B**), 2016 (**C**), 2017 (**D**), 2018 (**E**).




C
SEASON
Spring
Summer
Fall
Winter
Matrix Coding
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75
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20/1/16
1/3/16
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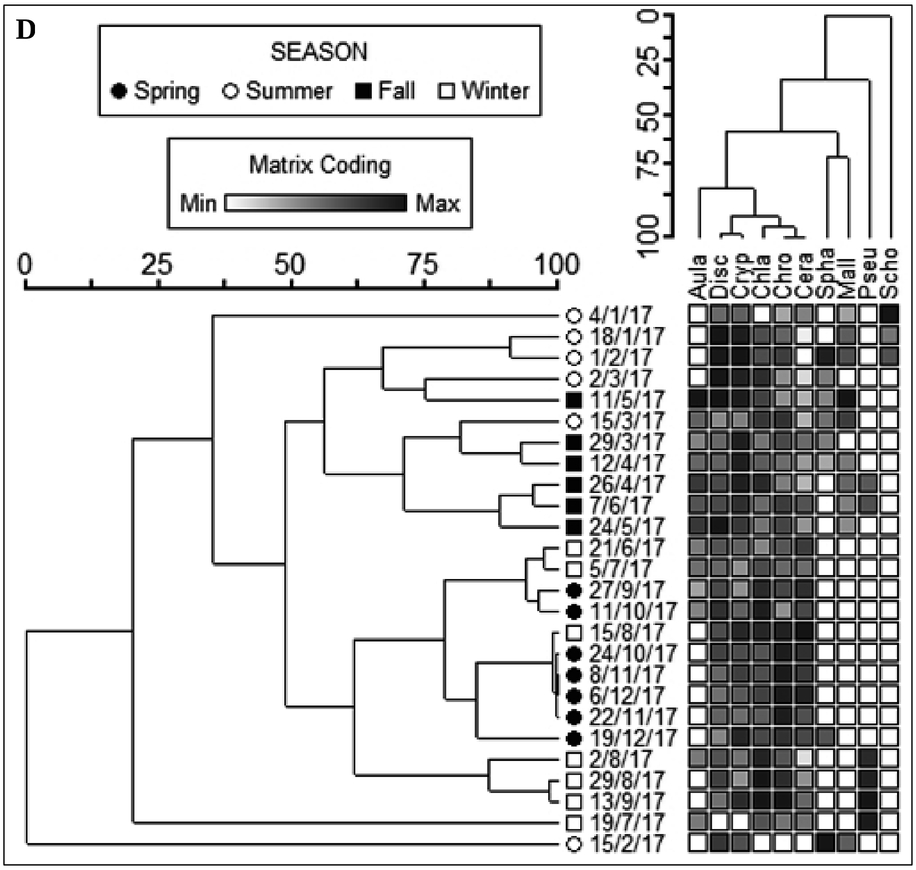
3/2/16
15/3/16
17/2/16
26/4/16
10/5/16
2/8/16
16/8/16
30/8/16
13/9/16
24/5/16
5/7/16
19/7/16
21/6/16
27/9/16
11/10/16
7/12/16
26/10/16
8/11/16
22/11/16
20/12/16
7/6/16
Disc
Mono
Uros
Chla
Mall
Chro
Cryp
Nitz
Cera
Scho
Pseu
Thal
Syne


D
SEASON
Spring
Summer
Fall
Winter
Matrix Coding
Min
Max
0
25
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100
4/1/17
18/1/17
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2/3/17
11/5/17
15/3/17
29/3/17
12/4/17
26/4/17
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6/12/17
22/11/17
19/12/17
2/8/17
29/8/17
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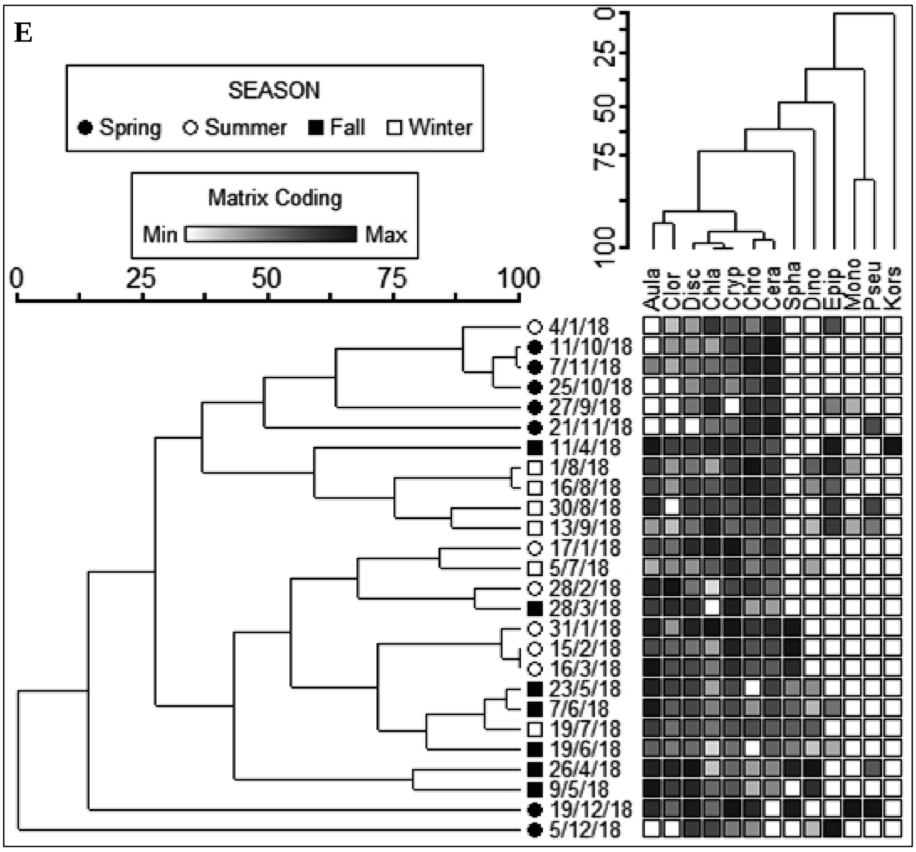
Spha
Mall
Pseu
Scho

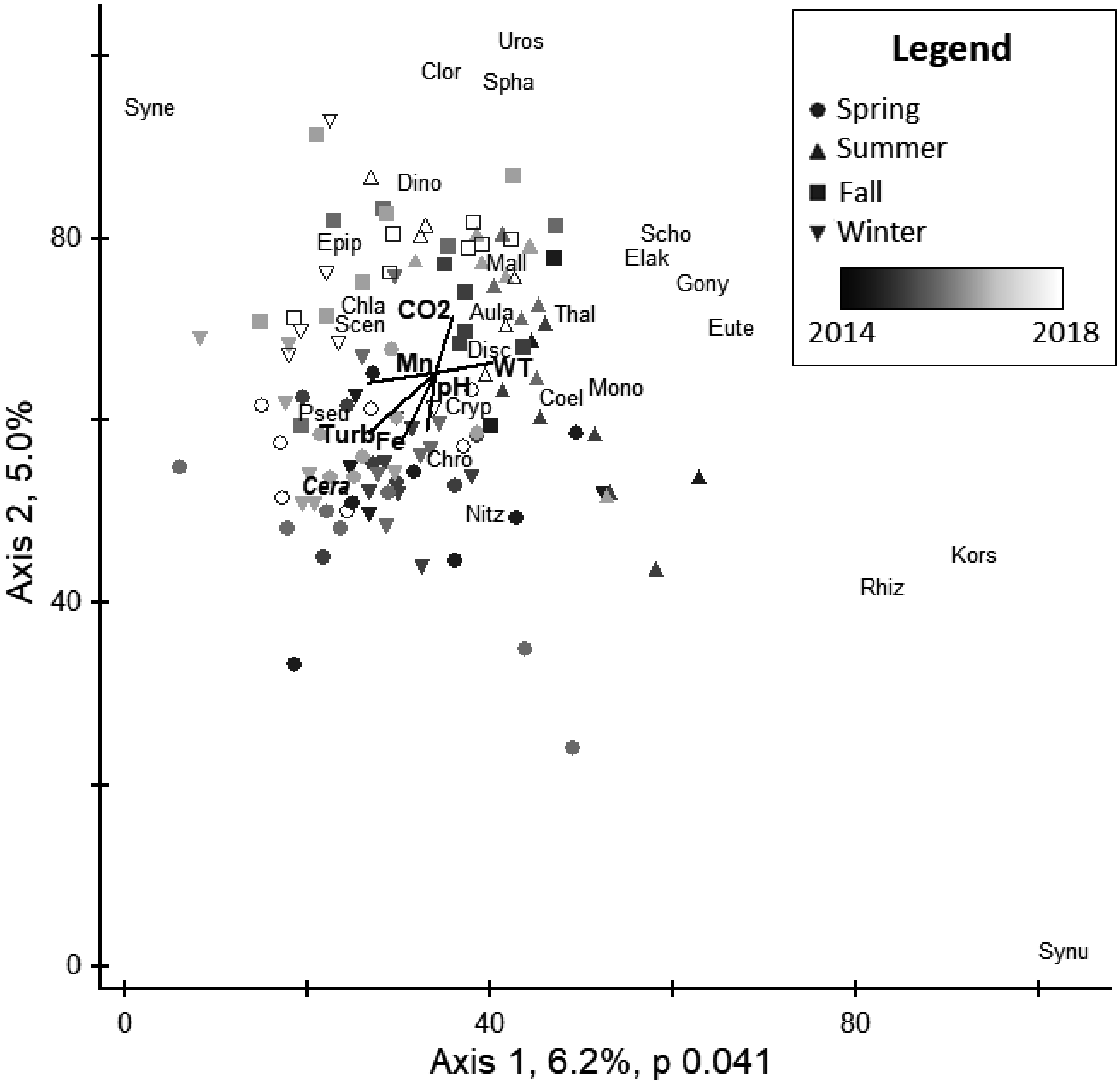


Legend: Aula: Aulacoseira; Disc: Discostella; Nitz: Nitzschia; Rhiz: Rhizosolenia; Thal: Thalassiosira; Uros: Urosolenia; Chla: Chlamydomonas; Clor: non-identified genus of Chlorophyta; Coel: Coelastrum; Elak: Elakatothrix; Eute: Eutetramorus; Kors: Korshikoviella; Mono: Monoraphidium; Scen: Scenedesmus; Scho: Schroederia; Spha: Sphaerocystis; Chro: Chroomonas; Cryp: Cryptomonas; Dino: Dinobryon; Epip: Epipyxis; Mall: Mallomonas; Synu: Synura; Pseu: Pseudanabaena; Syne: Synechococcus; Cera: Ceratium; Gony: Gonyostomum.

Phytoplankton and the environmental variables

The CCA ordination for 25 biotic variables (densities of the genera) and 19 abiotic variables explained a total of 11.2% of data variability in the first two axes (p 0.042) (Fig. 9). The most important biotic variables were *Discostella* (r = 0.5), *Monoraphidium* (r = 0.50), *Rhizosolenia* (r = 0.42), and *Cryptomonas* (r = 0.41) in the composition of the first axis (6.2%); while a non-identified genus of Chlorophyta (r = 0.49), *Sphaerocystis* (r = 0.42) and *Ceratium* (r = -0.41) in the composition of the second axis (5%). From the abiotic variable, only six were plotted: manganese (r = -0.67), turbidity (r = -0.66), and water temperature (r = 0.52) were the principal variables in the first axis; while iron (r = -0.57), turbidity (r = -0.54), CO_2 (0.41), and pH (r = -0.50), were the most important for the second axis. The CCA showed a positive relationship between *Ceratium*, *Chroomonas*, turbidity, and iron, which seemed associated with spring and winter (throughout all the study period, but lower in the last two years: 2017 and 2018). The invader showed a negative relationship with *Discostella*, *Aulacoseira* and *Mallomonas* which showed a tendency towards summer, principally of the first three years of study. *Epipyxis, Chlamydomonas* and *Dinobryon* showed a tendency towards fall and winter of the last years; *Thalassiosira, Schroederia, Elakatothrix,* and *Gonyostomum* towards summer. *Urosolenia,* *Sphaerocystis* and the non-identified genus of Chlorophyta appeared to be associated with fall and summer from 2016-2018 while species like *Rhizosolenia, Korshikoviella, Coelastrum, Monoraphidium,* and *Eutetramorus* showed a tendency towards summer and fall from 2014-2015 (Fig. 9).

Fig. 9 Canonical correspondence analysis (CCA) based on the biotic (densities of the genera) and abiotic variables (meteorological, physical, and chemical).



Legend of biotic variables and abiotic variables

Aula: Aulacoseira; Disc: Discostella; Nitz: Nitzschia; Rhiz: Rhizosolenia; Thal: Thalassiosira; Uros: Urosolenia; Chla: Chlamydomonas; Clor: Cloroficeas; Coel: Coelastrum; Elak: Elakatothrix; Eute: Eutetramorus; Kors: Korshikoviella; Mono: Monoraphidium; Scen: Scenedesmus; Scho: Schoederia; Spha: Sphaerocystis; Chro: Chroomonas sp; Cryp: Cryptomonas; Dino: Dinobryon; Epip: Epipyxis; Mall: Mallomonas; Synu: Synura; Pseu: Pseudanabaena; Syne: Synechococcus; Cera: Ceratium; Gony: Gonyostomum ***(Biotic).*** *Turb: turbidity; Org: organic matter; Fe: iron, Mn: manganese; WT: water temperature; CO2: carbon dioxide; DO: dissolved oxygen; NH4: Ammonium; PO4: Phosphate; Cond: conductivity; Rain (7): weekly precipitation; Tmax: daily maximum temperature; Tmed: daily mean temperature; wind (2): mean wind speed (sampling day and day before)* ***(Abiotic).***

Correlation analysis

During the first year of study *Ceratium furcoides' density* only correlated negatively with *Monoraphidium* and *Rhizosolenia* but not with any general phyla. In the second year, it correlated negatively with three members of Bacillariophyta (*Discostella, Nitzschia,* and *Rhizosolenia)* and *Coelastrum,* and with Bacillariophyta phylum. During the third year the negative correlations continued with two members of Bacillariophyta (*Discostella* and *Urosolenia*), *Chlamydomonas*, *Monoraphidium*, *Dinobryon*, *Mallomonas* and with three different phyla (Bacillariophyta, Chlorophyta, and Ochrophyta). In the fourth year the negative correlations decreased to only *Discostella, Sphaerocystis, Mallomonas, Schroederia,* and two phyla (Bacillariophyta, Ochrophyta) and a positive correlation started to appear with *Chroomonas* and Cryptophyta. During the last year *Ceratium furcoides' density* correlated negatively only with *Aulacoseira*, *Discostella*, the non-identified genus of Chlorophyta and three phyla (Bacillariophyta, Ochrophyta, and Chlorophyta) and the positive correlation with *Chroomonas* and Cryptophyta continued. In summer only negative correlations took place (with *Urosolenia* *Monoraphidium*, and *Coelastrum*), In fall both positive (*Aulacoseira, Nitzschia,* and *Cryptomonas*) and negative (*Urosolenia*, *Chlamydomonas,* the non-identified genus of Chlorophyta, *Schroederia,* and *Sphaerocystis,* and the Chlorophyta phylum) took place, in winter multiple positive (*Aulacoseira, Discostella, Chroomonas* and Bacillariophyta phylum) and negative (*Chlamydomonas,* *Mallomonas*, *Pseudanabaena*, Chlorophyta, Ochrophyta and Cyanobacteria) occurred, and during spring a lot of groups did not appeared (*Urosolenia*, *Rhizosolenia*, *Eutetramorus,* and *Korshikoviella*) the invader presented negative correlations (with *Chlamydomonas* and *Mallomonas*) and also positive ones (with *Aulacoseira, Discostella*, and *Chroomonas*). Furthermore, throughout all the years and the seasons, *Ceratium furcoides' density* showed negative correlation with species richness (number of genera) (Tables 3 and 4).

Regarding the meteorological, physical, and chemical data, the variables that correlated positively with *Ceratium furcoides' density* along the study period were turbidity, pH, organic matter, iron, manganese, and DO. Turbidity correlated from 2015 to 2017 (low to moderate); pH during 2017 and winter (moderate and low); organic matter from 2015 to 2018 (positively low to strong) and during spring, summer, and winter (low); iron during 2015 and 2017 and fall (low to moderate); manganese from 2016 to 2017 (low to moderate); and dissolved oxygen in 2015, 2018, spring and winter (low). Along the study, there were also some abiotic variables that correlated negatively including water temperature, ammonium, CO_2, and conductivity. Water temperature correlated negatively during 2015 and fall (low to moderate); ammonium during 2018 and in winter (low); CO_2 during 2017, 2018, and spring (low); and conductivity during 2014 and 2017 (low to moderate) (Table 5).

Table 3 Spearman´s correlation between *Ceratium furcoides’* density (ind.mL^{-1}) and the phytoplankton genus (only significant correlations values, $p<0.05$). (Legend Fig. 9)

		Aula	Disc	Nitz	Uros	Rhiz	Chla	Clor	Coel	Mono	Scho	Spha	Chro	Cryp	Mall	Pseu	Dino
Years	2014				ND	-0.56	ND	ND		-0.58	ND	ND					
	2015		-0.56	-0.53	ND	-0.45			-0.47		ND	ND					
	2016		-0.67		-0.51	ND	-0.49			-0.63					-0.55		-0.40
	2017		-0.38			ND	ND				-0.37	-0.48	0.55		-0.67		
	2018	-0.42	-0.57			ND	ND	-60					0.52		-0.31		
Seasons	Fall	0.46		0.46	-0.57		-0.51	-0.73			-0.48	-0.50		0.47			
	Spring		-0.34		ND	ND								0.35			
	Summer				-0.59				-0.43	-0.37						ND	
	Winter	0.56	0.39			ND	-0.63				ND		0.36		-0.57	-0.39	

Table 4. Spearman´s correlation between *Ceratium furcoides’* density (ind.mL^{-1}) and the phytoplankton phyla (only significant correlations values, $p<0.05$).

		Bacillariophyta	Chlorophyta	Cryptophyta	Ochrophyta	Cyanobacteria	Richness
Years	2014						-0.59
	2015	-0.49					-0.45
	2016	-0.55	-0.59		-0.57		-0.7
	2017	-0.48		0.37	-0.49		-0.6
	2018	-0.57	-0.43	0.44	-0.35		-0.5
Seasons	Fall		-0.39				-0.45
	Spring						-0.51
	Summer						-0.37
	Winter	0.38	-0.55		-0.54	-0.39	-0.54

Table 5. Spearman´s correlation between *Ceratium furcoides’* density (ind.mL^{-1}) and the meteorological, physical, and chemical variables (only significant correlations values, $p<0.05$). (Legend Fig. 9)

		WT	Turb	pH	DO	Org	NH_4	PO_4	Fe	Mn	CO_2	Cond	Rain(7)	Tmax	Tmed	Wind(2)
Years	2014											-0.58				
	2015	-0.55	0.39		0.49	0.38			0.56					-0.44	-0.43	
	2016		0.56			0.51				0.54						
	2017		0.50	0.60		0.77		0.70	0.41	0.35	-0.43	-0.40				
	2018				0.49	0.51	-0.47				-0.47					
Seasons	Fall	-0.38							0.59							
	Spring				0.47	0.43					-0.41					0.40
	Summer					0.41										
	Winter			0.48	0.36	0.35	-0.41						0.37			

DISCUSSION

In South America, the recent invasion of *Ceratium* is largely a consequence associated with changes in the hydrological regime and water quality of rivers following the construction of numerous reservoirs and their cascades (Padisák et al., 2016). Other factors influencing the dispersal of species of this genus into the continent include human activities like navigation, commercial and sport fishing, ornamental trade, ecotourism, and recreational activities (Incagnone et al., 2015). But although the arrival of cells or cysts is a prerequisite for the establishment of a non-resident species, to be considered invasive, or successful, it is necessary that freshwater habitats provide adequate conditions for cell survival, growth, and the formation of blooms (Meichtry et al., 2016). Cavalcante et al. (2016), after comparing *Ceratium furcoides* blooms, stated that subtropical systems tend to have better conditions for the development of this species.

Southern Brazil, along with southeastern Brazil, southeastern Paraguay, northeastern Argentina and other regions in South America have been demonstrated by Meichtry de Zaburlín et al. (2016) to show the conditions required by *Ceratium furcoides* for its potential establishment and distribution. In the case of Southern Brazil, *Ceratium furcoides* has shown aggressive behaviors, quickly reaching high biomasses after the colonization on a number of systems including Faxinal, Maestra, and in this case also Marrecas, evidencing the invasive nature of this dinoflagellate (Cavalcante et al., 2016, 2013). *Ceratium furcoides' density* during the study (mean of 744.2 ind.mL^{-1}, maximum of 15,865 ind.mL^{-1} and 35 registers above the 500 ind. mL^{-1}) was considerably high when compared with other reservoirs and natural lakes in South America including: Riogrande II reservoir (Colombia) with a maximum of 41 ind.mL^{-1} (Bustamante-Gil et al., 2012), Furnas reservoir (Brazil) a maximum of 29 ind.mL^{-1} (Silva et al., 2012), Yacyreta´ reservoir (Argentina) with a peak of 15 ind.mL^{-1} (Meichtry de Zaburlin et al., 2014), Maestra and Faxinal reservoirs (Southern Brazil) with peaks of 2,680 and 2,819 ind.mL^{-1} (Cavalcante et al., 2016), Xinó reservoir (north-central Brazil) with peaks of 5,600 ind.mL^{-1} , and in a urban shallow lake (Southern Brazil) a density peak of 10,170 ind.mL^{-1} (Silva et al., 2019). When compared with the bloom of 21,455 ind.mL^{-1} at the Billing reservoir in São Paulo, Brazil (Matsumura-Tundisi et al., 2010), the highest density reported in the literature, the 744 ind.mL^{-1} mean and even the maximum density of Marrecas (15,865 ind.mL^{-1}) seemed rather small. However, according to Cavalcante et al. (2016), the peak observed in Billings reservoir was a typographical mistake as the graphical representation of Matsumura-Tundisi et al. (2010) did not exceed the 25 ind.mL^{-1}. If that so, the peak reported in the present study during the spring of 2014 would be considered the highest register of *Ceratium furcoides' density* until now.

The extremely high-density peak during 2014, could be associated with the climatic conditions of the new environment. The process of filling of Marrecas started in November of 2013, it is known that during the first months of this process the concentration of nutrients (trophic upsurge) and the turbidity of the water increases considerably due to resuspension and the existence of terrestrial vegetation before the filling (Geraldes & Boavida, 1999), leaving light as a limiting factor. In Marrecas, although the nutrients measured (nitrate and phosphate) were not higher in the first year, CO_2, organic matter, iron, conductivity and turbidity (2nd highest) were. These conditions of low levels of light and oxygen, and high levels of turbidity, resuspension and some nutrients could have generated opportunities of establishment to a mixotroph such as *Ceratium furcoides* with partial independence of light and the ability to produce cysts under stressful conditions (Cavalcante et al., 2016).

Many studies have described seasonality in *Ceratium* spp., evidencing the relevance of climatic variables regarding *Ceratium* abundance and dominance (Cavalcante et al., 2016; Hickel, 1988; Lindström, 1992; Pollingher, 1988). In this study, the invader showed a seasonal preference towards spring which might be in function of the temperature of this season which corresponds to the optimum for this species (15−23°C, when overlapped the 15-25 ºC of Pollingher, 1988; Van Ginkel et al., 2001; and the 12-23 ºC from Heaney et al., 1988). Other factors including the mixing regime, the availability of nutrients, among other abiotic variables might also be contributing to the seasonality of this species as spring showed higher values of turbidity, manganese, iron, dissolved oxygen, nitrates (although not significant), phosphates, and organic matter; and lower values of conductivity, CO_2, and ammonium; and some of these variables even correlated with the invader density. Spring is a season when an important change in the phytoplankton community occurs in the Northern hemisphere (Forsström et al., 2007), as it follows the strong winter characterized by extremely cold temperatures, surface ice, and snow. It is possible that during the invasion process, *Ceratium furcoides* remains with this tendency towards spring even in subtropical environments. This preference for spring has been observed in other reservoirs in South America including Faxinal, a southern Brazilian reservoir very close to Marrecas (Cavalcante et al., 2016), in an urban shallow lake in southern Brazil (Silva et al., 2019), and in Rio Grande II reservoir in Antioquia, Colombia (Bustamante-Gil et al., 2012). Nevertheless, most of the literature show *Ceratium furcoides* peaks in other seasons including winter (Silva et al., 2012) and fall (Almanza et al., 2016; Chou & Wu, 1998), which were also observed in this study although not as frequent as in spring. But despite summer was the least preferred season for *Ceratium furcoides* in this study, it has been associated with high peaks in Maestra, a reservoir located only 20 km from Marrecas, that differs greatly from Faxinal and Marrecas regarding its trophic state (eutrophic to hypertrophic) which appears to be very important in the Dinoflagellate dynamics (Cavalcante et al., 2016); and in Europe where the species blooms are often in this season (Hickel, 1988; Napiórkowska-Krzebietke et al., 2017; Nõges et al., 2011). In the case of *Ceratium hirundinella*, a close relative of *Ceratium furcoides*, it has shown preference for summer in Spain (Moore, 1981), for summer and the beginning of fall in East Holstein, Germany (Schernewski et al., 2005; Sommer, 1993) and for mid-spring-winter in the Spanish Island of Mallorca (Moyá & Ramón, 1984) showing, as well as *Ceratium furcoides*, a variability of seasonal preferences depending on the area, time, and trophic state of the water body.

The invader showed a positive relationship with turbidity (CCA) and correlated positively from 2015 to 2017. Furthermore, all the invader's high-density peaks (>2500 ind./mL) occurred with turbidities above 10 NTU and the highest peak occurred at the highest turbidity (18 NTU). As Marrecas is considered a mesotrophic reservoir, the turbidities observed in the study were very low, thus they could be either biogenic (consequence of the phytoplankton abundance) or abiogenic (due to abiotic elements like nutrients and metals). As metals such as manganese and iron, which are more abundant in the hypolimnion (Becker et al., 2008a), correlated positively with the invader and showed the same relationship with turbidity in the CCA, we can say that at least partially this positive relationship between turbidity, these metals, and *Ceratium furcoides* might be associated with the mixing regime as stated in Cavalcante et al. (2016). During the mixing period, the sediments from the bottom including metals are resuspended to the epilimnion increasing their levels in the surface and therefore the turbidity (Becker et al., 2008b). This relationship between the invader and the mixing regime is associated with its life cycle. *Ceratium furcoides* can produce cysts or resistant dormant propagules (Hickel, 1988) that are then sunk to the bottom where they persist. During the mixing period, the cysts are resuspended to the epilimnion and the high levels of light and temperature in this upper layer interrupt the dormancy and enable the development of the cysts through a process of excystment (Hickel, 1988). This link between turbulence and *Ceratium* highlights the influence of hydraulic dynamics as one of the primary factors determining the structural and temporal changes in phytoplankton communities regardless of the nutrient concentration, which is characteristic of tropical high-mountain reservoirs (Moreira et al., 2015).

Despite the importance of the mixing regime, it is not the only driver for the species as most of the blooms occurred in spring but it was winter, which corresponds with the period of mixing in nearby reservoirs (Becker et al., 2008b), the season where the resuspension was higher. The temperature might also be explaining the invader population dynamics as all *Ceratium furcoides* peaks occurred in a water temperature range between 14 and 24 °C (mean 19.2) which corresponds to the optimum for this species (15−23°C, Heaney et al., 1988; Pollingher, 1988; Van Ginkel et al., 2001). However, winters in Marrecas often showed temperatures below these values and therefore it might not have been warm enough for the population to grow optimally. The species avoided also the extremely high temperatures of summer (mean of 25°C) as it corresponded to the period of population decline in other studies (Pollingher & Hickel, 1991).

Ceratium furcoides' density showed also a positive correlation with organic matter (2015-2018 and spring, summer, and winter), pH (CCA), and dissolved oxygen (2015, 2018, spring and winter). It is not clear if high organic matter, well-oxygenated, with low CO_2, and neutral to slightly basic waters are favorable condition for the development of this species, as it has been established for other dinoflagellates (Popovsky & Pfiester, 1990) or if these conditions are the results of its presence and development, since *Ceratium furcoides* exhibits high representation and biomass in the phytoplankton community and oxygen is a by-product of the photosynthetic process which decreases CO_2 and increases pH. This possible increase of dissolved oxygen as a result of the invader's photosynthetic activity has been detected in other studies (Silva et al., 2018). However, it is important to continue the monitoring of this variable along with the invader as Nicholls et al. (1980) found out that the collapse of a population of *Ceratium hirundinella* after a massive bloom in Heart Lake (Ontario) resulted in the death of large quantities of fish.

Biological invasions can cause important alterations in the structure of ecosystems including modifications in the composition of species due to local extinctions or to the facilitation of new colonizers, they can also change the community dominance and affect local species (Gurevitch & Padilla, 2004; Mooney & Cleland, 2001). The understanding of the ecological interactions between the local and exotic species over the colonization and establishment process is key for the assessment of the impacts on the system regarding the invader (Crossetti et al., 2018; Silva et al., 2019). In the case of phytoplankton, there are few studies in different tropical and subtropical aquatic systems that unveiled some of the responses of the local phytoplankton against the invasion of *Ceratium furcoides*. In general, the arrival of the dinoflagellate seems to overturn the cyanobacterial dominance in these systems (Cavalcante et al., 2016; Crossetti et al., 2018; Nishimura et al., 2015) however, in some cases the invader has shown coexistence with the cyanobacteria during each other blooms (de Almeida et al., 2016; Silva et al., 2012) and more recently a potential competition pattern between these taxa has been detected after three years of the arrival of *Ceratium furcoides* in an urban shallow lake (Silva et al., 2019).

In this study *Chroomonas*, *Cryptomonas*, *Discostella*, and after 2016 also *Chlamydomonas* were the only taxa co-occurring during *Ceratium* peaks, all of them were present in more than 90% of the samples so their presence may not have been a result of *Ceratium* dominance but may just be explained in function of their endurance and high tolerance (Reynolds et al., 2002); however their abundance might, as the first two genus correlated positively with the invader while the last two correlated negatively, these interactions will be explained further on in the following paragraphs.

Although Cyanobacteria has co-occurred with *Ceratium* in some studies (de Almeida et al., 2016; Silva et al., 2012), in Marrecas during the period of study, *Pseudanaeba*, a member of this phylum, appeared in 2016 and increased its dominance alternating with *Ceratium furcoides* dominance during the last years, and correlated negatively in winter (-0.39) when its densities were higher. This interaction between Cyanobacteria and *Ceratium furcoides* was similar to the one detected by Silva et al. (2019) inferring, although not conclusively, competition between these groups.

Even though *Discostella* was observed during the dinoflagellate peaks, it correlated negatively with the invader during the whole period of study, except in winter. As the rest of the members of Bacillariophyta, it rarely (only 2 occasions in October 2014 and September 2015) showed values above the mean during a *Ceratium furcoides* peak (density and/or dominance). Additionally, this diatom showed a clear preference towards summer and fall (the least favorite for the invader), which was shared with *Urosolenia* another member of the Bacillariophyta that appeared for the first time in 2016. During all *Ceratium furcoides* peaks (>1000 ind.mL^{-1}, >30%), *Urosolenia* was not present, moreover, its density correlated negatively with the invader. *Rhizosolenia* also showed negative correlation with the invader during the first two years (-0.56 and -0.45) and afterwards it disappeared of the reservoir, suggesting, although not conclusively, a local extinction result from competition with the invader. But although this negative relationship between Bacillariophyta and *Ceratium furcoides* might be due to interspecific competition, as has been suggested in other studies (Almanza et al., 2016), their positive correlation in winter, and in fall with *Aulacoseira* and *Nitzschia*, members of this phylum, suggests competition only as a partial driver. The higher densities of Bacillariophyta in summer and fall might be in function of its preference for clear waters (Reynolds et al., 2002) as turbidity decreases in these seasons. Furthermore, its decrease in spring might be explained by the vulnerability of these taxa to pH rise and CO_2 decrease (Reynolds et al., 2002), conditions met in this season.

After *Ceratium*, the highest peaks observed throughout the study were caused by Chlorophyta, these always occurred in summer, except in 2015 were it occurred in late spring. Chlorophyta is a common component of the freshwater phytoplankton in Brazilian tropical and subtropical lakes and usually co-occur with *Ceratium* blooms (Cassol, 2014; Hackbart et al., 2015). However, in Marrecas, the Chlorophyta (represented principally by *Eutetramorus* and *Korshikoviella*, responsible for the peak in 2014; *Schroederia* and *Monoraphidium* responsible for the peaks in 2015 and 2016; and *Sphaerocystis* responsible for the peaks in 2017 and 2018) appeared to avoid *Ceratium* peaks. Furthermore, the last three genera correlated negatively with the invader (in at least two of the five years and one season). In general, chlorophytes are opportunistic organisms, which grow rapidly and depend on high levels of nutrients and light intensity (Olrik, 1994), this negative interaction with *Ceratium* might be a result of competition for phosphate as it was very low during fall and summer and its population decrease in winter and spring might be due to the mixing, as this group is very susceptible to it (Reynolds et al., 2002). Chlamydomonas, another genus of Chlorophyta, also showed negative correlation with the invader during 2016 (-0.49), fall and winter (-0.51 and -0.63), this has also been observed in other south American reservoirs (Bustamante-Gil et al., 2012) and it is probably due to the high vulnerability of the genus (functional group X2) to mixing (Vanessa Becker, Huszar, & Crossetti, 2009; Reynolds et al., 2002), conditions preferred by *Ceratium furcoides* in this study.

Ochrophyta represented by *Mallomona*s and *Dinobryon*, correlated negatively with the invader in 2016-2018 and during winter. These two genera are very susceptible to low levels of CO_2 which might be the reason why it avoided springs, even though they are well represented in mesotrophic lakes they tend to be sensitive to nutrient enrichment and the additional demands that high biomass may place on the carbon and light fluxes (interspecific competition) (Reynolds et al., 2002). Its negative correlation with the invader in winter might be due to the lower levels of light and higher turbidity resulting in competition for this resource.

In a variety of reservoirs, clear positive interactions between the local phytoplankton and *Ceratium* have been detected, especially with Cyanobacteria, Chlorophyta, and Euglenozoa (de Almeida et al., 2013; Crossetti et al., 2018; Silva et al., 2012; Silva et al., 2019). In Marrecas, although *Ceratium furcoides* did not correlated positively with these groups it did with *Chroomonas* during the last years of the study (0.55, 0.52, respectively) and in winter (0.36), with *Cryptomonas* during spring (0.35) and fall (0.47), and with *Aulacoseira* during fall (0.46) and winter (0.56). These positive interactions might be in function of shared preferences between the groups. Like *Ceratium* in this study, *Chroomonas* and *Cryptomonas*, as they are well adapted to low light levels (group Y, Reynolds et al., 2002), have been associated with turbulent waters and periods of high water-column mixing in different studies (Klaveness, 1988; Sommer, 1981). *Aulacoseira* has also shown high resistance to mild-light conditions and it has shown vulnerability towards stratified waters, preferring turbulent conditions (Reynolds et al., 2002). However, there is not enough ecological information available on these groups, especially regarding their interactions with *Ceratium* species, and consequently, this field is yet to be explored.

One of the major general threats regarding biological invasions is the loss of species through local extinctions (Gurevitch & Padilla, 2004; Mooney & Cleland, 2001). Almanza et al. (2016) found a decrease in biodiversity and species richness related to the colonization process *Ceratium furcoides* and its blooms in a Chilean eutrophic lake. Throughout the present study, the same phenomenon was observed, *Ceratium furcoides' density* showed negative correlations (2014-2018: -0.59, -0.45, -0.70, -0.60 and -0.50, respectively; fall -0.45, spring -0.51, summer -0.37, and winter -0.54) with the species richness (number of genera) of the reservoir. This negative interaction might be a result of interspecific competition observed in other aquatic systems during *Ceratium furcoides* blooms (Almanza et al., 2016; Silva et al., 2019). *Ceratium furcoides* has been proven to be an optimal competitor as it has the ability to encyst in order to survive harsh conditions (Hickel, 1988), it also has two flagella that enable it to migrate vertically reaching the most favorable conditions of nutrients and light (Baek et al., 2008), its morphology confers it a low rate of cell sinking and herbivory (Febvre-Chevalier & Febvre, 1994; Sommer et al., 2003), and as a mixotroph it can predate bacteria or even other phytoplankton and survive with low levels of nutrients (Pollingher, 1988; Smalley et al., 2003) outcompeting the phytoplankton in multiple countries around the world.

During the study, especially in the last years, the invader's density and its peaks (amount and intensity) decreased considerably. The above might be a consequence of the interspecific competition resulting from the establishment of a higher number of taxa in the last three years, which would explain the decreased of peaks in the rest of the groups as well, leading to an equilibrium state, clear of blooms as happened recently in an urban shallow lake in Southern Brazil (Silva et al., 2019). However, more monitoring is needed to corroborate this phenomenon. The decrease in *Ceratium furcoides* blooms might also be related with abiotic factors such as weaker or shorter mixing periods during the last years and therefore low cyst resuspension, nevertheless this would not explain the decrease in the blooms of other groups. Finally, another possibility might be associated with an increase in the herbivory evidencing a top-down control in the phytoplankton, due to the arrival of new taxa with the time passed, creating an environment rich in zooplankton (as copepods, cladocerans), and predators (as other dinoflagellates species) that have proven effective reducing *Ceratium* blooms (Nielsen, 1991; Olseng et al., 2002). However, this is only speculative as the study did not assess the zooplankton and did not found representative (>10%) populations of other dinoflagellates that could predate *Ceratium furcoides*.

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