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Predatory behavior of *Frontonia leucas* (Ehrenberg, 1833) (Alveolata, Ciliophora, Hymenostomatida) in aquatic sites in the semiarid region of Brazil

Comportamento predatório de *Frontonia leucas* (Ehrenberg, 1833) (Alveolata, Ciliophora, Hymenostomatida) em diferentes corpos d'água do semiárido brasileiro

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Abstract: Aim: To investigate the predatory behavior of the ciliated microeukaryote *Frontonia leucas* (Ehrenberg, 1833) in aquatic environments in the semiarid region of Brazil. **Methods:** Water samples were collected in three lotic and two lentic aquatic sites in southwestern Bahia State, Brazil. Individuals of *Frontonia leucas* were observed and recorded *in vivo* for a total of 20 hours using an optical microscope with an attached camera. The following physical-chemical variables were recorded during sample collection: total dissolved solids, water transparency, pH, electrical conductivity, and water temperature. **Results:** The ingestion of 18 food types were observed – i) Amoebozoa (7 *taxa*), ii) Bacillariophyta (2 *taxa*), iii) Ciliophora (1 *taxa*), iv) Zygnematophyceae (5 *taxa*), and v) Rotifera: (3 *taxa*). Thirteen food items were recorded here for the first time (5 species of testate amoebas from the genera *Cylindrifflugia, Difflugia,* and *Netzelia*, one genus of the ciliate *Vorticella*, four genera of microalgae, three desmids [*Micrasterias, Pleurotaenium,* and *Cosmarium*], one filamentous Zygnematophyceae [*Spirogyra*], and three micrometazoans *taxa* Rotifera [*Lecane,* and Bdelloidea]. The size of the food items ranged from 50 to 1100 μm in length, with many of them larger than the ciliate predator itself. **Conclusions:** The results indicate *F. leucas* as an omnivorous predator that can contribute to population control in aquatic ecosystems.

Keywords: ciliate; food items; predator; prey.

Resumo: Objetivo: Análise do comportamento predatório do microeucarioto ciliado *Frontonia leucas* (Ehrenberg, 1833) em cinco corpos aquáticos do sudoeste da Bahia, região semiárida brasileira. **Métodos:** As amostras de água foram coletadas em cinco corpos aquáticos do Sudoeste da Bahia, Brasil, sendo três lóticos e dois lênticos. Os indivíduos foram analisados *in vivo* com auxílio de microscópio óptico com câmera fotográfica acoplada, totalizando 20 horas de observação. Durante a coleta das amostras foram registradas as seguintes variáveis físico-químicas: sólidos totais dissolvidos, transparência da água, pH, condutividade elétrica e temperatura da água. **Resultados:** Foi observada a ingestão de 18 tipos de alimentos por *F. leucas* distribuídos nos seguintes grupos: i) Amoebozoa: (7 *taxa*), ii) Bacillariophyta (2 *taxa*), iii) Ciliophora (1 *taxa*), iv) Zygnematophyceae (5 *taxa*) e v) Rotifera: (3 *taxa*), e incluem 13 *taxa* aqui registrados pela primeira vez, sendo cinco espécies de amebas testadas dos gêneros *Cylindrifflugia, Difflugia* e *Netzelia*, um gênero de ciliado *Vorticella*, quatro gêneros de microalgas sendo três desmidias (*Micrasterias*, *Pleurotaenium* e *Cosmarium*) e uma filamentosa Zygnematophyceae (*Spirogyra*) e três *taxa* de micrometazoários Rotifera (*Lecane* e Bdelloidea). O tamanho dos itens alimentares variou de 50 a 1100 µm de comprimento, sendo muitos deles maiores que o próprio ciliado. **Conclusões:** Os resultados revelam a plasticidade alimentar de *F. leucas* em condições naturais, alimentando-se de protistas, microalgas e até mesmo pequenos animais, podendo assim ser considerado como onívoro, tendo importante contribuição para o controle de populações em ecossistemas límnicos.

Palavras-chave: ciliados; itens alimentares; predador; presa.

1. Introduction

Frontonia leucas (Ehrenberg, 1833) is a ciliate species belonging to the family Frontoniidae Kahl, 1926, class Oligohymenophorea de Puytorac et al., 1974, of the phylum Ciliophora (Alveolata), which encompasses highly diversified microeukaryotes (Dunthorn et al., 2015; Fernandes & Schrago, 2019). *Frontonia leucas* is found in lotic and lentic waters throughout the year, living close to sediments and in plankton (Dias & D'Agosto, 2006).

Frontonia is reported to have a wide food spectrum composed of bacteria, heterotrophic and autotrophic flagellated protists, diatoms, "microalgae" up to 50 µm in diameter, naked amoebas, testate amoebae, ciliates, and even small metazoans such as Rotifera; cases of cannibalism have been reported (Beers, 1933; Devi, 1964; Foissner et al., 1999; Dias & D'Agosto, 2006). *Frontonia leucas* is able to feed on items larger than the width of its own body.

Studies of the predatory behavior of *F. leucas* allow us to understand how it interacts with other organisms in aquatic environments, reveal details of the complex ecological dynamics of these ecosystems, and indicates its role in regulating the populations of several species and the stability of these environments.

The semiarid region of Brazil is characterized by complex climate patterns and irregular rainfall. It comprises numerous aquatic ecosystems with the potential for harboring *F. leucas*, including artificial reservoirs, shallow natural lakes, streams, and rivers (Medeiros & Maltchik, 2001; Maltchik & Medeiros, 2006;). The organisms that populate these ecosystems are known to exhibit significant changes in their compositions and dynamics (Cardoso et al., 2012).

The present work recorded the organisms ingested by *Frontonia leucas* in five aquatic bodies (three lotic and two lentic) in the semiarid region of Bahia State (BA), Brazil. Our results may have practical implications for bioremediation processes such as bioaugmentation – a technique in which microorganisms are introduced into a given ecosystem to accelerate natural biological processes (Zhang et al., 2017; Shah, 2017) that can improve water quality. This research also provides a broader view of evolutionary strategies and behavioral adaptations in ciliates and other predatory organisms in limnic environments.

2. Material and Methods

Samples were collected during three temporal periods: C1 - April/2023; C2 - May/2023; and C3 - June/2023. Sampling in C1 was carried out in the Boa Nova National Park (PARNA) and the Boa Nova Wildlife Refuge (REVIS), both located in the central southern region of Bahia State, in the municipality of Boa Nova. *Frontonia leucas* was recorded in samples from three streams (Cachoeira Sete de Setembro, Riacho das Traíras, and Rio Uruba). Sampling in C2 was carried out in lakes at Lagoa Fazenda, Rio dos Porcos, and Barra do Choça in Bahia State. Sampling in C3 was carried out in Deinho Lake, located in the rural area of Poções, Bahia. Collections were made at as many localities as possible during each sampling period to verify the occurrence of *F. leucas* as well as the breadth of the variety of food items ingested.

Samples of approximately 500 ml of water were collected at each site, including scraping of approximately 2 cm of sediment from the borders of the aquatic bodies. Sediment sampling was carried out using a ladle. The samples were stored in plastic bottles, accommodated in isothermal boxes, and transported for microscopic analysis at the Limnologia e Biomonitoramento Laboratory of the Universidade Federal da Bahia – Instituto Multidisciplinar em Saúde – Campus Anísio Teixeira (UFBA/IMS/CAT).

Simultaneously, the following physical-chemical properties were recorded in the field: electrical conductivity (µS/cm), pH, total dissolved solids (ppm), and water temperature (°C), using a portable multiparameter probe (AKSO®). Water transparency (cm) and depth (cm) measurements were carried out using a Secchi disk and a graduated tape respectively.

The samples were observed in the laboratory using a Sedgwick-Rafter chamber under an optical microscope with an attached photographic camera (Olympus® Model CX31RTSF). Photomicrographs and films were recorded to better observe the behavior and morphology of *F. leucas*, totaling 20 hours of observation. Taxonomic identifications of *F. leucas* and its food items were carried out through the *in vivo* observation of specimens and consulting the specific literature: Ciliophora: Foissner et al. (1994) and Foissner & Berger (1996); Amoebozoa: Gauthier-Liévre & Thomas (1958), Decloitre (1962), Ogden & Hedley (1980), and Silva et al. (2009); microalgae: Bicudo & Menezes (2006) and Oliveira et al. (2014); and Rotifera: Koste (1978) and Koste & Shiel (1986)

The taxonomic identification of *F. leucas* was based on morphological characteristics, mainly its single contractile vacuole with long collecting channels, and its oral apparatus (located at the end of the first quarter of its body) which is small when compared to its cell size (Foissner et al., 1994).

3. Results and Discussion

A total of 55 *Frontonia leucas* individuals were recorded ingesting 18 different *taxa*, distributed into the following groups: i) Amoebozoa (7 *taxa*); ii) Bacillariophyta (2 *taxa*); iii) Ciliophora (1 *taxa*); iv) Zygnematophyceae (5 *taxa*); and v) Rotifera (3 *taxa*) (Table 1, Figure 1, Figure 2).

Records of *F. leucas* were distributed among three municipalities (Boa Nova, Poções, and Barra do Choça, with 24, 20, and 11 individuals observed respectively), with the identification of 109 food items. Based on these data, the numerical frequency percentages (NF%) of each item were calculated in each type of environment [lentic (Barra do Choça, and Poções) and lotic (Boa Nova)]. Additionally, considering the number of food items and their quantities, the frequency percentages of each food item in each aquatic body were calculated. *Arcella hemisphaerica undulata* was the food item with the highest observed total NF% (30.3%); at site 4 (Córrego José Miguel, Boa Nova - BA), this was the only food item observed (100%); at site 5 (Riacho das Traíras, Boa Nova-BA), four types of food items were recorded, with 90.6% of all of the food items

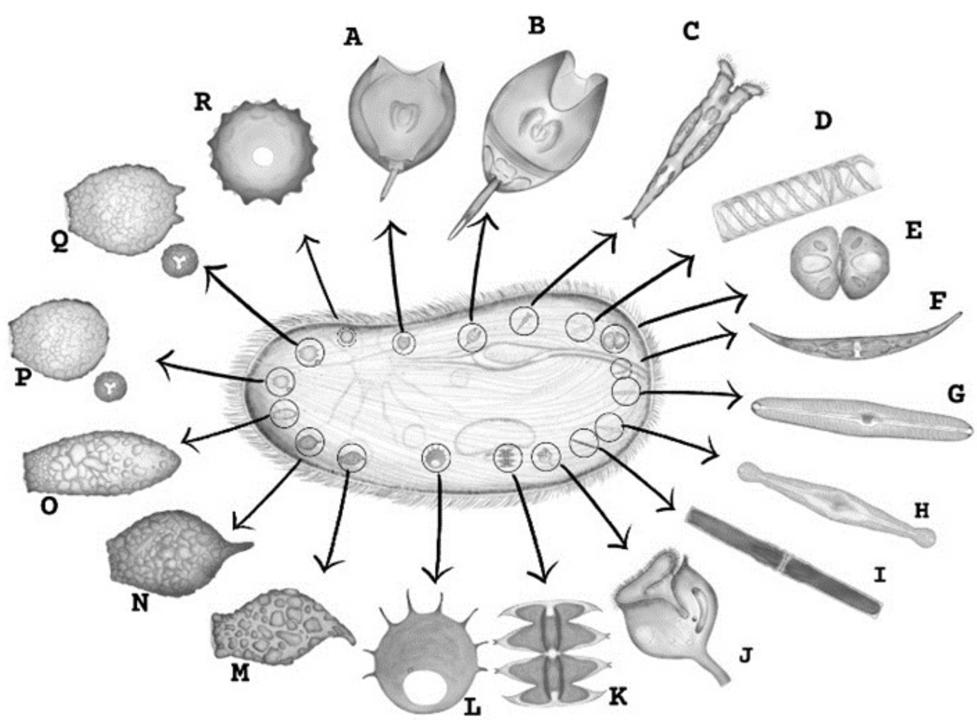

Figure 1. Schematic representation of food items ingested by *Frontonia leucas* in lentic and lotic aquatic environments in the semiarid region of Brazil. **A:** *Lecane cornuta,* **B:** *Lecane bulla,* **C:** Bdelloidea, **D:** *Spirogyra* sp., **E:** *Cosmarium* sp., **F:** *Closterium* sp., **G:** *Pinnularia* sp.1., **H:** *Pinnularia* sp.2, **I:** *Pleurotaenium trabecula* var. *elongatum*, **J:** *Vorticella* sp., **K:** *Micrasterias* sp., **L:** *Centropyxis aculeata,* **M:** *Difflugia angustata,* **N:** *Cylindrifflugia elegans,* **O:** *Cylindrifflugia lanceolata,* **P:** *Netzelia lobostoma,* **Q:** *Netzelia lobostoma cornuta*, **R:** *Arcella hemisphaerica undulata.*

Table 1. Numerical frequency of food items consumed by *Frontonia leucas* in lentic and lotic environments in the semiarid region of Brazil.

Food items	Barra do Choça	Poções	PARNA E REVIS de Boa Nova				NFt (%)
	1	2	3	4	5	6	
AMOEBOZOA							
Arcellidae Ehrenberg, 1843							
Arcella hemisphaerica undulata Deflandre, 1928	3.6	0	0	100	90.6	0	**30.3**
Centropyxidae Jung, 1942							
Centropyxis aculeata (Ehrenberg, 1838)	0	0	0	0	3.1	0	**0.9**
Cylindriflugiidae González-Miguéns et al., 2022							
Cylindrifflugia elegans (Penard, 1890)	0	16.3	0	0	0	0	**6.4**
Cylindrifflugia lanceolata (Penard, 1890)	0	0	0	0	3.1	0	**0.9**
Difflugiidae Awerintzew, 1906							
Difflugia angustata (Deflandre, 1926)	0	4.7	0	0	0	0	**1.8**
Netzeliidae Kosakyan et al., 2016							
Netzelia lobostoma (Leidy, 1874)	3.6	2.3	0	0	0	0	**1.8**
Netzelia lobostoma cornuta (Gauthier-Liévre & Thomas, 1958)	25	0	0	0	0	0	**6.4**
BACILLARIOPHYTA							
Pinnulariaceae D.G.Mann							
Pinnularia sp1.	3.6	0	0	0	3.1	0	**1.8**
Pinnularia sp2.	0	14	0	0	0	0	**5.5**
CILIOPHORA							
Vorticellidae Ehrenberg, 1838							
Vorticella sp.	0	0	100	0	0	0	**0.9**
CHAROPHYTA							
Zygnematophyceae Round ex Guiry							
Closteriaceae Bessey							
Closterium sp.	14.3	0	0	0	0	0	**3.7**
Desmidiaceae Ralfs							
Cosmarium sp.	21.4	0	0	0	0	0	**5.5**
Micrasterias sp.	7.1	0	0	0	0	0	**1.8**
Pleurotaenium trabecula var. *elongatum* (Cedergren)	10.7	0	0	0	0	0	**2.8**
Spirogyraceae Bessey							
Spirogyra sp.	10.7	44.2	0	0	0	0	**20.2**
METAZOA							
ROTIFERA							
Bdelloidea	0	0	0	0	0	100	**1.8**
Lecanidae Rename, 1933							
Lecane bulla (Gosse, 1851)	0	14	0	0	0	0	**5.5**
Lecane cornuta (Muller, 1786)	0	4.7	0	0	0	0	**1.8**
Number of *Frontonia leucas* individuals observed	**11**	**20**	**1**	**2**	**19**	**2**	**55**
Number of food items identified	**28**	**43**	**1**	**3**	**32**	**2**	**109**

(1) Fazenda Rio dos Porcos, Barra do Choça – BA; (2) Lagoa do Deinho, Poções – BA; (3) Cachoeira Sete de Setembro, Boa Nova - BA; (4) Córrego José Miguel, Boa Nova - BA; (5) Riacho das Traíras, Boa Nova – BA; (6) Rio Uruba, Boa Nova - BA. NFt (%): Total Numerical Frequency.

consumed by *F. leucas* individuals being observed at this site (Table 1).

The food items recorded here corroborate data available in the literature (Dias & D'Agosto, 2006), but include 13 *taxa* recorded for the first time (five species of testate amoebae of the genera *Cylindrifflugia*, *Difflugia,* and *Netzelia*, a genus of ciliate *Vorticella*, four genera of microalgae (three desmids [*Micrasterias*, *Pleurotaenium,* and *Cosmarium* and one filamentous Zygnematophyceae (*Spirogyra*)], and three micrometazoan Rotifera *taxa* (*Lecane* sp. and Bdelloidea). This variety of food items consumed by *F. leucas* evidences its omnivorous nature and its great plasticity for occupying aquatic bodies having different trophic levels. Under more eutrophic conditions with abundant bacteria, they can become facultative bacterivores (Primc, 1988).

Considering the 18 food items ingested, testate amoebae represented 48.5%, followed by microalgae (41.3%), rotifers (9.1%), and ciliates (0.9%). *Arcella hemisphaerica undulata* was the

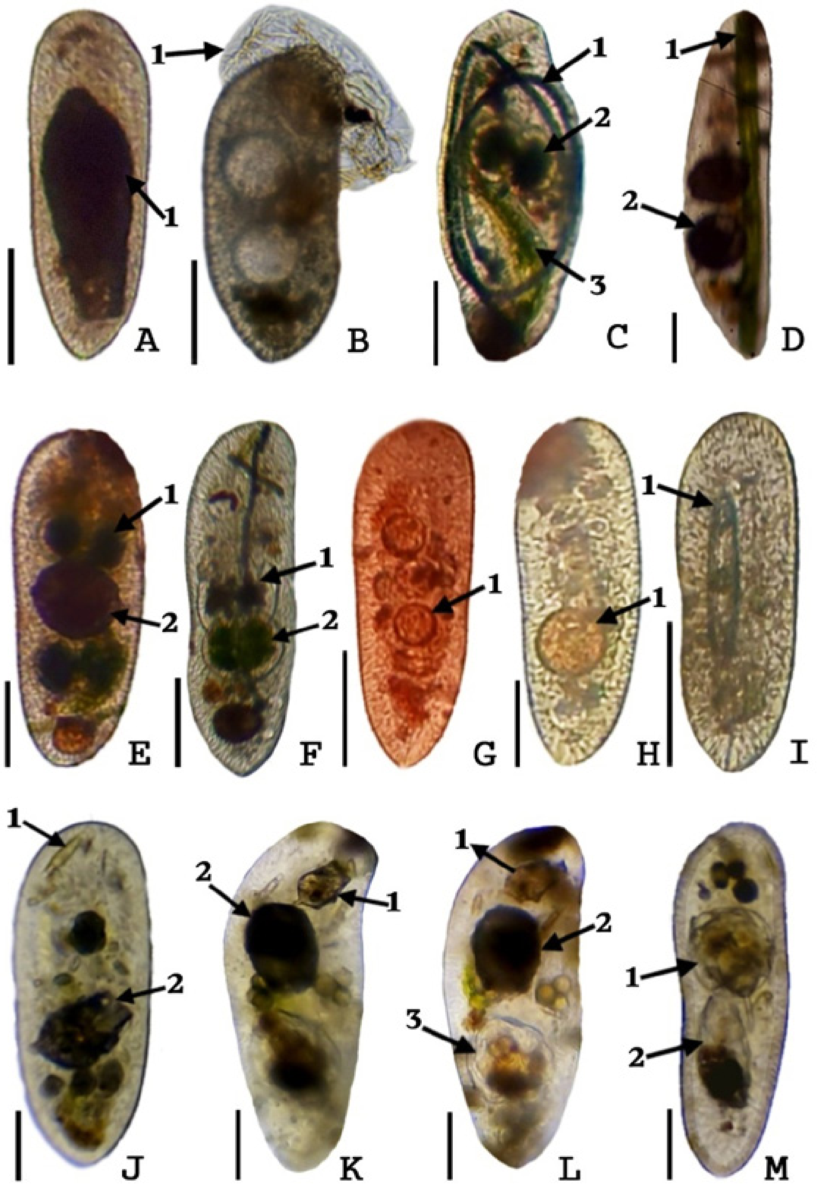

Figure 2. Food items ingested by *Frontonia leucas* in aquatic sites in the Brazilian semiarid region. **A:** 1 - *Cylindrifflugia lanceolata*; **B:** 1 - Bdelloidea; **C:** 1 - *Spirogyra* sp., 2 - *Cosmarium* sp.; 3 - *Closterium* sp.; **D:** 1 - *Pleurotaenium trabecula* var. *elongatum*, 2 – *Netzelia lobostoma cornuta;* **E:** 1- *Cosmarium* sp.; 2 – *Netzelia lobostoma cornuta;* **F:** 1 - *Micrasterias* sp.; 2 - *Cosmarium* sp.; **G** and **H:** 1 - *Arcella hemisphaerica undulata;* **I:** 1 -*Pinnularia* sp.1.; **J:** 1 - *Pinnularia* sp.2, 2 - *Cylindrifflugia elegans;* **K:** 1 - *Difflugia. angustata,* 2 - *Netzelia lobostoma;* **L**: 1 - *Difflugia angustata,* 2 - *Netzelia lobostoma,* 3 *Lecane bulla;* **M:** 1 - *Lecane cornuta*, and 2 - *L. bulla*. Bars = 100 µm.

most consumed food item (30.3%), followed by *Spirogyra* sp. (20.2%) (Table 1). This is the only study that has provided quantitative data on the food items ingested by *F. leucas*, making comparisons impossible.

Considering all of the aquatic sites examined, lentic environments presented the greatest diversity of consumed *taxa* (13) as compared to lotic environments (6) (Table 1). Microalgae were the food items most consumed in lentic environments (62%), principally *Spirogyra* sp. (31%), followed by testate amoebae (26.8%) and rotifers (11.3%), while in lotic environments testate amoebae were the predominant item in the diet of *F. leucas*, representing 89.5% of all food items, followed by microalgae and rotifers (5.3% each) (Table 1). These differences reveal the plasticity of food consumption by *F. leucas* and reflect the fact that planktonic communities respond to alterations of the hydrological and abiotic characteristics of their environments, with microalgae being predominant in lentic environments (Nascimento & Bortolini, 2022).

This study demonstrated, as reported by Foissner et al. (1994), large variations in the observed sizes of *F. leucas* individuals, ranging from 160 to 700 µm in length. These variations are strictly related to the environment and the food item ingested, as this microeukaryote has the ability to expand up to two-thirds of its original body size during food ingestion without any cellular damage (Goldsmith, 1922). The largest individual of *F. leucas* was recorded in Barra do Choça (700 µm long); it had ingested both *Pleurotaenium trabecula* (660 µm) and *Netzelia lobostoma* var. *cornuta* (100 µm) and stood out from other specimens observed in the same location (450 to 500 µm long); it was likewise observed ingesting other types of foods during the observation period [such as *Micrasterias* sp. (90 µm), *Cosmarium* sp. (90 µm), *Closterium* sp. (200 µm), and *Spirogyra* sp. (1100 µm)]. *Spirogyra* sp. was the largest food item ingested, and that microalgae was arranged in a spiral inside *F. leucas* within a spherical food vacuole, representing one of five digestive mechanisms reported by Goldsmith (1922) and Dias & D'Agosto (2006).

The smallest food items recorded were *Arcella hemisphaerica undulata* (50 µm diameter), *Vorticella* sp. (50 µm), and *Pinnularia* sp. 2 (60 µm). *Arcella hemisphaerica undulata* is the food item associated with the greatest observed variations in body size of *F. leucas*, with records of 160, 180, 220, 300, and 450 µm (the latter being recorded at site 4 - Córrego José Miguel, Boa Nova).

The Lagoa do Deinho, Poções site (Site 2) was the only one where rotifers [*Lecane bulla* (130 µm), *Lecane cornuta* (120 µm), and Bdelloidea (225 µm)] were observed being ingested. Variations in the body sizes of *F. leucas* (350, 410, and 500 µm) were also observed at that site. The individual that measured 500 µm had ingested two loricate rotifers simultaneously. Interestingly, when rotifers were ingested together with testate amoebae [such as *Netzelia lobostoma* (120 µm) and *Difflugia angustata* (70 µm)] reductions in cell dimensions were observed. The smallest cell size of *F. leucas* was recorded in Poções (250 µm) after the ingestion of testate amoebae such as *Cylindrifflugia elegans* (70 µm) and diatoms such as *Pinnularia* sp. (100 µm). The largest testate amoeba observed was *Cylindrifflugia lanceolata* (200 µm) inside a 400 µm individual of *F. leucas* (Figure 2). At Riacho das Traíras in Boa Nova, Bahia, a *F. leucas* specimen (440 µm) was observed to have ingested an individual of *Centropyxis aculeata* (110 µm).

Other authors previously reported the polyphagous habit of *F. leucas* (Bick & Kunze, 1971), which was corroborated in the present study. The predation of rotifers by larger individuals of *F. leucas* (Bereczky, 1977), as well as the predation of testate amoebae of the genera *Arcella* and *Difflugia* (Burger, 1908), had also been previously reported. Finlay et al. (1988) observed that *F. leucas* fed on algae up to 50 µm long, although the present study demonstrated that it is capable of feeding on even larger algae, such as *Micrasterias* sp. (90 µm), *Cosmarium* sp. (90 µm), and *Closterium sp*. (200 µm). Kusano (1985) reported the predation of other ciliates, which is corroborated here by the observation of predation on *Vorticella* sp. While incidences of cannibalism by *F. leucas* have been reported (Devi, 1964), no examples were observed in the present study. Dias & D'Agosto (2006) reported observing *F. leucas* preying on diatoms, desmids (*Closterium*), filamentous cyanobacteria, testate amoebae (*Arcella, Centropyxis*), and rotifers; these same groups were also observed as ingested food items in the present study. The present study was therefore able to complement and corroborate observations previously reported by other authors, as well as add additional data relating to the feeding habits of *F. leucas.*

In general, all of these observations of predation by *Frontonia leucas* on different organisms of varying sizes reinforce the polyphagous nature and morphological plasticity of the species. It was observed that the larger sizes and/or the greater quantities of sequentially ingested items led to larger body sizes of *F. leucas* individuals. Additionally, our microscopic observations revealed that predation by that species directly reflects food item availability in the environment, with the preferential ingestion of the most abundant organisms.

The ingestion mechanisms of *F. leucas* involve traction exerted on the food item by the circumoral cilia; movement of its cilia in the direction of the food item; a series of ordered changes in the positions of the cilia with reference to the food item that allows it to subsequently pass more easily along the aboral surface of the ciliate; superficial contractions of the aboral surface of the ciliated microeukaryote – forming points of tension and cyclosis (Goldsmith, 1922).

The formation of food vacuoles within the cytoplasm of *F. leucas* as well as the deformation of its original oval shape were observed when large food items were ingested (such as *Cylindrifflugia lanceolata*, *Closterium* sp., and *Pleurotaenium trabecula elongatum*) (Figure 2A, 2C and 2D). This condition was also noted by Goldsmith (1922) after the ingestion of *Oscillatoria* and *Closterium* sp., and by Dias & D'Agosto (2006) after the ingestion of cyanobacteria and testate amoebae of the genus *Centropyxis*.

Another recorded food capture strategy was the absorption of the body contents of large loricate rotifers (thus avoiding the ingestion of the chitinous lorica, which is difficult to degrade). Therefore, we assume that when predating high-volume organisms, *F. leucas* can selectively absorb only their body contents without ingesting the entire individual.

Regarding the analysis of abiotic variables, and considering all of the environments sampled, water depths ranged from 32 to 63 cm, with an average of 53 ± 14.79 cm. Water transparency ranged from 22.7 to 53 cm, with an average of 28 ± 12.17 cm. The pH ranged from 6.9 to 7.84, with an average of 7.3 ± 0.36. Electrical conductivity ranged from 16 to 247.3 µS/cm, with an average of 122.7 ± 97.49 µS/cm. Total dissolved solids ranged from 7.5 to 123 ppm, with an average of 61.3 ± 48.44 ppm. The temperature ranged from 21.7 to 25.3 ºC, with an average of 23.55 ± 1.5 ºC.

The species appears to tolerate different degrees of electrical conductivity, total dissolved solids, and pH. The data presented here contributes to greater knowledge about the autoecology of *F. leucas* and expands available information concerning the occurrence of that species in terms of variables such as water transparency, total dissolved solids, and depth, which have not been previously reported in the literature.

This study highlights the versatile predatory behavior of *Frontonia leucas* in different aquatic environments in the Brazilian semiarid region. Our results demonstrate that *F. leucas* feeds on a significant variety of organisms, including testate amoebae, microalgae, rotifers, and ciliates, and thus contributes to the regulation of their populations in limnic ecosystems. Furthermore, our observations revealed preferences for certain *taxa*, such as *Arcella hemisphaerica undulata* and *Spirogyra* sp.

The possibility of using *F. leucas* in bioremediation processes, especially in aquatic environments showing significant increases in the populations of *taxa* that are consumed by this ciliated microeukaryote, offers a promising perspective for the control and restoration of environmental quality. In short, the results of this study highlight the importance of understanding trophic interactions in aquatic ecosystems and highlight the potential of *F. leucas* as a natural population control agent and bioremediator as well as its potential to contribute to the conservation and sustainability of vital environments.

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