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Abundance and size structure of planktonic protist communities in a Neotropical floodplain: effects of top-down and bottom-up controls

Abundância e estrutura de tamanho da comunidade de protistas planctônicos em uma planície de inundação neotropical: efeitos dos mecanismos de controle *top-down* e *bottom-up*

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Abstract: Aim: We aimed to assess the influence of bottom-up and top-down control mechanisms on the abundance and size structure of protist communities (heterotrophic flagellates and ciliates). We formulated the following hypothesis: bottom-up control mechanisms, related to the availability of resources in the environment, are responsible for structuring the abundance of these communities, whereas top-down control mechanisms, related to predation effects, determine the size pattern of these organisms. **Methods:** Samples for planktonic organisms were taken in 20 shallow lakes belonging to the upper Paraná River floodplain. We evaluated linear regression models to select the best model which predicts the patterns observed according to Akaike Information Criterion. **Results:** The best models selected to explain the abundance of heterotrophic flagellates included negative relations with picophytoplankton abundance and positive with rotifers abundance, while for their size structure, negative relationships were found with heterotrophic bacteria, ciliates and rotifers biovolumes. In relation to the ciliates, their abundances were positively related to the rotifers and picophytoplankton abundances and negatively with the heterotrophic bacteria abundance. On the other hand, for the size structure, the best models selected strong negative relations with the microcrustaceans biovolumes, in addition to relations with the different fractions of the phytoplankton. **Conclusion:** For both flagellates and ciliates, their abundance is being mainly regulated by a bottom up control mechanism, whereas for the size structure the results showed that both food resources and predators were important, indicating that bottom-up and top-down mechanisms act simultaneously in determining the size of these microorganisms.

Keywords: protist; plankton; freshwater; size structure; shallow lakes; microbial food web.

Resumo: Objetivo: Esse estudo objetivou analisar a influência dos mecanismos de controle *bottom up* e *top down* sobre a abundância e a estrutura de tamanho das comunidades de protozoários planctônicos (flagelados heterotróficos e ciliados). Assim, a seguinte hipótese foi testada: mecanismos de controle *bottom up*, relacionados à disponibilidade dos recursos alimentares no ambiente, controlam a abundância das comunidades de protozoários, enquanto que mecanismos de controle *top down,* relacionados ao efeito da predação, controlam o padrão de tamanho destes organismos. **Métodos:** As amostras para análise dos organismos planctônicos foram obtidas em 20 lagoas pertencentes a três diferentes subsistemas da planície de inundação do alto rio Paraná (Paraná, Baía e Ivinhema). Foram utilizadas regressões lineares para selecionar o melhor modelo que prediz os padrões observados de acordo com o Critério de Informação de Akaike. **Resultados:** Os melhores modelos selecionados para explicar a densidade de flagelados heterotróficos incluíram relações negativas com o picofitoplâncton e positivas com os rotíferos, enquanto que para sua estrutura de tamanho, foram encontradas relações negativas com as bactérias heterotróficas, ciliados e rotíferos. Já em relação aos ciliados, suas densidades estiveram relacionadas positivamente com os rotíferos e picofitoplâncton e negativamente com as bactérias heterotróficas. Por outro lado, para o biovolume os melhores modelos selecionaram fortes relações negativas com os microcrustáceos, além de relações com as diferentes frações do fitoplâncton. **Conclusão:** Para ambos protistas, o mecanismo de controle *bottom-up* foi o principal regulador de suas densidades, enquanto que para a estrutura de tamanho dos mesmos, os resultados mostraram que tanto os recursos alimentares quanto os predadores foram importantes, indicando que os mecanismos *bottom-up* e *top-down* atuam conjuntamente na determinação do tamanho destes microrganismos.

Palavras-chave: protistas; plâncton; ambientes aquáticos continentais; estrutura de tamanho; ambientes lênticos; teia alimentar microbiana.

1. Introduction

The understanding of the ecosystem functioning occurs mostly through the knowledge of species interactions within its food webs, through which the energy and matter flow (Pomeroy, 1974). In aquatic ecosystems, since the concepts of microbial loop (Azam et al., 1983) and microbial food web (Sherr & Sherr, 1988), studies approaching the interactions among its components were recognized as a key stone for understanding the food web structure, due to its crucial role in nutrient cycling, biomass accumulation, and carbon flow (Weisse, 2002).

The components of microbial food webs can be strongly affected by both bottom-up control – related to resource availability in the environment (Gasol et al., 1995; Šimek et al., 2003) – and top-down control, which is related to predation effects (Šimek et al., 1997; Auer et al., 2004). The impact of bottom-up mechanisms usually occurs slowly within the ecosystem (Sommer, 2008), and food resources are the main drivers of community abundance (Palijan, 2012; Weisse, 2002). The predator-prey relationship is directly linked to the size of the organisms, since no predator feeds the entire size spectrum of their resources, and they are able to select their prey by size classes through selective predation (Jürgens & Matz, 2002). Thus, if the abundance and biomass of lower trophic levels remain unchanged, the top-down control will certainly be visible in the size structure of organisms, which is known as "partial trophic cascade" (Sommer, 2008).

Among the microbial components, heterotrophic protozoa (flagellates and ciliates) are often considered as the main consumers of bacteria and phytoplankton (Auer et al., 2004; Comte et al., 2006; Palijan, 2012; Weisse, 2002). In addition, studies suggest that these microorganisms prefer to consume picocyanobacteria instead of bacteria (Callieri et al., 2002; Fontes & Abreu, 2012; Tarbe et al., 2011), and that ciliates can meet their carbon needs with a diet based exclusively on picophytoplankton. This small size fraction of the phytoplankton represents an important food source when compared to the largest size fractions, which can be lost by either sedimentation or integration into the classic food web. Ciliates can also have strong impacts on the heterotrophic flagellate community through predation (Auer et al., 2004). Furthermore, ciliates act as competitors in relation to rotifers and can be consumed by them and other larger predators, such as cladocera and copepoda (Agasild et al., 2013; Müller et al., 1991).

We aimed to assess the influence of bottom-up and top-down control mechanisms on the abundance and size structure of protist communities (heterotrophic flagellates and ciliates). Specifically, we formulated the following hypothesis: bottom-up control mechanisms, related to the availability of resources in the environment, are responsible for structuring the abundance of both flagellate and ciliate communities, whereas top-down control mechanisms, related to predation effects, determine the size pattern of these organisms. Considering this hypothesis, we formulated the following predictions: (i) bottom-up control mechanisms regulate both flagellate and ciliate abundances resulting in a positive relationship between food resources (bacteria and phytoplankton) and protist abundance (heterotrophic flagellates and ciliates); (ii) top-down control mechanisms determine the size pattern of flagellates and ciliates, resulting in a negative relationship between the protist biovolume and predators biovolume (zooplankton).

2. Material and Methods

2.1. Study area

The Upper Paraná River floodplain (Figure 1), encompassing the boundaries between Paraná and Mato Grosso do Sul states, is the last undammed stretch of this river and drains an area of over 2,800.000 km^2. Its great heterogeneity is due to the presence of different types of environments, such as shallow lakes, which can be permanent or temporary, backwaters, channels and rivers, supporting a high diversity of terrestrial and aquatic species (Thomaz et al., 2007).

2.2. Sampling design

Samples for planktonic organisms were taken at the low water period, in 20 shallow lakes belonging to three different subsystems of the upper Paraná River floodplain (Paraná, Baía and Ivinheima rivers). Samples were taken at the subsurface (20 cm depth) of all environments with polyethylene bottles and near the bottom (20 cm above the sediment) of habitats more than 1 meter deep using a Van Dorn bottle.

For bacterioplankton, picophytoplankton and flagellate analyses, 100mL of water samples were preserved with Lugol/ buffered

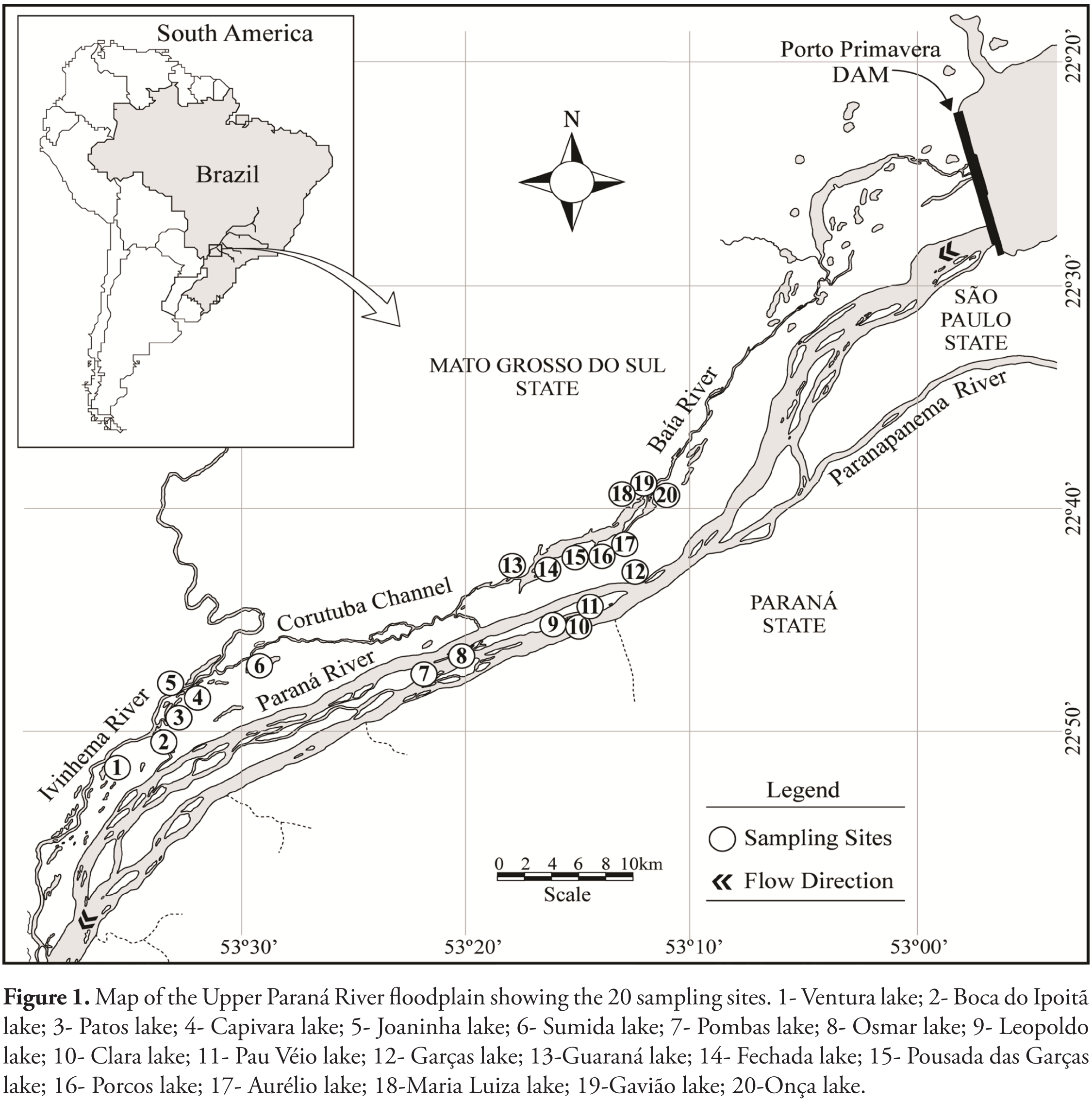

Figure 1. Map of the Upper Paraná River floodplain showing the 20 sampling sites. 1- Ventura lake; 2- Boca do Ipoitã lake; 3- Patos lake; 4- Capivara lake; 5- Joaninha lake; 6- Sumida lake; 7- Pombas lake; 8- Osmar lake; 9- Leopoldo lake; 10- Clara lake; 11- Pau Véio lake; 12- Garças lake; 13-Guaraná lake; 14- Fechada lake; 15- Pousada das Garças lake; 16- Porcos lake; 17- Aurélio lake; 18-Maria Luiza lake; 19-Gavião lake; 20-Onça lake.

formaldehyde/thiosulfate (Sherr & Sherr, 1993). For ciliates, four liters of water samples were concentrated in the laboratory to 100 mL using a 5 μm net, to direct in vivo counting. For phytoplankton analysis, 50mL were collected using sterilized glass bottles and preserved in situ with Lugol´s solution. For zooplankton samples, 200 liters were filtered using a motorized pump and plankton net (68 μm) and samples were fixed with 4% buffered formaldehyde.

2.3 Laboratory analysis

Bacterioplankton abundance was estimated by filtering 200 μL water subsamples on black 0.2 μm Nuclepore/Watchman polycarbonate membranes, stained with 1 mL of DAPI (4,6´- diamidino-2-phenylindole). Bacteria were randomly counted and measured under an epifluorescence microscope (Olympus BX51) at a ×1000 magnification, using UV excitation (blue-white emission), from captured images taken from the fields using Image Pro Express software. 10 fields were counted and 100 bacterial cells were measured per sample (Porter & Feig, 1980). Abundance was estimated according to Waterbury et al. (1986). Biovolume was also calculated (μm^3; Posch et al., 1997).

Picophytoplankton was estimated based on the natural fluorescence of the pigments (chlorophyll and phycobilins; Waterbury et al.,1986), using the same methodology of bacterioplankton, but filtering 2 to 5 mL water sample. A filter set that provided blue excitation (450 to 490 nm) was used to detect chlorophyll a, while green excitation (546 nm) was used to detect phycoerythrin and phycocyanin pigments of some cyanobacteria (Waterbury et al.,1986). 30 fields/100 cells were counted to estimate the abundance (Okada et al., 2007) and 50 cells of each sample were measured in length and width to estimate the biovolume (Waterbury et al.,1986).

Phytoplankton abundance was estimated using an inverted microscope according to the Utermöhl method (Utermöhl, 1958). Sedimented volume was defined according to the sample algae concentration, and sedimentation time was at least three hours for each centimeter of the chamber height (Margalef, 1983). Fields were counted until the number of individuals of the dominant species reached a total of at least 100 (Lund et al., 1958). Abundance was calculated according to APHA (1998). To estimate of biovolume were measured up to 20 individuals of each species and the volume of each cell was calculated according to the formula for the most similar standard geometric figure (Sun & Liu, 2003). Phytoplankton was grouped according to the size classes of nanophytoplankton (2-63 μm) and microphytoplankton (64-500 μm).

Heterotrophic flagellate abundance was estimated using the same methodology of bacterioplankton, but filtering 10 mL water samples on black 0.8 μm Nuclepore/Watchman polycarbonate membranes. They were also counted and measured under an epifluorescence microscope (Olympus BX51) at a ×1000 magnification, using UV and green excitation to differentiate the heterotrophic from the autotrophic flagellates. 100 fields were counted and all cells measured (length and width) to estimate the biovolume (μm^3; Ohno et al., 2013).

Ciliates were analyzed in vivo, abundance was estimated using an Olympus CX41 optical microscope under magnifications of 100 × and 400 × and identification was performed based on taxonomic literature (Corliss, 1979; Foissner et al., 1999). Biovolume was calculated from length and width measurements and geometric shapes known from each species (Foissner & Berger, 1996; Foissner et al., 1999; Müller & Geller, 1993).

Zooplankton abundance was estimated by counting at least 50 individuals of each group (rotifers and microcrustaceans - cladocerans, young and adult copepods) in Sedgewick-Rafter chambers, according to Botrell et al. (1976), with three sub-samples taken with Hensen-Stempell (2.5 mL) pipettes and counted under optical microscope. Samples with small number of organisms were entirely counted. Biovolume was estimated from measurements of 50 individuals of each group, considering the largest diameter, excluding thorns, spines and ornaments (rotifers: Ruttner-Kolisko,1977; microcrustaceans: Lawrence et al., 1987).

2.4. Data analyses

To test the predictions, we evaluated linear regression models to select the best model which predicts the patterns observed according to Akaike Information Criterion (AIC) (Burnham & Anderson, 2002). We tested different models considering the explanatory variables which, according to the literature, are the main controllers of the abundance and biovolume of the heterotrophic flagellates (HF) and ciliates (CIL). In these models, *a* and *b* coefficients are the intercept and the slope, respectively.

For example, considering a top-down control and according to the available data, the following linear models were tested to select the best model that predicts abundance and biovolume of heterotrophic flagellates:

(1) HF = a + b[abundance or biovolume of ciliates]

(2) HF = a + b[abundance or biovolume of rotifers]

(3) HF = a + b[abundance or biovolume of microcrustaceans]

Considering a bottom-up control, the following models were tested to predict if the abundance and biovolume of flagellates are being controlled by the resources:

(4) HF = a + b[abundance or biovolume of bacteria]

(5) HF = a + b[abundance or biovolume of picophytoplankton]

(6) HF = a + b[abundance or biovolume of nanophytoplankton]

For ciliates, considering a top-down control and according to the available data, the following linear models were tested to select the best model that predicts abundance and biovolume:

(1) CIL = a + b[abundance or biovolume of rotifers]

(2) CIL = a + b[abundance or biovolume of microcrustaceans]

Considering a bottom-up control, the following models were tested to predict if the abundance and biovolume of ciliates are being controlled by the resources:

(3) CIL = a + b[abundance or biovolume of bacteria]

(4) CIL = a + b[abundance or biovolume of picophytoplankton]

(5) CIL = a + b[abundance or biovolume of nanophytoplankton]

(6) CIL = a + b[abundance or biovolume of microphytoplankton]

(7) CIL = a + b[abundance or biovolume of HF]

Other models considering the joint effect of predators and resources with different possible combinations were also tested. We calculated the AICc differences for each model. The best approximating model have $\Delta i = 0$. However, models with $\Delta i < 2$ have similar levels of empirical support and may be considered for inference (Burnham & Anderson, 2002). All analyses were performed using the freeware statistical package Spatial Analysis in Macroecology (SAM) (Rangel et al., 2006).

3. Results

Abundance and biovolume values of all communities are shown in Table 1. Heterotrophic bacteria were almost entirely constituted by small cocci, with cell diameter varying between 0.4 and 0.8 µm. Picophytoplankton cell size ranged from 0.8 to 1.5 µm and was the most abundant among the phytoplankton size fractions (Table 1). Regarding the protists, HF showed higher mean densities than ciliates, whereas ciliates showed higher mean biovolume (Table 1), since ciliates are usually larger in size. Among the zooplankton components, rotifers showed the highest mean densities, whereas higher mean biovolume values were found for microcrustaceans (Table 1).

3.1. Influence of top down and bottom up control mechanisms on the abundance and biovolume of protists

The best-approximated model to explain the variation of the flagellate abundance, according to the AIC*c* differences (Δi), included only the rotifer abundance. Since the standardized regression

Table 1. Mean, minimum and maximum values of abundance and biovolume of each community.

Communities	Abundance			Biovolume (µm³)		
	Mean	Min	Max	Mean	Min	Max
HB (cels/mL)	8.92×10^5	3.11×10^5	2.57×10^6	0.11	0.04	0.29
PPP (cels/mL)	8.20×10^3	1.79×10^1	4.16×10^4	0.47	0.24	1.48
HF (cels/L)	2.71×10^4	6.69×10^3	2.08×10^5	87.33	8.18	1.23×10^3
Nanophytoplankton (ind/mL)	7.07×10^2	10.0	1.83×10^3	0.35	0.001	2.47
Microphytoplankton (ind/mL)	5.16×10^2	2.0	4.40×10^3	2.16	0.19	13.62
Ciliates (cels/L)	8.95×10^2	2.50×10^1	2.53×10^3	5.18×10^5	2.78×10^4	2.45×10^6
Rotifer (ind/m³)	3.88×10^4	7.95×10^2	2.48×10^5	5.22×10^5	1.55×10^5	1.53×10^6
Microcrustaceans (ind/m³)	3.29×10^4	4.05×10^2	1.49×10^5	2.13×10^8	4.55×10^7	9.66×10^8

HB= heterotrophic bacteria; PPP= picophytoplankton; HF= heterotrophic flagellates.

coefficient (*beta* coefficient) was positive, we can infer that the increase of the flagellate abundance was associated with an increase in the rotifer abundance (Table 2, Figure 2). The second best model included only the densities of the picophytoplankton, and the other six models showed AIC*c* ≤ 2.

To explain the variation on the ciliate abundance, according to the AIC*c* differences (Δ*i*), the best model also included rotifer abundance, showing a positive standardized regression coefficient. However, two other models including the densities of picophytoplankton and bacterioplankton showed AIC*c* ≤ 2. Thus, rotifer and picophytoplankton densities were included in the second best model, and rotifer and bacterial densities were included in the third best model (Table 2, Figure 2).

To explain the variation in the biovolume of flagellates, the best-approximated model, according to the AIC*c* differences (Δ*i*) included the biovolumes of the bacteria and rotifers. Nonetheless, other

Table 2. Models considered parsimonious in explaining the abundance and biovolume of flagellates and ciliates. As a criterion for selection of models, those with AICc < 2 were considered the best approximate models, according to Burnham & Anderson (2002). For each model, AICc is the corrected Akaike Information Criterion, Δ AICc is the the difference between the AICc of each model and the minimum AICc and *wi* is the Akaike weight and indicates the likelihood of a particular model, among all tested, to be the most parsimonious.

Models	coef. β	r^2	AICc	Δ AICc	w*i*
Flagellates abundance					
Rotifers	0.17	0.029	142.21	0	0.091
Picophytoplankton	-0.16	0.021	142.53	0.319	0.078
Ciliates abundance					
Rotifers	0.49	0.238	40.805	0	0.165
Rotifers, Picophytoplankton	0.49; 0.15	0.258	42.219	1.414	0.081
Rotifers, bacterioplankton	0.49; -0.10	0.248	42.747	1.942	0.062
Flagellates biovolume					
Bacterioplankton, rotifers	-0.54; -0.49	0.273	74.250	0	0.263
Bacterioplankton, rotifers, ciliates	-0.54; -0.49; -0.13	0.285	76.201	1.951	0.099
Ciliates biovolume					
Picophytoplankton, microphytoplankton, rotifers, microcrustaceans	0.32; -0.27; 0.29; -0.30	0.271	63.589	0	0.076
Picophytoplankton, nanophytoplankton, microphytoplankton, rotifers, microcrustaceans	0.32; 0.15; -0.27; 0.29; -0.30	0.308	64.472	0.884	0.049
Picophytoplankton, microphytoplankton, rotifers	0.32; -0.27; 0.29	0.194	64.854	0.531	0.040
Picophytoplankton, rotifers, microcrustaceans	0.32; 0.29; -0.30	0.189	65.094	1.506	0.036
Picophytoplankton, microcrustaceans	0.32; -0.30	0.129	65.331	1.743	0.032

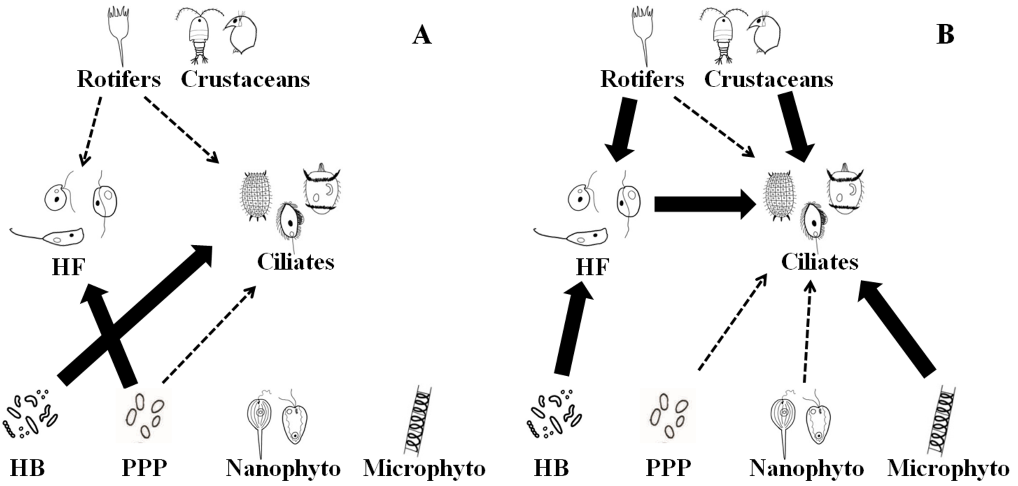

Figure 2. Schematic representation of the best models selected by the Akaike criterion to explain the variation in abundance (A) and biovolume (B) of protists. The continuous arrows represent the negative relations, whereas the dashed arrows represent the positive relations. HF= heterotrophic flagellates; HB= heterotrophic bacterias; PPP= picophytoplankton; Nanophyto= nanophytoplankton and Microphyto= microphytoplankton.

model showed AICc ≤ 2 including the biovolumes of bacteria, rotifers, and ciliates (Table 2, Figure 2).

The best model explaining the variation of ciliate biovolume included the biovolumes of picophytoplankton, microphytoplankton, and microcrustaceans. However, other four models showed AICc ≤ 2, with the second model including the same explanatory variables as the first model, with the addition of nanophytoplankton biovolume (Table 2, Figure 2).

4. Discussion

In the last few decades, the importance of the food resources (bottom-up) and the influence of the predators (top-down) on protozoa community structuring has been widely discussed (Agasild et al., 2013; Jack & Gilbert, 1997). These two mechanisms act simultaneously by altering the abundance and biomass of the communities (Gasol et al., 1995) so one should not evaluate which one of these factors is acting separately, but instead, determine which attributes each one is altering.

As expected, protist abundance was related to their main food resources, such as heterotrophic bacteria and picophytoplankton. Heterotrophic flagellates and ciliates are known to be the main consumers of picoplankton in aquatic ecosystems (Fontes & Abreu, 2012; Sherr & Sherr, 2002; Tarbe et al., 2011). Therefore, it is no surprise that the abundance of these protists is associated with high densities of their food resources, since they are usually not capable of suppressing the abundance of their prey due to elevated growth rates and short life cycle of picoplankton organisms (Callieri & Stockner, 2002), which evidences the importance of bottom up mechanisms in controlling the abundance of both heterotrophic flagellates and ciliates.

Rotifers were the only potential predators influencing the densities of both heterotrophic flagellates and ciliates, although their correlation with these two communities was positive. Rotifers occupy an intermediate level of the food web, being consumed mainly by microcrustaceans and acting as predators or competitors of both flagellates and ciliates, items often present in their diet, as well as heterotrophic bacteria and several size fractions of the phytoplankton (Stoecker & Egloff, 1987). Therefore, although some studies found a strong negative impact of rotifer predation on ciliates (Lischke et al., 2016; Weisse & Frahm, 2002), the positive relationships evidenced in our study suggest that they are both benefiting from the same resource, in this case, heterotrophic bacteria and/or picophytoplankton, or, alternatively, that they are being controlled by the same predators, such as microcrustaceans (Li et al., 2016). What would explain the positive relations found between ciliates and rotifers for both abundance and biovolume.

Regarding the size of protists, the biovolume of heterotrophic flagellates was apparently regulated by the predation by rotifers and ciliates (negative relationships), besides the influence of food resources (bacteria). As opposed to microcrustaceans, which are not efficient in capturing small particles (smaller than 5 μm), rotifers are able to capture and ingest, by filtration, particles with a wide range of size (0.5–200 μm), including bacteria, flagellates, and ciliates (Rothhaupt, 1990).

Correlations between rotifers and heterotrophic flagellates have been widely documented in aquatic ecosystems (Cushing, 1976; Dolan & Gallegos, 1991). Arndt (1993) developed long-term experiments in microcosms and found that rotifers were capable of selecting different flagellate species with similar sizes, which seemed to be the main food item in their diet. Therefore, although predation by rotifers is usually not capable of decreasing flagellate abundance, as previously discussed, they showed a negative effect on the size of these protists, which may indicate that zooplankton is exerting a selective predation in certain size classes.

Similarly, ciliates did not show negative impacts on flagellate abundance, but were negatively related to their biovolume. These results suggest that ciliate predation is also acting only in certain size fractions of heterotrophic flagellates. This relationship was also observed in other studies, for example, Chen et al. (2012) found that ciliate can consume up to 100% of nanoflagellate production, and that this consumption was more pronounced for flagellates smaller than 5 μm.

Besides predators, food resources such as heterotrophic bacteria were also related to HF size. Flagellates are one of the main bacterial consumers in aquatic environments (Gonzalez et al., 1990), being able of actively selecting the largest bacterial cells (Šimek & Chrzanowski, 1992). This selective predation of HF on certain size classes of bacteria is known to cause changes in the size distribution of bacterial populations, due to a top-down control (Šimek et al., 1995). However, our results indicate that food resources could also be related to predator size, which suggests that resource selectivity may also affect the size of consumers.

Negative relationships between microcrustaceans and ciliates are commonly found in aquatic ecosystems, since these organisms are known to be the main ciliate predators (Jack & Gilbert, 1997; Wickham, 1998; Wickham & Gilbert, 1993). Several studies indicate a selective predation of zooplankton on some ciliate groups (Agasild et al., 2013; Jack & Gilbert, 1997). For instance, Jack & Gilbert (1997) found strong negative effects of copepod predation on ciliates and that large cladocerans suppressed up to 90% of certain ciliate populations through direct predation. Agasild et al. (2013) also found, through an experimental approach, that copepods and cladocerans may strongly suppress large-bodied ciliates, such as species belonging to the order Gymnostomatida. Moreover, Jürgens & Jeppesen (2000) found that during the dominance of *Cyclops vicinus*, a cyclopoid copepod species, ciliates of larger cell sizes were selectively consumed by these predators, and only small sized ciliates remained in the environment. Therefore, the negative effects between microcrustacean and ciliate biovolumes found in our study suggest a selective top-down control.

On the other hand, food resources were also important to maintain the biovolume of the ciliates. These protists have a wide range of body sizes, thus consuming food resources of a wide variety of sizes as well, such as the distinct fractions of phytoplankton (pico, nano, and microphytoplankton). Thus, the size spectrum of food resources present in the environment may determine the persistence of certain size classes of ciliates instead of others. Therefore, for both flagellates and ciliates the best models predicting their biovolume included food resources as well as predators, indicating that bottom-up and top-down mechanisms act simultaneously in determining the size of these microorganisms. On the other hand, their abundance is being mainly regulated by a bottom up control mechanism.

5. Conclusion

Several studies have shown that food resource availability affects protist community (Palijan, 2012; Segovia et al., 2015), however these resources vary widely in size and quality (Li et al., 2016; Pernthaler et al., 1996) and may affect not only protist abundance but also their size classes. It is important to notice that both food resources and predators are important in controlling the protist community, and thus, bottom up and top down mechanisms act simultaneously in structuring this community. However, these mechanisms may act in a different manner on certain community attributes, as evidenced in our results. Therefore, a better comprehension regarding how bottom up and top down mechanisms control the abundance and size structure of heterotrophic flagellates and ciliates in aquatic environments is essential, considering that these protists form an important link in the transfer of matter and energy to higher trophic levels in aquatic food webs, besides participating in the nutrient cycling.

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