

Does predation by planktonic organisms influence the size structure of phytoplanktonic algae in a black water lake in the Amazon?

Predação por organismos planctônicos influencia a estrutura de tamanho das algas fitoplanctônicas em um lago de água preta na Amazônia?

Raize Castro-Mendes^{1*}, Edinaldo Nelson dos Santos-Silva¹, Bruno Machado Leão¹, Renan Gomes do Nascimento¹, Maiby Glorize da Silva Bandeira¹, Luis José de Oliveira Geraldes-Primeiro¹

¹Laboratório de Plâncton – Instituto Nacional de Pesquisas da Amazônia – Manaus, Amazonas Av. André Araújo, 2936, Aleixo, Manaus, Amazonas – CEP 69060-001.

*Email: raize.mendes@gmail.com

Received: 25, February 2019: / Accepted: 31, July 2019 / Published: 5, August 2019

Resumo Organismos do fitoplâncton podem pertencer às categorias de tamanho pico, nano e microplâncton e organismos do zooplâncton ao micro, meso e macroplâncton. Por terem tamanhos diferentes, os organismos zooplânctônicos podem se alimentar de diferentes tamanhos do fitoplâncton. O objetivo foi avaliar se microcrustáceos e rotíferos planctônicos consomem o pico, nano e microfitoplâncton de forma homogênea nos períodos de seca enchente do lago Tupé. Um experimento foi colocado durante 24 horas no período de seca e enchente no lago Tupé. Amostras de zooplâncton e fitoplâncton foram coletadas com um tubo de PVC de 4 m de comprimento e os organismos zooplânctônicos foram contados e medidos. A amostra de fitoplâncton foi fracionada em pico, nano e microfitoplâncton para ser medida a biomassa de cada fração. No período de seca, a biomassa inicial total foi 1,92 µg/L, especificamente pico 0,82, nano 0,55 e micro 0,55 µg/L, sendo o valor da biomassa final 1,09 µg/L correspondente ao pico 0,55, nano 0,27 e micro 0,27 µg/L. No período de enchente, a biomassa inicial foi 2,91 µg/L, especificamente pico igual a zero, nano 0,54 µg/L e micro 2,37 µg/L, sendo o valor da biomassa final 0,81 µg/L correspondente apenas ao picoplâncton. A maior densidade de organismos foi encontrada no experimento do período de seca. Concluímos que a pressão de predação do zooplâncton não influencia a estrutura de tamanho do fitoplâncton no ambiente estudado, uma vez que atua de forma similar sobre as diferentes classes.

Palavras-Chave: Fitoplâncton, nanoplâncton, microplâncton, mesocosmo, biomassa.

Abstract Phytoplanktonic organisms may be categorized as pico, nano and microplankton, and zooplanktonic organisms as micro, meso and macroplankton. Because they are different sizes, zooplanktonic organisms can feed on varying sizes of phytoplankton. The study objective was to test whether microcrustaceans and planktonic rotifers consumed pico-, nano- and microphytoplankton non-selectively during low- and high-water periods in Lake Tupé, Amazonian Brazil. An experiment was carried out across 24 hours in the low- and high-water periods, with zooplankton and phytoplankton samples collected from the lake with a PVC tube 4 m in length. Zooplankton were counted and measured, while the phytoplankton sample was divided into pico-, nano- and microphytoplankton and the biomass of each fraction measured. During low water, total initial biomass was 1.92 µg/L and, by fraction, contained pico 0.82, nano 0.55 and microphytoplankton 0.55 µg/L. Total biomass was 1.09 µg/L, corresponding to pico- 0.55, nano- 0.27 and microphytoplankton 0.27 µg/L. During high water, total initial biomass was 2.91 µg/L and by fraction, contained pico- equal to zero, nano- 0.54 µg/L and micro- 2.37 µg/L. Total biomass was 0.81 µg/L corresponding only to picophytoplankton. The highest density of organisms occurred in the low-water sample. We conclude that predation pressure from zooplankton does not influence phytoplankton size structure in the studied environment, since it impacts the different size classes equally.

Keywords: Picoplankton; Nanoplankton; Microplankton; Mesocosm; Biomass.

Introduction

In continental aquatic environments cladocerans, copepods and rotifers are the major abundant zooplanktonic organisms. These organisms are endowed with morphological and chemical devices to propitiate their success in these environments (Tian *et al.* 2019). For feeding, the cladocerans have as devices, the filtering bristles and, it has the capacity to select their prey by size (Lampert 1994; Dumont & Negrea 2002; Holynska *et al.* 2003). The copepods present buccal appendages such as jaws, maxilla, maxillula and maxillipeds, which gives them the ability to capture individual food particles and to select the appropriate food (Dussart & Defaye 1995; Dussart & Defaye 2001; Dumont & Negrea 2002; Holynska *et al.* 2003). The rotifers have a filtering mouthpiece called corona ciliata and, it has a specialized muscular pharynx called mastax. In the presence of food, rotifers perform movements with the cilia of the corona ciliata creating a flow, and then the food is sent into the organism body. In the mastax a chitinous jaws (trophi) process, the food particles ingested (Nogrady *et al.* 1993).

These organisms present different shapes and sizes in aquatic environments. In freshwater environments, rotifers are approximately 100 to 500 μm in size and microcrustaceans (cladocerans and copepods) between 200 to 3000 μm (Dumont & Negrea 2002). So, differences in body length can have great effects on the filtration rate and food size.

Phytoplankton also presents different sizes and, it's the main zooplankton's feeding item (Round 1983; Raven *et al.* 1996; Lourenço

2006; Frau *et al.* 2019). Sieburth *et al.* (1978) classified by size the planktonic organisms (including the phytoplankton and the zooplankton). Algae were included in the categories of picoplankton (0.02 to 2 μm), nanoplankton (2.1 to 20 μm) and microplankton (20.1 to 200 μm). The zooplankton was included in the categories of microplankton (20.1 to 200 μm), mesoplankton (200.1 to 2000 μm) and macroplankton ($> 2000 \mu\text{m}$).

In this context, algae with smaller sizes may be more consumed, since large and small sizes of zooplanktonic organisms can consume them. As an example, in the study by Filetto *et al.* (2004) it was observed that nanoplanktonic algae are the most suitable for feeding cladocerans, from newborn to breeding stage, and that the limit of particle sizes ingested by these herbivores depends on body size and filtering bristles.

Studies on the phytoplankton-zooplankton relationship have been carried out in laboratory experiments (Lampert 1994; Diaz-Castro & Hardy 1998; Hardy & Castro 2000; Pagano 2008; Chen *et al.* 2015) and in natural environments (Frau *et al.*, 2019). However, for the natural environments of the Amazon region, there are few that approached the size structure of the organisms and, neither, those that approached the predation of the zooplankton on the biomass of the different phytoplankton size classes. According to Rai (1982) and Romero & Arenas (1990) studying the populations of the phytoplanktonic community starting from their size allows a deeper understanding about the participation and efficiency of these fractions in total community biomass and environments dynamics.

Specifically, in the phytoplankton-

zooplankton relationship, studies of this nature provide elements to understand the complexities of trophic chains for the various types of aquatic environments of the Amazon. Especially for black water environments, such as Tupé Lake, studies on the taxonomy, composition and abundance of these organisms are great (Melo *et al.* 2005a; 2005b; Previattelli *et al.* 2005; Brandorff & Hardy 2009; Ghidini & Santos-Silva 2009; Pereira 2009; Calixto *et al.* 2011; Leão 2012; Souza 2012), however almost nothing or none about the influence of zooplankton on the specific categories of algal size.

Thus, the objective of this study is to understand the relationship and influence of zooplankton on phytoplankton size fractions in different periods of a blackwater Amazon lake, Tupé Lake. The hypothesis tested was that neither predation by zooplankton nor the river regime phases studied affect the size structure of the phytoplankton community populations.

Materials and Methods

Study Area

Lake Tupé (3° 2'36 "S and 60° 15'18" W)

is located in the Tupé Sustainable Development Reserve (Tupé RDS), left bank of the Rio Negro, 25 km from the port of Manaus, Amazonas State, Brazil (Figure 1). It is a black water lake, into which eight streams flow and it is connected to the Rio Negro by a channel that, during the dry season, is some 20 m wide, 0.5 m deep and 150 m long. When the level of the Rio Negro, in the port of Manaus, is below 19 m a.s.l. (above sea level), the river has no influence on the lake, and, for the lake, this period is considered low-water. When the level of the Rio Negro at the port of Manaus is exceeds 19 m m.s.l., then river waters have an influence on those of the lake, flowing in and causing the water level of the lake to rise, flooding its banks. This is considered to be the high-water period. Maximum depths of the lake vary between 4.5 m in the low-water season to 15 m in the high-water season. During high-water temperature in Lake Tupé varies between 27.8° C and 30.9° C, oxygen saturation 0.4 and 88.5% (4.6 mg.L⁻¹) and pH between 3.05 and 4.67. During low-water the temperature varies between 24.8 and 32.0° C, oxygen saturation 0.8 and 135, 6% and pH 3.89 to 5.95 (Darwich *et al.* 2005).

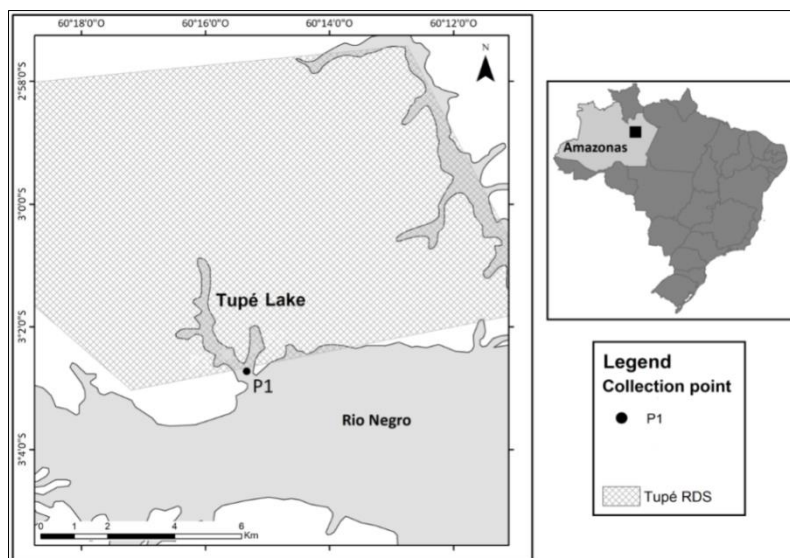


Figure 1 - Map of Tupé RDS, showing Lake Tupé and collection points within it.

In situ experiments

Phytoplankton

In order to evaluate the consumption of phytoplankton by planktonic microcrustaceans and rotifers, an *in situ* experiment was carried out in the low-water (December 2015), and high-water seasons (May 2016). The criterion for choosing a mesocosm for each period studied was due to already established information about the zooplankton in Tupé Lake, which consists of the spatial distribution of the wealth of cladocerans, copepods and rotifers to be homogeneous in the lake (Calixto *et al.* 2011).

The experiment was performed once in each period, for 24 hours at a single point on the lake.

The mesocosm consisted of a sturdy 60 L plastic bag, secured between two hoops of floating material. This assemblage was placed between three wooden poles from which it was suspended by ropes (Figure 2). The plastic bag contained 60 L of lake water, and so contained the planktonic organisms present at that moment in the lake. Collection occurred using the same procedure used to collect phytoplankton and zooplankton (see below). Simultaneously, a sample of zooplankton and phytoplankton were collected from the lake, and this was considered representative of the organisms present in the environment at the beginning of the experiment. After 24 hours, the volume of water in the mesocosm was measured and 1 L was withdrawn to measure the final biomass of the size fractions used in this study. The remainder was filtered through a 55 µm plankton sieve. Samples were then prepared using canonical methods and

transported to the National Institute of Amazonian Research (INPA) Plankton Laboratory for processing.

When collecting water for biomass analysis of pico-, nano-, and microphytoplanktonic and to obtain zooplanktonic organisms for use in the experiment (initial time T1), the limit of the euphotic zone was estimated *via* water transparency using a Secchi disk. The value obtained was multiplied by three to give a final value that was then considered as the limit of the Euphotic Zone, that is, the depth at which the value of photosynthetically-active light in the water column is 1% of the light incident on the surface (Esteves, 1998). After euphotic zone depth estimation, phytoplankton was collected with a PVC tube 4.5 m in length and 5 cm in diameter with a water-retaining valve coupled at its far end. The tube was inserted vertically into the water column, to the limit of the euphotic zone. Once the desired depth was reached, movement was paused and the valve activated, thus collecting an integrated sample of the entire euphotic zone. After this, the tube was pulled back into the boat and its contents dumped into a bucket. The sample volume of the drought period was 47.1 m³ and the sample volume of the flood period was 58.8 m³.

The collected water was homogenized and 2L (initial) sample withdrawn. After 24 hours, the water from the experiment was again homogenized and the final 2L sample was withdrawn. Sample vials were wrapped in foil and placed in black plastic bags to avoid any influence of light. These were then labelled and packed in an ice-filled expanded polystyrene chest, then

transported to the laboratory where they were refrigerated until analysed. At the INPA Water Chemistry laboratory, 1L of each sample was sequentially filtered through a graded filter battery with porosities of 20 μ m, 2 μ m and 0.2 μ m. The first was a sieve made of 20 μ m mesh. The other two filters were fiberglass. With this procedure three phytoplankton fractions (pico, nano and micro) were obtained for chlorophyll-a extraction,

which was used to estimate biomass. Chlorophyll-a concentration was used as an estimate of the biomass of each size class, and was extracted and measured using the spectrometric method proposed by Lorenzen (1967), at wavelengths 663 nm and 750 nm. Calculation of chlorophyll-a values followed Golterman et al. (1978).

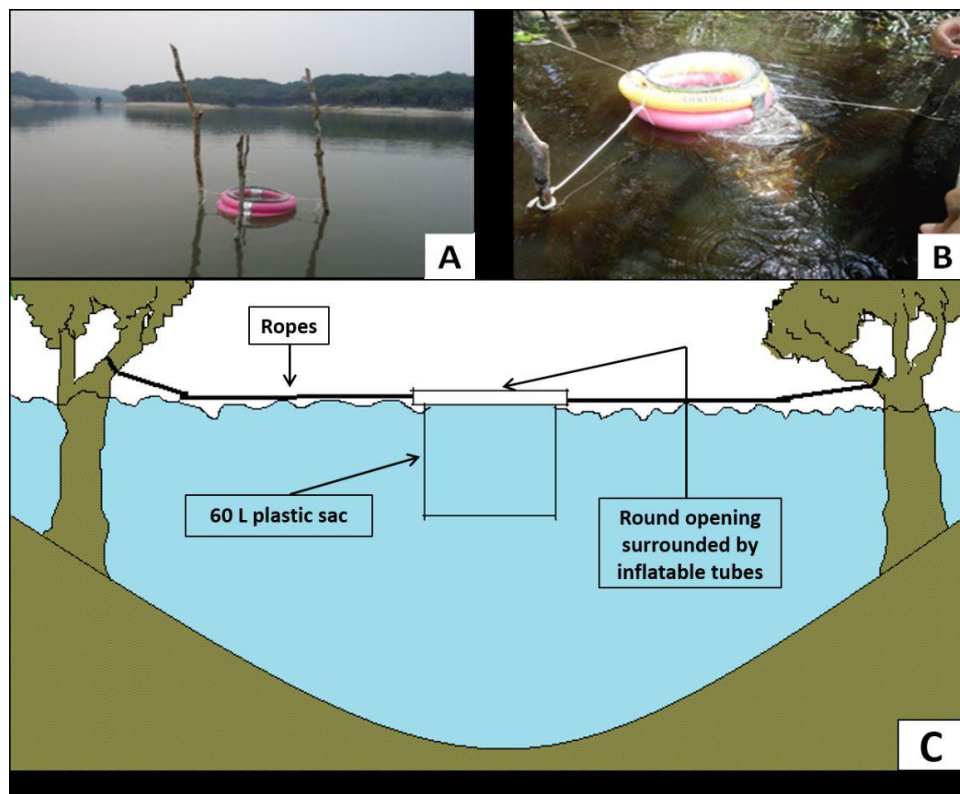


Figure 2 - **A)** Mesocosm in the low-water period, and **B)** Mesocosm in the high-water period. Photos: Castro-Mendes (2016); **C)** Diagram showing the mesocosm structure. Source: (Modified) Couto (2009).

Zooplankton

Zooplanktonic organisms were also sampled with the PVC tube and placed in the mesocosm previously mentioned above. At the same time, an initial sample of zooplanktonic organisms was collected with a 55 μ m mesh net. The net was drawn vertically through the water column, and the sample filtered and packed in 100 ml vials and fixed with 6% buffered formalin.

After 24 hours, the mesocosm was broken down and the zooplankton present were filtered out with a 55 μ m mesh net to obtain final zooplankton sample. These samples were packed and transported to the INPA Plankton Laboratory.

In counting zooplankton each sample was fractionated in the Laboratory using a Folsom-type sample fractionator, until 1/8 of the original sample was obtained. This one-eighth fraction of

the sample was concentrated and placed in Petri dish with a millimeter-gridded underside to facilitate counting. The taxonomic level used for the zooplankton identification was at the order level for microcrustaceans and phylum for rotifers.

Rotifers, cladocerans and copepods in each sample were then counted using a stereoscopic microscope. From each sample, 15 subjects were randomly selected for measurement. For this, a composite microscope equipped with a millimeter eyepiece was used. The measured individuals were classified by size according to the classification of Sieburth *et al.*, (1978). Density was expressed as organisms/m³, with the formula proposed by Tonolli (1971) used for its calculation. To determine the filtered volume in the trawl: $V_f = \pi \cdot r^2 \cdot h$. Where: r = radius of the PVC tube ($r = 2.5$ cm), h = water column height. The volume of water filtered was used to calculate the density of individuals per m³, *via* the formula: $N^\circ \text{ of individuals} = n/V_f$. Where: n = number of individuals counted, V_f = filtered volume.

Data analysis

A G test was conducted to test whether significant differences existed between the sizes

of collected zooplanktonic organisms, this being an alternative to χ^2 (Chi-squared). The G-test was calculated based on the observed and expected values, assuming a significance level of $G > 3.84$ and $P < 0.05$. Analysis was done using the BioEstat statistical program (version 5.3).

Results

Size of zooplanktonic organisms

None of the sampled cladocerans, copepods and rotifers classified into microplankton and mesoplankton size categories was larger than 2 mm. In the low-water season, the smallest was a 33.2 μm rotifer, and the largest size was 1079 μm adult Calanoid copepod. Most zooplanktonic organisms occupied the mesoplankton size-class (Table 1). There was a statistically significant differences between the microplankton and mesoplankton ($G = 39.8613$, $P < 0.0001$) for both the initial and final samples of the experiment ($G = 41.7093$, $P < 0.0001$). There was no statistically significant difference between the initial and final microplankton ($G = 0.1023$ and $P > 0.05$) samples, nor was there any statistically significant difference between the initial and the final mesoplankton samples ($G = 0.2203$ and $P > 0.05$).

Zooplankton (μm)	Initial			Last		
	Min.	Max.	Mean \pm SD	Min.	Max.	Mean \pm SD
Cladocera	91.3	499	301.6 \pm 138.7	141.1	464.8	264.4 \pm 84.9
Nauplius	107	298.8	184.2 \pm 67.8	83	332	207.5 \pm 81
Young-Copepods	232.4	747	417 \pm 127.4	323.7	572.7	441 \pm 63.8
Adults-Copepods	290.5	1079	691.6 \pm 301.1	415	921.3	488.5 \pm 122.1
Rotifera	33.2	307.1	146.6 \pm 86.3	33.2	415	135.5 \pm 104.5

Table 1 – Size of zooplanktonic organisms in the low-water season at Lake Tupé.

For the high-water sample, the smallest recorded size was for a nauplius (49.8 μm), and the largest size was an adult Calanoida copepod (1120.5 μm). Recorded sizes occupied both the micro- and mesoplankton classes (Table 2). There were differences between the micro- and mesoplankton ($G = 71.3441$ and $P < 0.0001$) for both the initial

and final samples of the experiment ($G = 83.231$ and $P < 0.0001$). As in the low-water season, there was no difference between the initial and final microplankton ($G = 0.196$ and $P > 0.05$), nor between the initial and final mesoplankton values ($G = 2.8263$ and $P > 0.5873$).

Zooplankton (μm)	Initial			Last		
	Min.	Max.	Mean \pm SD	Min.	Max.	Mean \pm SD
Cladocera	132.8	664	253.8 \pm 148.9	166	224.1	253.9 \pm 19.8
Nauplius	99.6	232.4	146.6 \pm 40.1	49.8	182.6	133.9 \pm 38.6
Young-Copepods	207.5	456.5	350.2 \pm 72.1	207.5	498	393.4 \pm 77.7
Adults-Copepods	448.2	946.2	766.9 \pm 118	315.4	1120.5	650 \pm 210.6
Rotifera	99.6	141.1	121.1 \pm 13.2	91.3	149.4	120 \pm 15.3

Table 2 – Size of zooplanktonic organisms in the high-water season at Lake Tupé.

Zooplankton Density

The highest densities were found during the low-water period experiment. At this time the rotifers were the most abundant organisms, while at high-water, the copepods had the greater numbers. After 24 hours, in both low and high-

water experiments, there was an increase in the density of the three studied zooplanktonic groups, but during high-water the overall number of organisms was lower than in low-water season (Figures 3 and 4).

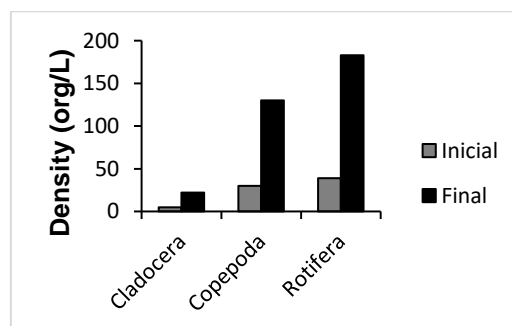


Figure 3 – Initial and final zooplanktonic densities in the low-water mesocosm.

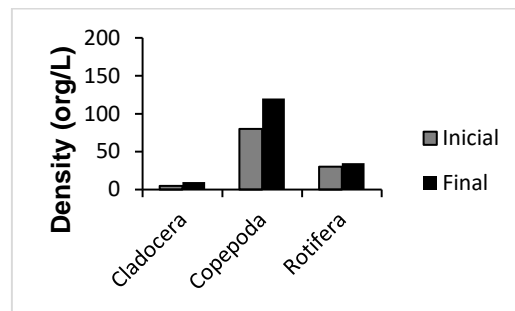


Figure 4 – Initial and final zooplanktonic densities in the high-water mesocosm.

Phytoplankton Biomass

In the low-water season, the initial biomass was 1.92 $\mu\text{g/L}$, and the final biomass 1.09 $\mu\text{g/L}$. For high-water, the initial biomass was 2.91 $\mu\text{g/L}$, and the final 0.81 $\mu\text{g/L}$. Initial and final biomass of the pico-, nano- and

microphytoplankton are shown in Table 3. Both in the low and high-water samples there was decrease in the biomass of all three phytoplanktonic size fractions after 24 hours. Possibly the phytoplankton in the three fractions were consumed by zooplanktonic organisms.

Biomass ($\mu\text{g/L}$)	Low-water		High-water	
	Initial	Last	Initial	Last
Picophytoplankton	0.82	0.55	0	0.81
Nanophytoplankton	0.55	0.27	0.54	0
Microphytoplankton	0.55	0.27	2.37	0

Table 3 – Initial and final biomass of mesocosm phytoplankton fractions in the low- and high-water periods at Lake Tupé.

Discussion

Zooplankton sizes

Freshwater cladocerans are generally 0.2 to 3 mm long, while rotifers are usually smaller, length ranging from 100 to 1000 μm , although in the current study rotifers less to 33.1 μm were recorded. Copepods range from <1 mm to more than 1 mm, and in this study the largest copepod was an 1120.5 μm adult Calanoid. Micro- and mesoplanktonic organisms sizes found in the Lake Tupé agree with those reported by Gliwicz (1977), Gliwicz (1990), Ghidini e Santos-Silva (2009) and Trevisan & Forsberg (2007).

The fact that members of the of micr and mesoplankton size-classes were found is related to the presence of certain species that are dominant in these time-periods. The most abundance cladocerans species during the low-water season are *Bosminopsis deitersi*, which occurs in both micro- and mesoplankton classes, and the mesoplanktonic species *Moina minuta*, *Ceriodaphnia cornuta* and *Diaphanosoma polypina*. *Bosminopsis deitersi* is the most abundant cladoceran in the transition period between low and high waters (Ghidini 2007; Brandorff & Hardy 2009; Ghidini & Santos-Silva

2009; Calixto *et al.* 2011; Ghidini, 2011). Ghidini & Santos-Silva (2009) analysed the biomass and size of the four most abundant cladocerans during the lake's low and high-water seasons, and found *B. deitersi* and *M. minuta* to be co-dominant at low-water. These species also had the highest biomass. While at high-water, *B. deitersi* was both the most dominant species and had the higher biomass. Both in low- and high-water seasons, *Oitona amazonica* is the most abundant cyclopoid species (Brandorff & Hardy 2009; Calixto *et al.* 2011; Segundo 2013; Raid 2015) and the calanoid *Aspinus acicularis* (Raid 2015). For rotifers, 72 planktonic species have been recorded in Lake Tupé (Calixto *et al.*, 2011; Vásquez 2011). Possibly, these same species may have formed part of the assemblage sampled during the mesocosm experiment. If so, then the sizes recorded agree with those already reported for the lake. It is known that most of the organisms recorded belonged more to the mesoplankton than the microplankton size class, so it is possible that that most of the organisms within the mesocosm were large-sized organisms, which may have fed on all available food particles, so making it difficult to ascertain if small species did, indeed, feed on smaller particles.

Zooplankton Density

Zooplanktonic density was higher in the dry season, a pattern already recorded in other zooplankton studies at this site (Brandorff & Hardy 2009; Ferreira & Robertson 2009; Calixto *et al.* 2011; Ghidini 2011; Vasquez 2011; Segundo 2013). This occurs because high-water season is accompanied by changes in the environmental characteristics of the lake, which

occur when the waters of the Rio Negro enter the lake, increasing its volume, and causing a dilution effect and so physically diminishing the zooplankton populations (Brandorff & Andrade 1978; Hamillton *et al.* 1990; Aprille & Darwich, 2005). However, this high-water decrease in the zooplanktonic density may also be related to predation by *Chaoborus* sp. (Santa-Rita & Santos-Silva, 2009), and plankton-feeding fish that enter the lake during this period from the Rio Negro (Prevattelli *et al.* 2005; Soares & Yamamoto, 2005). Rotifers were denser in the dry season because as it has a higher richness and abundance in the lake compared to copepods and cladocerans (Calixto *et al.* 2011; Vasquez 2011). Trevisan & Forsberg (2007), studying three types of Amazon lakes in both white and black water systems, found that rotifers comprised 80% of zooplanktonic abundance. Copepod numbers were much higher at high-water, but this was due to the greater number of nauplii. According to Melão (1997) the developmental period from nauplii to copepodite I is protracted in Amazonian copepods.

In the smaller time scale of 24 hours, two main factors are likely to have influenced the development of organisms, temperature and food. In the bag, food would have been concentrated and zooplankton feed on algae. Cladocerans and rotifers can reproduce by cyclic parthenogenesis (Nogrady *et al.* 1993) and so can produce large quantities of offspring very quickly. Ghidini & Santos-Silva (2009) studying the most abundant Cladocera species of Lake Tupé, *Bosminopsis deitersi*, stated that the density of the species increases in 24 hours mainly at 18 hours. On the other hand, calanoid and cyclopoid copepods

reproduce only by sexual reproduction (Dussart & Defaye 2001), though with large numbers of eggs per cycle. In the experimental samples egg-bearing females were recorded from all three

Phytoplanktonic biomass in relation to zooplankton

The mesocosm method used to provide an *in situ* experiment was effective in allowing some of the simpler of lacustrine environment plankton dynamics to be simulated and investigated. This method has already been used in other studies involving phytoplankton and zooplankton, such as those of Dodson (1974), Northcote *et al.* (1990), Gliwicz & Lampert (1994), Armengol *et al.* (2001), Arcifa & Guagnonil (2003), DeMott & Donk (2004), Filletto *et al.* (2004), Castilho-Noll & Arcifa (2007), Bukovinszky *et al.* (2012), Hansson *et al.*, (2013).

The decrease in biomass at the end of the 24 hours period indicates predation by zooplanktonic organisms on the three phytoplankton fractions had. This could happen because of the variety of zooplankton sizes found which, as discussed above, ranged from tiny nauplii and small rotifers to large adult calanoids. However, Geller & Muller (1981) argue that when an organism grows in size this does not mean that the filtering bristles and food collecting apparatus always increase allometrically, pointing out that in some species of cladocerans the swimming bristles that filter food particles remain the same size even as body size increases. However, they also show that, in still other species, the size of the filtering apparatus and bristles does increase in size as the body grows. Predation by zooplankton

groups, indicating that individuals that were sampled and counted may have hatched during the experimental period, thus increasing the density within the sampled 24 hours.

of phytoplanktonic organisms is corroborated by the results found by Northcote *et al.* (1990) and Gliwicz & Lampert (1994).

Northcote *et al.* (1990) report that predation of phytoplankton by zooplankton occurs more frequently when zooplankton are not predated by fish. In their mesocosm-based experiments with fish both the density and biomass of phytoplankton increased, since it had not been so heavily consumed by the zooplankton. A second experiment without fish recorded a decrease in phytoplankton density and biomass. During low-water season at Lake Tupé zooplanktivorous fish are not greatly abundant (Soares & Yamamoto 2005), but larval *Chaoborus* sp. are (Santa-Rita & Santos-Silva 2009). Such larvae were present in the mesocosm, but not at densities enough to impact zooplanktonic organisms and to influence their biomass and the size-range profile of the surviving population. During high-water, zooplankton apparently did not impact the three phytoplankton size-fractions. This may have occurred because of low density and because zooplanktonic organisms may have been themselves predated by *Chaoborus* sp. larva during the experiment. According to Castilho-Noll & Arcifa (2007), during experiments with mesocosms in lakes, some populations of zooplankton, such as *Daphnia gessneri*, can be regulated by the predation of invertebrates,

particularly by *Chaoborus* sp.

On the other hand, Trevisan & Forsberg (2007), evaluating the predation pressure of zooplanktonic organisms on phytoplankton in the lacustrine systems, found highest zooplankton densities for small-sized organisms, and concluded that phytoplankton was free of high predation pressure and was able to increase its biomass to the limit of available resources. This is considered a frequent occurrence in tropical systems where small forms, such as Rotifera or *Bosmina* sp., dominate zooplankton communities (Nöges 1997). Such small individuals are not able to regulate the relationships between nutrients and phytoplankton biomass in the way that occurs in temperate systems, where phytoplankton numbers are suppressed by the larger, more competitive, crustaceans (Trevisan & Forsberg 2007).

However, Filleto *et al.*, (2004) tested the influence of different phytoplankton size fractions on the growth and reproduction of cladocerans in Monte Alegre Lake, southeaster Brazil, by feeding cladocerans from recently-hatched up to breeding stage on different sizes of phytoplankton (micro- and nanoplankton). They concluded that nanoplankton was most suitable for most cladocerans, with particle size ingestion by these herbivores depended on body size and filtering bristle dimensions. Caraballo (2011), investigating the cladocerans *Diaphanosoma spinolosum* and *Ceriodaphnia cornuta*, observed that, although they grew when fed on phytoplankton from a range of size-fractions, population performance was best when fed on the <30 µm size fraction. Consequently, they suggested that the different fractions tested produce different rates of population growth and

isotopic signatures in cladocerans.

For Tupé Lake, it was observed that there is the presence of zooplankton species of small and large sizes (micro and mesoplankton) and that there are species of phytoplankton from different sizes. It was also observed that the zooplankton's organisms acted in the biomass of the three fractions of phytoplankton's size, thus, it isn't possible to state that there is a dominance of large or small species of phytoplankton since zooplankton's organisms equally prey the three sizes fractions.

Conclusions

Cladocerans, copepods and rotifers did not affect the size-structure of the phytoplankton community or the total biomass of these organisms. In addition, at the community-level, they did not exert selective predation pressure on any of the size fractions of the organisms studied.

It is possible that the result of predation on phytoplankton organisms can be conserved only when heavy predation pressure or selective predation alters the size and/or density structure of some zooplankton size fractions.

The size structure of the phytoplankton was the same in low- and high-water samples, and this may mean that these organisms are also not influenced by the hydrological changes caused by the water from the Negro River into the lake during the flooding period.

Acknowledgements

This research was funded by the Biotupé Project and the National Institute of Amazonian

Research (Instituto Nacional de Pesquisas da Amazonia: INPA). We thank the residents of the Tupé Reserve for their help and participation, and CNPq for a master's degree grant. Adrian Barnett helped with the English writing.

References

- Aprile, F. M. & Darwich, A. J. 2005. Modelos Geomorfológicos para o Lago Tupé. In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (1^a. ed.) Biotupé: meio físico, diversidade biológica e sócio-cultural. Manaus, Amazonas: Instituto Nacional de pesquisas da Amazônia, p. 3-17.
- Arcifa, M. S. & Guagnoni, W. 2003. A new modelo of enclosure for experiments in lentic water. *Acta Limnologica Brasiliensia* 16: 76-79.
- Armengol, X.; Boronat, L.; Camacho, A. & Wurtsbaugh, A. 2001. Grazing by a dominant rotifer *Conochilus unicornis* Rousselet in a mountain lake: in situ measurements with synthetic microspheres. *Hydrobiologia* 446/447: 107-114.
- Brandorff, G. O. & Andrade, E. R. 1978. The relationship between the water level of the Amazon river and the fate of the zooplankton population in lake Jacaretinga. A várzea lake in the central Amazon. *Studies on Neotropical Fauna and Environment* 13: 63-70.
- Brandorff, G. O. & Hardy, E. R. 2009. Crustacean zooplankton of Lago Tupé, a neotropical black water lake in the Central Amazon. In: Santos-Silva, E.N.; Aprile, F.M.; Scudeller, V.V.; Melo, S. (2^a. ed.) Biotupé: meio físico, diversidade biológica e sócio-cultural. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 37-52.
- Bukovinskyl, T.; Verschoor, A. M.; Helmsing, N. R.; Bezemer, T. M.; Bkker, E. S.; Vos, M. & Domis, L. N. S. 2012. The good, the bad and the plenty: interactive effects of food quality and quantity on the growth of different *Daphnia* species. *PLoS One* 7: 1-8.
- Calixto, L. S. F., Ghidini, A. R., Silva, E. A. & Santos-Silva, E. N. 2011. Distribuição espaço-temporal da riqueza e abundância do zooplâncton no lago Tupé, baixo rio Negro, Amazonas, Brasil. In: Biotupé: meio físico, diversidade biológica e sociocultural do baixo rio Negro, Amazônia Central. Santos-Silva, E. N.; Scudeller, V. V. & Cavalcanti, M. J. (3^a. ed.) Manaus: Rizoma Editorial, p. 203-233.
- Caraballo, P.; Sanchez-Caraballo, A. F.; Forsberg, B. & Leite, R. 2011. Crescimento populacional e análise isotópica de *Diaphanosoma spinolosum* e *Ceriodaphnia cornuta* (Crustacea: Cladocera), alimentadas com diferentes frações de seston natural. *Maringá* 33: 11-19.
- Castilho-Noll, M. S. M. & Arcifa, M. A. 2007. Mesocosm experiment on the impact of invertebrate predation on zooplankton of a tropical lake. *Aquatic Ecology* 41: 587-598.
- Chen, R.; Xu, N.; Zhao, F.; Wu, Y.; Huang, Y. & Yang, Z. 2015. Temperature-dependent effect of food size on the reproductive performances of the small-sized cladoceran *Moina micrura*. *Biochemical Systematics and Ecology* 59: 297-301.

- Darwich, A. J.; Aprile, F. M. & Robertson, B. A. 2005. Variáveis limnológicas: contribuição ao estudo espaço-temporal de águas pretas amazônicas. In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (3^a. ed.) Biotupé: meio físico, diversidade biológica e sócio-cultural. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 19-33.
- Diaz-Castro, J. G. & Hardy, E. R. 1998. Life history of *Moina micrura* (Kurz) fed with three algae species, in the laboratory. *Amazoniana* 15: 25-34.
- Dodson, S. I. 1974. Zooplankton competition and predation; an experimental test of the size efficiency hypothesis. *Ecology* 55: 605-613.
- Dumont, H. J. & Negrea, S. V. 2002. Introduction to the Class Branchiopoda. Leiden, Backhuys Publishers.
- Dussart, B. H. & Defaye, D. 1985. Reportoire Mondial des Copépodes Cyclopoides. Paris: Editions du C.N.R.S.
- Dussart, B. H. & Defaye, D. 2001. Introduction to the Copepoda. 2 edn. Backhuys Publishers, Leiden. Frisch, D.; Green, A.J. & Figuerola, J. High dispersal capacity of a broad spectrum of aquatic invertebrates via waterbirds. *Aquatic Sciences* 69: 568-574.
- Esteves, F. A. 1998. Fundamentos de Limnologia. 2.ed. Rio de Janeiro: Interciência.
- Ferreira, C.P.B.; Robertson, A.B. 2009. Composição e abundancia de cladóceros planctônicos no período diurno e noturno de um lago de água preta da Amazonia Central. Programa de Iniciação Científica. Instituto Nacional de Pesquisas da Amazonia.
- Filetto, C.; Ferrao-Filho, A. Arcifa, S.; Silva, L. 2004. Influence of phytoplankton fractions on growth and reproduction of tropical cladocerans. *Aquatic Ecology* 38: 503-514.
- Frau, D.; Batauz, Y.; Alvarenga, P. F.; Scarabotti, P. A.; Mayora, G. & Sinistro, R. Assessing the relevance of top-down and bottom-up effects as phytoplankton structure drivers in a subtropical hypereutrophic shallow lake. *Aquatic Ecology* 53: 265-280.
- Geller, W. & Muller, H. 1981. The filtration apparatus of cladocera: filter mesh-sizes and their implications on food selectivity, *Oecologia* 49: 316-321.
- Ghidini, A. R. 2007. Distribuição vertical nictimeral de Cladocera (Crustacea: Branchiopoda) no lago Tupé, Rio Negro, Amazonas, Brasil. Dissertação de Mestrado, Instituto Nacional de Pesquisas da Amazônia/Universidade Federal do Amazonas.
- Ghidini, A. R. & Santos-Silva, E. N. 2009. Biomassa de quatro espécies de cladocera (Crustacea: Branchiopoda) e sua variação nictemeral no lago Tupé, Amazonas, Brasil In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (2^a. ed.) Biotupé: meio físico, diversidade biológica e sócio-cultural. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 53-62.
- Ghidini, A. R. 2011. Distribuição vertical nictemeral de Cladocera (Crustacea: Branchiopoda) no lago Tupé, rio Negro, Amazonas, Brasil. Dissertação de mestrado do Instituto Nacional de Pesquisas da Amazônia/Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior,

- Manaus, Amazonas.
- Gliwicz, Z. M. 1977. Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. *Ekologia Polska* 25: 179-225.
- Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. *Nature* 343: 638-640.
- Gliwicz, Z. M. & Lampert, W. 1994. Clutch-size variability in *Daphnia*: Body-size related effects of egg predation by cyclopoid copepods. *Limnology and Oceanography* 39: 479-495.
- Golterman, H. L.; Clymo, R. S. & Ohnstad, M. A. M. 1978. *Methods for Physical and Chemical Analysis of Freshwaters*. Oxford: Blackwell Scientific Publication.
- Hamilton, S. K.; Sippel, S. J.; Lewis, W. M. & Saunders, J. J. F. 1990. Zooplankton abundance and evidence for its reduction by macrophyte mats in two Orinoco floodplain lakes. *Journal of Plankton Research* 12: 345-363.
- Hansson, L. A.; Brodersen, J.; Chapman, B. B.; Ekvall, M. K.; Hargeby, A.; Hulthén, K.; Nicolle, A.; Nisson, P. A.; Skov, C. & Bronmark, C. 2013. A lake as a microcosm: reflections on developments in aquatic ecology. *Aquatic Ecology* 47: 125-135.
- Hardy, E.R. & Castro, J. G. D. 2000. Qualidade nutricional de três espécies de clorófitas cultivadas em laboratório. *Acta Amazonica*, 30: 39-47.
- Holynska, M.; Reid, J. W. & Ueda, H. 2003. Genus *Mesocyclops* Sars, 1914. Copepoda: Cyclopoida genera *Mesocyclops* and *Thermocyclops*. In: Ueda, H. & Reid, J. W. (eds.). *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*. Amsterdam: Backhuys Publishers, p. 12-213.
- Lampert, W. 1994. Phenotypic plasticity of the filter screens in *Daphnia*: Adaptation to a low-food environment. *Limnology and Oceanography* 39: 997-1006
- Lourenço, S. O. 2006. *Cultivo de microalgas marinhas: princípios e aplicações*. 1ª. ed. São Carlos: Rima.
- Leão, B.M. 2012. *Composição florística e flutuação espacial e temporal do fitoplâncton do lago Tupé (Amazonas, Brasil)*. Tese de Doutorado. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia/Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior.
- Melo, S.; Rebelo, S. R. M.; Souza, K. F.; Menezes, M. & Torgan, L. C. 2005. Fitoplâncton. In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (3ª. ed.) *Biotupé: meio físico, diversidade biológica e sócio-cultural*. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 87-98.
- Melo, S.; Rebelo, S. R. M.; Souza, K. F.; Soares, C.; Sophia, M. G. 2005. Desmídias com ocorrência planctônica. In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (3ª. ed.) *Biotupé: meio físico, diversidade biológica e sócio-cultural*. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 99-108.
- Melão, M. G. G. 1997. *A comunidade planctônica fitoplâncton e zooplâncton e produtividade secundária do zooplâncton de um reservatório oligotrófico*. Tese de

- Doutorado. São Carlos: UFSCar.
- Nogrady, T.; Wallace, P. L. & Snell, T. W. 1993. Rotifera: biology, ecology and systematics. In: Dumont, H. J. F. (cod). Guides to the identification of the microinvertebrates of the Continental Waters of the world. Netherlands: SPB Academic Publishing.
- Nöges, T., 1997, Zooplankton-phytoplankton interactions in lakes Võrtsjärv, Peipsi (Estonia) and Yaskhan (Turkmenia). *Hydrobiologia* 342/343: 175-183.
- Northcote, T. G.; Arcifa, M. S. & Munro, K. A. 1990. An experimental study of the effects of fish zooplanktivory on the phytoplankton of a Brazilian reservoir. *Hydrobiologia* 194: 31-45.
- Pagano, M. 2008. Feeding of tropical cladocerans (*Moina micrura*, *Diaphanosoma excisum*) and rotifer (*Brachionus calyciflorus*) on natural phytoplankton: effect of phytoplankton size-structure. *Journal of Plankton Research* 30: 401-414.
- Pereira, A.C. 2009. Pinnulariaceae (Bacillariophyta) de um lago de inundação amazônico (lago Tupé, Amazonas, Brasil): taxonomia e distribuição espacial e sazonal. Dissertação de Mestrado. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia.
- Previattelli, D.; Santos-Silva, E. N. & Darwich, A. J. 2005. Distribuição vertical do zooplâncton e sua relação com as variáveis ambientais. In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (3a. ed.) Biotupé: meio físico, diversidade biológica e sócio-cultural. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 109-121.
- Rai, H. 1982. Primary production of various size fractions of natural communities in a North German lake. *Archives fur Hydrobiologie* 95: 395-412.
- Raid, S. A. 2015. Dinâmica da comunidade de copepoda (Crustacea, Maxillopoda) no lago Tupé sob a influência do rio Negro, Manaus – AM. Dissertação de Mestrado. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia/Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior.
- Raven, H. P.; Evert, R. F. & Eichhorn, S. E. 1996. *Biologia vegetal*. 5^{ta}. ed., Rio de Janeiro: Guanabara Koogan.
- Romero, M. C. & Arenas, P. M. 1990. Aporte relativo de diferentes fracciones fitoplanctônicas a la producción primaria y concentración de clorofila, en la laguna de Chascomús (Prov. De Buenos Aires, Argentina). *Revista Brasileira de Biologia* 50: 327-333.
- Round, F. E. 1983. *Biologia das algas*. 2ed. London: Edward Arnold.
- Santa-Rita, A. M. & Santos-Silva, E. N. 2009. Abundância de *Chaoborus* sp. em três ciclos nictemerais no lago Tupé, Manaus-AM. XVIII Jornada Científica PIBIC, p. 439-442.
- Segundo, W. O. P. F. 2013. Riqueza, composição, abundância e distribuição de ciclopóides nas regiões litorânea e limnética do lago Tupé, Manaus, AM, Brasil. Dissertação de Mestrado. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia/Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior.

- Soares, M. G. M. & Yamamoto, K. C. 2005. Diversidade e composição da ictiofauna do lago Tupé. In: Santos-Silva, E. N.; Aprile, F. M.; Scudeller, V. V. & Melo, S. (3a. de.) Biotupé: meio físico, diversidade biológica e sócio-cultural. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia, p. 181-197.
- Souza, K. F. 2012. *Staurostrum meyen* Ralfs (Conjugatophyceae, Desmidiaceae) da bacia do rio Negro: taxonomia e distribuição geográfica. Tese de Doutorado. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia/Programa de Pós-Graduação em Biologia de Água Doce e Pesca Interior.
- Sieburth, J. N. N.; Smetacek, V. & Lenz, J. 1978. Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnology and Oceanography* 23: 1256-1263.
- Tian, X.; Ohtsuki, H. & Urabe, J. 2019. Evolution of asexual *Daphnia pulex* in Japan: variations and covariations of the digestive, morphological and life history traits. *BMC Evolutionary Biology* 19:122.
- Trevisan, G.V. & Forsberg, B. R. 2007. Relationships among nitrogen and total phosphorus, algal biomass and zooplankton density in the central Amazonia lakes. *Hydrobiologia* 586: 357-365.
- Tonolli, V., 1971. Zooplankton – methods of collection. In Edmondson, W. T. & Windberg, G. G. (eds), *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters*, IBP. Oxford and Edinburgh: Blackwell Scientific Publishers,
- Vásquez, E. R. 2011. Estrutura e Dinâmica de Rotíferos (Rotifera) em Vários Microhabitats de Um Lago de Água Preta (Lago Tupé) na Amazônia Central, Brasil. Tese de Doutorado. Manaus, Amazonas: Instituto Nacional de Pesquisas da Amazônia.