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How the structure of a phytophilous chironomid assemblage responds to a lake level drawdown for submerged macrophyte control in a tropical reservoir

Virginia Sanches Uieda* and Sandra Francisca Marçal

Department of Zoology, Biosciences Institute, São Paulo State University - UNESP, CEP: 18618-689 Botucatu, SP, Brazil.

* Corresponding author: vsuieda@gmail.com

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ABSTRACT

How the structure of a phytophilous chironomid assemblage responds to a lake level drawdown for submerged macrophyte control in a tropical reservoir

In hydropower reservoirs, lakes permanently connected to the river present high temporal and spatial stability, what favors the occurrence of macrophytes and a diverse Chironomidae fauna. However, the rapid proliferation of macrophytes causes problems for the diverse uses of the reservoir, being common the application of induced drought to expose the plants to desiccation. In a lake connected to Paranapanema River and under the influence of Salto Grande reservoir, the structure of the Chironomidae fauna associated with the submerged macrophyte *Egeria densa* was analyzed during an induced drought management to verify its consequences on the fauna structure. One sample was taken before starting the management (Control-C), three during the drought disturbance (1st, 7th and 11th days-DD) and one on the 49th day after the reservoir refilling (flood disturbance-FD). A Principal Coordinates analysis applied to density data of 28 Chironomidae taxa (nine replicates per date) indicated a temporal variation. Eight taxa had high correlation with the ordination, but only three with significant temporal difference in density (higher for *Caladomyia* in C, *Dicrotendipes* in FD and *Thienemanniella* in DD11). A temporal difference was also found for richness and diversity (lower at DD1). The higher values of diversity in the peak of the induced drought and after the refilling emphasize the strong effect on this fauna, with reduction of *Caladomyia* and increase of *Dicrotendipes* and *Thienemanniella* densities. Forty-nine days after refilling (FD), the richness and density did not return to pre-management values, with a distribution of abundance among diferent genera and none expressing dominance.

Key words: aquatic insects, density, diversity, *Egeria densa*, hydrological disturbance, temporal variation

RESUMO

Como a estrutura de uma assembléia de quironomídeos fitófilos responde à redução no nível de um lago utilizada para controle de macrófitas submersas em um reservatório tropical

Em reservatórios de hidrelétricas, lagos permanentemente conectados ao rio apresentam alta estabilidade temporal e espacial, o que favorece a ocorrência de macrófitas e uma fauna diversa de Chironomidae. No entanto, a rápida proliferação de macrófitas causa problemas para os diversos usos do reservatório, sendo comum a aplicação de seca induzida para expor as plantas à dessecação. Em um lago ligado ao Rio Paranapanema e sob influência do reservatório de Salto Grande, a estrutura da fauna de Chironomidae associada à macrófita submersa Egeria densa *foi analisada durante um manejo de seca induzida para verificar suas conseqüências na estrutura da fauna. Uma amostra foi retirada antes do início do manejo (Controle-C), três durante o distúrbio da seca (1º, 7º e 11º dias-DD) e uma no 49º dia após o enchimento do reservatório (perturbação por inundação-FD). Uma análise de Coordenadas Principais aplicada aos dados de densidade de 28 táxons de Chironomidae (nove réplicas por data) indicou uma variação temporal. Oito táxons tiveram alta correlação com a ordenação, mas apenas três com diferença temporal significativa na densidade (maior para* Caladomyia *em C,* Dicrotendipes *em FD e* Thienemanniella *em DD11). Uma diferença temporal também foi encontrada para riqueza e diversidade (menor em DD1). Os maiores valores de diversidade no pico da seca induzida e após o enchimento enfatizam o forte efeito sobre esta fauna, com* *redução de* Caladomyia *e aumento das densidades de* Dicrotendipes *e* Thienemanniella*. Quarenta e nove dias após o enchimento (FD), a riqueza e a densidade não retornaram aos valores pré-manejo, com distribuição da abundância entre diferentes gêneros e nenhum expressando dominância.*

Palavras chave: *insetos aquáticos, densidade, diversidade,* Egeria densa*, perturbação hidrológica, variação temporal*

INTRODUCTION

Dipterans of the family Chironomidae are dominant insects in macrophytes (Ogbeibu, 2001; Copeland *et al.*, 2012; Kaczorowska & Suchora, 2014), with composition, abundance and trophic structure dependent on the successional stage (Stripari & Henry, 2002; Nessimian & Henriques-de-Oliveira, 2005; Silva & Henry, 2018) and on the conditions of the aquatic environment (Silva *et al.*, 2015; Habib & Yousuf, 2015). Those insects also play an important role in the cycling of organic matter in freshwater ecosystems (Hirabayashi & Wotton, 1999).

These dipterans present rapid development and high adaptability as colonizers (Wiggins *et al.*, 1980), which allows them to live in a wide range of environmental conditions (Trivinho-Strixino, 2011), including floodplains with seasonal hydrological pulses (Santos *et al.*, 2013). In these environments, drought events are very common and cause hydric, thermal and low oxygen stress in the invertebrate fauna (Santos *et al.*, 2013). However, hydrological variations are usually gradual in these ecosystems, allowing invertebrates to adapt or alter their behavioral characteristics favoring their survival or recovery from disturbances (Otermin *et al.*, 2002; Frouz *et al.*, 2003).

In hydropower reservoirs, lateral lakes permanently connected to the river present high temporal and spatial stability due to lower frequency and intensity of hydrological disturbances (Ward *et al.*, 1999; Henry, 2005). These environmental conditions favor the occurrence of macrophytes and a diverse fauna of Chironomidae, adapted to hydrological stability and food availability (Habib & Yousuf, 2015; Silva *et al.*, 2015). Some Chironomidae species are favored by the intense eutrophication process and high organic matter availability, which over time causes the substitution of less tolerant species by species more resistant to environmental modifications (Brandimarte *et al.*, 1999; Dornfeld *et al.*, 2005; Penczak *et al.*, 2006). Unlike hydrologically stable environments, aquatic systems that are disturbed periodically tend to have a high diversified fauna, where dominance and competitive exclusion are intense (Huston, 1979).

Submerged macrophytes such as *Egeria densa* Planch have been favored in dams due to the low depth and turbulence and the high water column luminosity, with their rapid proliferation causing problems to reservoirs uses (Yarrow *et al.*, 2009; Silva *et al.*, 2012). The high *E. densa* density in shallow marginal lakes favors colonization by detritivorous invertebrates, as many Chironomidae taxa that become dominant (Trivinho-Strixino *et al.*, 2000; Dornfeld & Fonseca-Gessner, 2005) and specially benefited in these systems (Dvořák, 1996; James *et al.*, 2000; Weatherhead & James, 2001; Silva & Henry, 2013).

Due to the financial damages that the macrophytes profitable growth can cause, in recent years power companies have shown interest in understanding the dynamic of these plants in altered ecosystems. Some management techniques have been used in reservoirs and an efficient control of macrophytes density has been obtained by varying the reservoirs operational quota (Pompêo, 2008; Yarrow *et al.*, 2009; Curt *et al.*, 2010; Coetzee *et al.*, 2011) what leads to water level reduction and exposure of the plants to desiccation in the littoral zone (Debastiani-Júnior & Nogueira, 2015, Portinho & Nogueira, 2017). In a continuous monitoring program, from 2011 to 2018, the hydropower company responsible for the Salto Grande reservoir management (Duke Energy) estimated the macrophyte biomass one week before and about 100 days after the depletion and verified that the control of the plants occurred effectively in three years over this period, with a reduction of approximately 40 % (2012), 10 % (2015) and 30 % (2018), considering that without the depletion possibly the amount of plants today would be extremely higher (personal communication, M. G. Nogueira).

However, an induced drought for macrophyte management in environments controlled by dams can act as a significant disturbance with diverse consequences on the local fauna richness and diversity (Santos & Thomaz, 2007; Debastiani-Júnior & Nogueira, 2015, Portinho & Nogueira, 2017), interfering in the hydrodynamics, stability and trophy of the whole system.

The aim of our study was to evaluate the effects of hydrological disturbances, induced by the water level operational variation of a tropical reservoir to control *E. densa* biomass, upon the structure and stability of the phytophilous Chironomidae fauna in a marginal lake of the Paranapanema River. The hypothesis is that with the natural macrophyte decay due to the induced drought it will be a reduction in the fauna diversity immediately after the disturbance.

MATERIALS AND METHODS

Survey design

The work was conducted in the Pedra Branca lake (22º 56' 28" S, 49º 58' 02" W) that is connected to the Salto Grande reservoir, a run-of-river reservoir on the Paranapanema River on the border of São Paulo and Paraná States, Brazil (Fig. 1). The lake, located on the right bank of the river, has a surface area of 0.44 Km^2 and a mean depth of 2 m (which varies in response to the water level in the reservoir), and is densely colonized by the submerged aquatic macrophyte *Egeria densa* (Debastiani-Júnior & Nogueira, 2015; Portinho & Nogueira, 2017).

The survey schedule followed the operational lowering of the water level (drawdown) conducted by the electricity generating company (Duke Energy) every year during the dry season to expose shore macrophytes to dehydration with the aim of decreasing plant biomass. In 2011, the Salto Grande reservoir was drawdown by ~ 2 m over a period of 13 days (August 21 to September 2). A total of five collections were carried out between August 16 and October 22, the first seven days before the beginning of the water level management (Control - C) and four during the management, of which three occurred in the period of induced drought (on the 1^{st}, 7^{th} and 11^{th} days of the drought disturbance - DD) and one on the 49^{th} day after the reservoir refilling (flood disturbance – FD).

Although the studied area presented three precipitation events of no more than 5 mm each

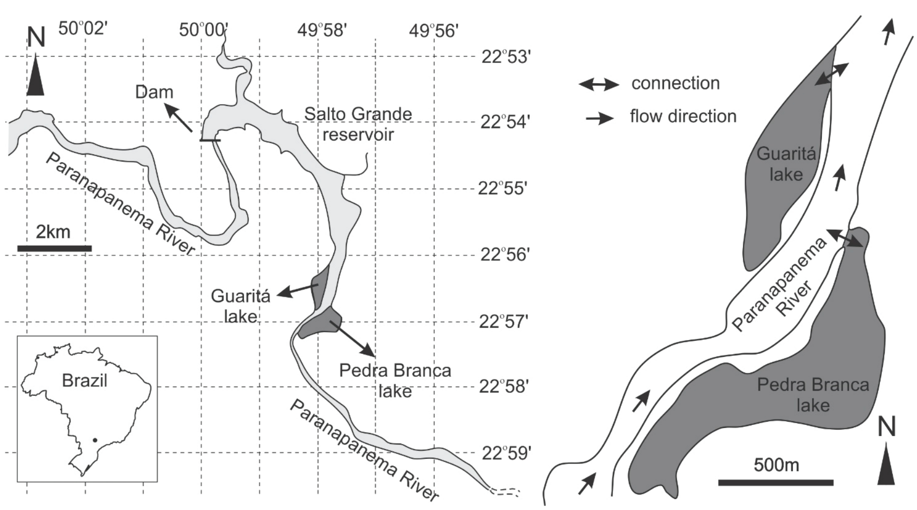

Figure 1. Location of Pedra Branca lake on the right margin of Paranapanema River and at a distance of ~ 6 Km from the dam of the Salto Grande reservoir (Source: Debastiani-Júnior & Nogueira, 2015). *Localização do lago Pedra Branca na margem direita do Rio Paranapanema e a uma distância de ~ 6 Km da barragem do reservatório Salto Grande (Fonte: Debastiani-Júnior & Nogueira, 2015).*

Table 1. List of taxa from the three Chironomidae subfamilies found associated with *Egeria densa* in the Pedra Branca lake (according to Trivinho-Strixino, 2011). *Lista de táxons das três subfamílias de Chironomidae encontrados associados com* Egeria densa *no lago Pedra Branca (de acordo com Trivinho-Strixino, 2011).*

CHIRONOMINAE	ORTHOCLADIINAE
Apedilum Townes, 1945	*Corynoneura* Winnertz, 1846
Asheum (Sublette, 1964)	*Cricotopus* v. d. Wulp, 1874
Beardius Reiss & Sublette, 1985 type1	*Paracladius* Hirvenoja, 1973
Beardius Reiss & Sublette, 1985 type2	*Thienemanniella* Kieffer, 1911
Caladomyia Sawedal, 1981	
Chironomus Meigen, 1803	**TANYPODINAE**
Dicrotendipes Kieffer, 1913	*Ablabesmyia* Johannsen, 1905
Endotribelus calophylli Roque & Trivinho-Strixino, 2008	*Labrundinia* Fittkau, 1962 sp2
Fissimentum Cranston & Nolte, 1996 sp3	*Labrundinia* Fittkau, 1962 sp5
Fissimentum Cranston & Nolte, 1996 sp4	*Labrundinia* Fittkau, 1962 sp9
Goeldichironomus Fittkau, 1965	*Larsia* Fittkau, 1962
Oukuriella Epler, 1986	
Parachironomus longistilus Paggi, 1977	
Polypedilum Kieffer, 1912 sp3	
Polypedilum Kieffer, 1912 sp5	
Polypedilum Kieffer, 1912 (*Tripodura*) sp3	
Pseudochironomus Malloch, 1915	
Riethia truncatucaudata (Edwards, 1931)	
Xenochironomus Kieffer, 1921	

during the drawdown period, the volume and depth of the Pedra Branca lake was strongly reduced, and the lake remained disconnected from the river following three days of drawdown and reconnected immediately when start refilling (Portinho & Nogueira, 2017). Due to this dynamic, some limnological characteristics of the lake showed significant changes over the operational management. At the end of the drawdown period, the lake presented the lowest pH and dissolved oxygen and the highest conductivity value, none returning to the values measured before the management (Portinho & Nogueira, 2017).

Field and laboratory work

Samples of *E. densa* were collected in three sites along the major longitudinal axis of the lake, one near the river connection, other in the middle and another in the end of this axis. Three replicates were taken per site, with a total of nine replicates for each date, using a polyvinyl chloride (PVC) cylinder with 25 cm in diameter by 40 cm in height, closed at one end by a 250 µm mesh for water drainage. The macrofauna samples were transfered to plastic bags with 70 % alcohol for preservation until its processing.

In the laboratory, the macrophytes were carefully washed in running water over granulometry screens (1.0, 0.50 and 0.25 mm mesh). The material retained in the sieves (fragments of macrophyte, organic matter and associated macroinvertebrates) was fixed in 70 % alcohol and screened under a stereoscopic microscope. From this material the macroinvertebrates were separated and the Chironomidae specimens were identified using Trivinho-Strixino (2011) keys and descriptions.

After the invertebrates removal, the macrophytes were dried in a forced aeration oven at 70 ºC until reaching constant weight (about 72 hours) and then weighed in analytical balance to determine the dry biomass, following the methodology of Pompêo & Moschini-Carlos (2003). The abundance of Chironomidae, analyzed at the family, subfamilies and genus levels, was transformed in density, considering the number of individuals per 100 gram of macrophyte dry weight (ind/100g DW).

Table 2. Mean absolute (n = ind/100g DW, mean of nine replicates) and relative density (%) of Chironomidae taxa associated with *Egeria densa* in the Pedra Branca lake. The samples were collected before (control) and during the management phases of the Salto Grande reservoir, Paranapanema River (DD = 1st, 7th and 11th days of the drought disturbance, FD = on the 49th day of the flood disturbance). *Densidade media absoluta (n = ind/100g peso seco, média de nove réplicas) e relativa (%) dos táxons de Chironomidae associados a* Egeria densa *no lago Pedra Branca. As amostras foram coletadas antes (controle) e durante as fases de manejo do reservatório Salto Grande, Rio Paranapanema (DD = 1º, 7º e 11º dias da perturbação de seca, FD = no 49º dia da perturbação de cheia).*

	Control		**DD1**		**DD7**		**DD11**		**FD**	
Taxa	n	%	n	%	n	%	n	%	n	%
Apedilum	12.80	0.19	0.90	0.03	-	-	0.49	0.13	0.69	0.05
Asheum	0.57	0.01	-	-	-	-	-	-	-	-
Beardius type1	0.93	0.01	2.56	0.10	6.11	0.74	1.02	0.27	2.61	0.19
Beardius type2	2.69	0.04	1.49	0,06	-	-	0.45	0.12	0.35	0.03
Caladomyia	5011.82	75.27	1567.87	60.74	431.17	52.33	62.14	16.78	460.10	33.61
Chironomus	0.57	0.01	-	-	-	-	-	-	-	-
Dicrotendipes	228.50	3.43	4.02	0.16	19.33	2.35	10.50	2.83	290.79	21.24
Endotribelus calophylli	4.81	0.07	1.07	0.04	0.62	0.08	1.47	0.40	-	-
Fissimentum sp3	0.57	0.01	-	-	-	-	-	-	-	-
Fissimentum sp4	-	-	-	-	0.76	0.09	-	-	-	-
Goeldichironomus	-	-	-	-	0.67	0.08	-	-	-	-
Oukuriella	-	-	-	-	-	-	-	-	0.69	0.05
Parachironomus longistilus	323.60	4.86	692.08	26.81	108.56	13.18	18.72	5.05	131.21	9.58
Polypedilum sp3	10.69	0.16	2.70	0.10	3.70	0.45	1.52	0.41	52.72	3.85
Polypedilum sp5	4.61	0.07	-	-	4.92	0.60	1.95	0.53	3.21	0.23
Polypedilum (*Tripodura*) sp3	-	-	-	-	0.67	0.08	-	-	0.69	0.05
Pseudochironomus	1.41	0.02	-	-	-	-	0.30	0.08	0.66	0.05
Riethia truncatucaudata	5.11	0.08	0.90	0.03	1.88	0.23	0.30	0.08	0.69	0.05
Xenochironomus	5.14	0.08	-	-	-	-	0.30	0.08	-	-
Corynoneura	49.50	0.74	31.37	1.22	1.34	0.16	6.93	1.87	9.18	0.67
Cricotopus	252.23	3.79	60.56	2.35	80.07	9.72	23.04	6.22	102.29	7.47
Paracladius	9.08	0.14	6.43	0.25	2.20	0.27	0.90	0.24	0.35	0.03
Thienemanniella	168.09	2.52	32.14	1.25	102.62	12.46	189.45	51.15	142.09	10.38
Ablabesmyia	344.25	5.17	110.73	4.29	48.80	5.92	26.82	7.24	120.52	8.80
Labrundinia sp2	1.09	0.02	1.33	0.05	0.58	0.07	0.32	0.09	-	-
Labrundinia sp5	201.09	3.02	63.59	2.46	6.92	0.84	16.89	4.56	49.85	3.64
Labrundinia sp9	13.71	0.21	-	-	2.97	0.36	5.97	1.61	-	-
Larsia	5.81	0.09	1.44	0.06	-	-	0.89	0.24	0.35	0.03

Data analysis

The total richness and mean density of Chironomidae determined by date (Control, DD1, DD7, DD11, and FD) were used to calculate the Shannon-Wiener diversity and the Simpson evenness indices (Krebs, 1989).

Given the lack of normality (Shapiro-Wilks; $\alpha = 0.05$) and homoscedasticity (Levene; $\alpha = 0.05$) even after data transformation, a Kruskal-Wallis non-parametric analysis of variance was applied to community attributes (richness, density, diversity and evenness), considering the nine replicates by date, in order to verify the existence of temporal differences (SYSTAT 13 for Windows, 2009). The significant results were followed by a pair-wise test (Dwass-Steel-Chritchlow-Fligner) and were presented in mean and standard error graphics (OriginPro 8; ORIGINLAB©, 2011).

The density data was transformed in log (x+1) and a resemblance matrix (Bray-Curtis similarity measure) was created to perform a Principal Coordinates analysis (PCO), with the add of vectors representing the Chironomidae taxa that presented a Pearson correlation > 0.6 with the ordination. This analysis provide a direct projection of the points in a two-dimensional space defined by the actual dissimilarities between the replicates (Permanova+ for Primer; Anderson *et al.*, 2008). The vector exploratory tool added to this analysis allowed the visualization of potential linear correlation between the variables and the ordination axis, with the length and direction of each vector indicating the strength and sign, respectively, of the relationship between that variable and the PCO axes.

RESULTS

A total of 28 Chironomidae taxa were identified, representing three subfamilies, being 19 Chironominae, four Orthocladiinae and five Tanypodinae (Table 1). Of these Chironomidae taxa, only 12 (43 %) were recorded on all dates and most taxa contributed with less than 10 ind/100g DW on each date (Table 2).

The analysis of Chironomidae community attributes showed a significant temporal difference in richness, density and diversity, with the smallest value of richness and diversity at the beginning (DD1) and of density at the end (DD11) of the drought disturbance (Table 3, Fig. 2).

The results of the analysis of variance applied to density data of the three subfamilies (Fig. 3) indicated significat temporal difference for Chironominae ($p = 0.002$), Orthocladiinae ($p = 0.043$) and Tanypodinae ($p = 0.046$). For Chironominae, the pairwise test differentiated the

Table 3. Community attributes calculated for Chironomidae sampled in the Pedra Branca lake, before (control) and during the management phases of the Salto Grande reservoir, Paranapanema River (DD = 1st, 7th and 11th days of the drought disturbance, FD = on the 49th day of the flood disturbance). Richness = total number of taxa in the nine replicates of each date. Density = mean of nine replicates, expressed by ind/100g DW (DW- dry weight of macrophytes). Diversity and evenness = mean of nine replicates, calculated from the total richness and the mean density. Results of non-parametric Kruskal-Wallis analysis, with p value that indicate significant temporal differences ($p < 0.05$) in bold. *Atributos da comunidade calculados para Chironomidae amostrado no lago Pedra Branca, antes (controle) e durante as fases de manejo do reservatório Salto Grande, Rio Paranapanema (DD = 1º, 7º e 11º dias da perturbação de seca, FD = no 49º dia da perturbação de cheia). Riqueza = número total de táxons nas nove réplicas de cada data. Densidade = média de nove réplicas, expressa em ind/100g PS (PS- peso seco de macrófitas). Diversidade e equitabilidade = média de nove réplicas, calculadas da riqueza total e da densidade média. Resultados do teste não-paramétrico Kruskal-Wallis, com o valor de p que indica diferenças temporais significativas (*p *< 0,05) em negrito.*

Community attributes	Control	DD1	DD7	DD11	FD	*p*
Richness	24	17	19	21	19	**0.005**
Density	6927.10	2626.96	863.98	408.08	1397.32	**0.013**
Diversity	2.371	1.911	2.159	2.206	2.122	**0.007**
Evenness	0.970	0.966	0.968	0.962	0.966	0.813

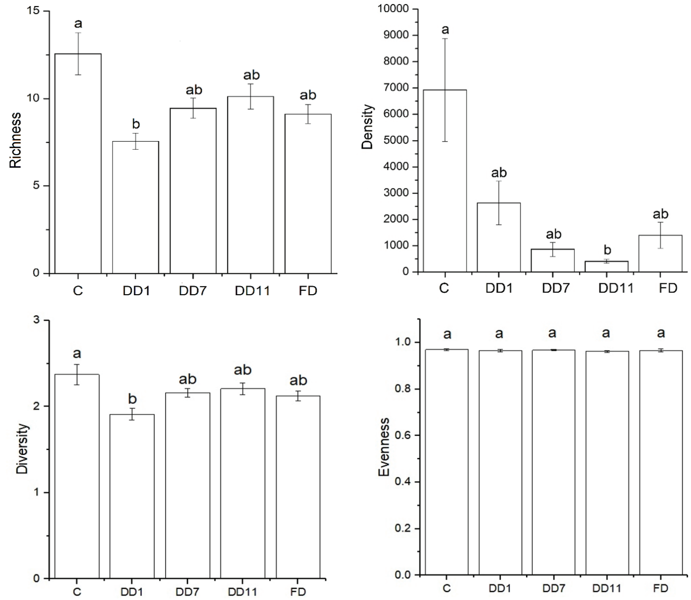

Figure 2. Mean and standard error of the richness, density, diversity and evenness of Chironomidae, analysed before (C = control) and during the management phases of the Salto Grande reservoir, Paranapanema River (DD = 1st, 7th and 11th days of the drought disturbance; FD = on the 49th day of the flood disturbance). Results of pairwise test: different letters indicate values significantly different. *Média e erro padrão da riqueza, densidade, diversidade e equitabilidade de Chironomidae analisada antes (C = controle) e durante as fases de manejo do reservatório Salto Grande, Rio Paranapanema (DD = 1º, 7º e 11º dias da perturbação de seca; FD = no 49º dia da perturbação de cheia). Resultados do teste pairwise: letras diferentes indicam valores significativamente diferentes.*

Control from DD11. For the other two subfamilies, although the variance analysis indicated a significant difference, the pairwise test did not differentiate the dates (Fig. 3).

A significant temporal variation was also found for two Chironominae taxa (*Caladomyia* $p = 0.001$ and *Dicrotendipes* $p = 0.008$), two Orthocladiinae (*Cricotopus* $p = 0.003$ and *Thienemanniella* $p = 0.014$) and one Tanypodinae (*Labrundinia* sp9 $p = 0.012$). These five taxa with a significant difference in density showed different responses to the management, evidenced by the pairwise test (Fig. 4). The Chironominae *Caladomyia* and *Dicrotendipes* presented a strong decrease in density during the drought disturbance but their response to the management was different. For *Caladomyia* the smallest density occurred at the end of the drought disturbance (DD11) and not recovered to control values after refilling, whereas the smallest density of *Dicrotendipes* occurred at the beginning of the drought disturbance (DD1) and the value after refilling was higher than in the control (Fig. 4). The Orthocladiinae *Cricotopus* and *Thienemanniella* also presented a reduction in density during the drought disturbance, the first at the end (DD11) and the second at the beginning (DD1) of the drought disturbance, but both not recovering the control values after refilling (Fig. 4). For the Tanypodinae *Labrundinia* sp9 there was no occurrence at the beginning of the drought disturbance and after refilling (Fig. 4).

The two first axes of the Principal Coordinates analysis (PCO) explained together 52.2 % of the Chironomidae density data (Fig. 5). The first axis, with the highest percentage of total variation, separated most replicates of control and DD1 in the negative side and all replicates of DD11 and most of DD7 and FD in the positive one. Eight Chironomidae taxa showed high correlation with the ordination (Fig. 5), from which only three showed significant temporal difference by the variance analysis: *Caladomyia* with a high density in Control, *Dicrotendipes* in FD and *Thiene-*

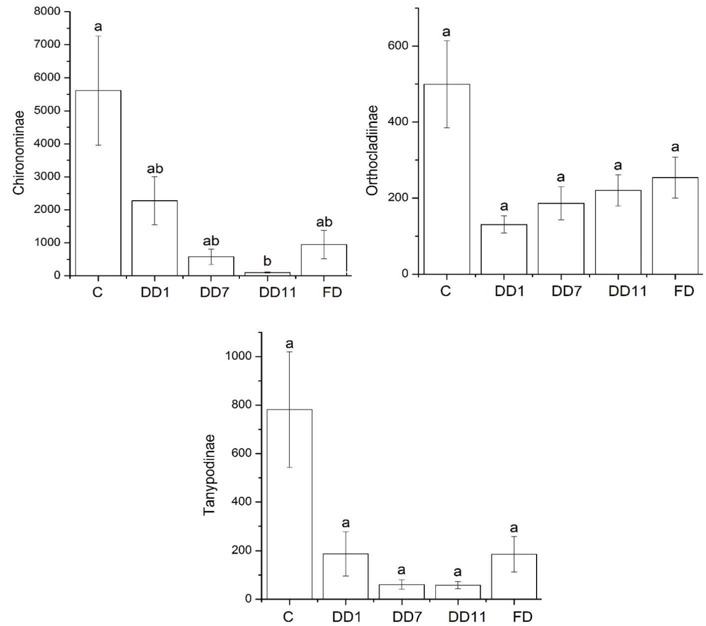

Figure 3. Mean density and standard error of the three Chironomidae subfamilies, analysed before (C = control) and during the management phases of the Salto Grande reservoir, Paranapanema River (DD = 1st, 7th and 11th days of the drought disturbance, FD = on the 49th day of the flood disturbance). Results of pairwise test: different letters indicate values significantly different. *Densidade média e erro padrão das três subfamílias de Chironomidae, analisada antes (C = controle) e durante as fases de manejo do reservatório Salto Grande, Rio Paranapanema (DD = 1º, 7º e 11º dias da perturbação de seca; FD = no 49º dia da perturbação de cheia). Resultados do teste pairwise: letras diferentes indicam valores significativamente diferentes.*

manniella in DD11 (Fig. 4 and 5).

The management of the reservoir led to four types of fauna response when compared each date with the previous one, with positive effects through increase in density or emergence of new taxa and with negative effects through reduction in density or absence (Table 4). At the beginning of the drought disturbance the percentage of negative effects was higher (78 %) than positive ones, equally by reduction in density or absence of many taxa; at days seven and eleven of the drought disturbance the percentage of positive and negative effects was similar. When considered the flood disturbance comparatively to control, the percentage of negative effects was higher (57 %), similarly by reduction in density or absence of taxa (Table 4). The emergence of new taxa that had not been recorded in the previous date or in the control occurred more at the end of the drought disturbance (DD7 and DD11).

DISCUSSION

Dipterans of the Chironomidae family stand out in freshwater aquatic ecosystems for abundance and diversity (Coffman & Ferrington, 1996; Kaczorowska & Suchora, 2014). Their greater numerical representativeness is generally associated with a set of morphological, physiological and behavioral mechanisms that make them capable of tolerating the most diverse environmental conditions, including those unfavorable for most invertebrates (Penczak *et al.*, 2006; Trivinho-Strixino, 2011). Environmental factors, such as food availability, water and sediment oxygenation, and composition of macrophyte coverage, can determine the qualitative and quantitative structure of Chironomidae assemblages (Kaczorowska & Suchora, 2014). Santana *et al.* (2015) observed that changes in aquatic systems and changes in water level due to rainfall or dam control may cause changes in the

Table 4. Effect of the operational management of the Salto Grande reservoir on the density of Chironomidae taxa, sampled during four management phases, determined by comparing the mean relative density of the drought disturbance date with the one preceding it (DD1 compared with control) and comparing the density of the flood disturbance date with the control value. (DD = 1st, 7th and 11th days of the drought disturbance, FD = on the 49th day of the flood disturbance). Positive effects: increase (+), emergence of new taxa (1); negative effects: reduction (-), absence (0). *Efeito do manejo operacional do reservatório Salto Grande sobre a densidade dos táxons de Chironomidae, amostrados durante as quatro fases de manejo, determinado comparando a densidade relativa média na data da perturbação de seca com a anterior (DD1 comparada com o controle) e comparando a densidade da data da perturbação de cheia com o valor do controle. (DD = 1º, 7º e 11º dias da perturbação de seca, FD = no 49º dia da perturbação de cheia). Efeitos positivos: aumento (+), aparecimento de novos táxons (1); efeitos negativos: redução (-), ausência (0).*

Taxa	DD1	DD7	DD11	FD
Apedilum	-	0	1	-
Asheum	0	0	0	0
Beardius type1	+	+	-	+
Beardius type2	+	0	1	-
Caladomyia	-	-	-	-
Chironomus	0	0	0	0
Dicrotendipes	-	+	+	+
Endotribelus calophylli	-	+	+	0
Fissimentum sp3	0	0	0	0
Fissimentum sp4	0	1	0	0
Goeldichironomus	0	1	0	0
Oukuriella	0	0	0	1
Parachironomus longistilus	+	-	-	+
Polypedilum sp3	-	+	-	+
Polypedilum sp5	0	1	-	+
Polypedilum (*Tripodura*) sp3	0	1	0	+
Pseudochironomus	0	0	1	+
Riethia truncatucaudata	-	+	-	-
Xenochironomus	0	0	1	0
Corynoneura	+	-	+	-
Cricotopus	-	+	-	+
Paracladius	+	+	-	-
Thienemanniella	-	+	+	+
Ablabesmyia	-	+	+	+
Labrundinia sp2	+	+	+	0
Labrundinia sp5	-	-	+	+
Labrundinia sp9	0	1	+	0
Larsia	-	0	1	-
% Increase (+)	22	36	28	39
% Emergence (1)	0	17	19	4
% Reduction (-)	39	14	28	25
% Absence (0)	39	33	25	32

community structure of Chironomidae to adjust to the new environment.

In the present study, the Chironomidae density was hampered by the drought disturbance and presented a slow recovery after the reservoir refilling. According to Lake (2000), the effects of droughts and floods on the abiotic environment and on the biota differ greatly. The drought disturbances have longer effects, as the recovery of the biota is slower and some species can be eliminated; in contrast most floods have short-term effects, but some also can cause drastic changes in species composition (Lake, 2000).

Among the most successful adaptations of invertebrates to withstand drought are those related to the life cycle (diapause stages and resistance forms) and dispersal capacity (Boulton, 1989; Otermin *et al.*, 2002). Each Chironomidae species has its own strategy for surviving desiccation, but in general species typical of artificial reservoirs present high dehydration tolerance because they are frequently exposed to hydrological variations (Suemoto *et al.*, 2004), emerging from the sediment soon after the flood (Benigno & Sommer, 2008). However, some species do not have physiological adaptations to desiccation,

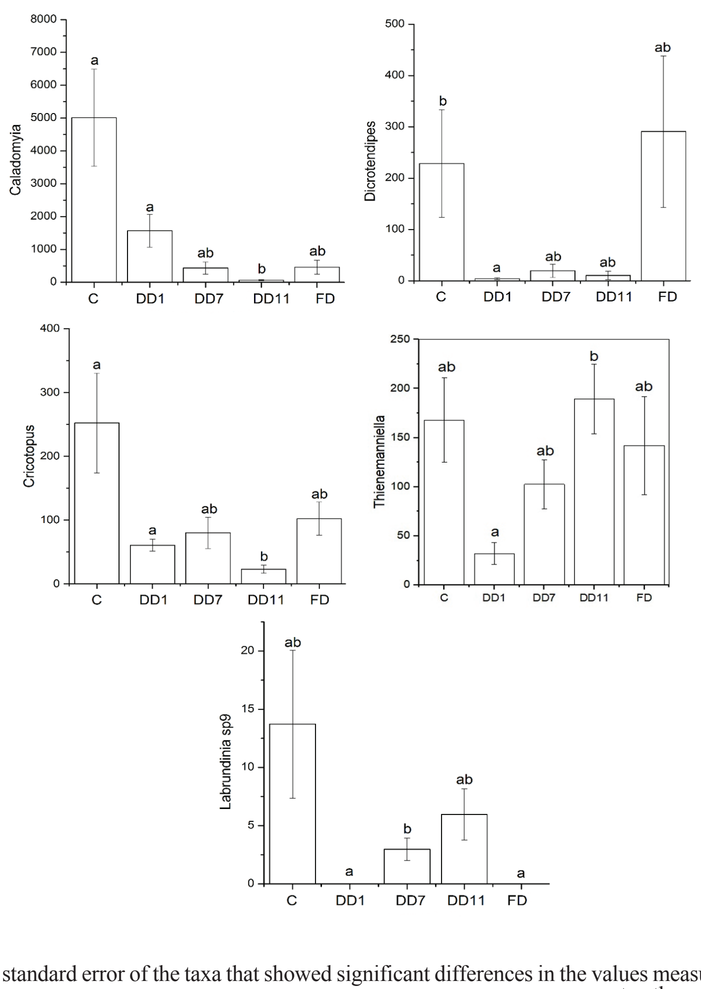

Figure 4. Mean density and standard error of the taxa that showed significant differences in the values measured before (C = control) and during the management phases of the Salto Grande reservoir, Paranapanema River (DD = 1st, 7th and 11th days of the drought disturbance, FD = on the 49th day of the flood disturbance). Results of pairwise test: different letters indicate values significantly different. *Densidade média e erro padrão dos táxons que mostraram diferença significativa entre os valores mensurados antes (C = controle) e durante as fases de manejo do reservatório Salto Grande, Rio Paranapanema (DD = 1º, 7º e 11º dias da perturbação de seca; FD = no 49º dia da perturbação de cheia). Resultados do teste pairwise: letras diferentes indicam valores significativamente diferentes.*

surviving no more than two hours under drought conditions or being able to complete the larval phase of their life cycle before the environment completely dries up (Suemoto *et al.*, 2004).

Due to its fragile structure, *E. densa* rapidly dried in the margins of the lake by the effect of induced drought, concentrating in the center of about one meter deep, which probably caused changes in the abiotic parameters and, consequently, caused changes in the Chironomidae assemblage composition due to its low tolerance to environments subject to hydric stress. With macrophytes senescence, the groups of microorganisms and invertebrates that participate in the macrophytes degradation may vary (Gullberg *et al.*, 1997), with a greater supply of ecological niches and food resources for detritivorous groups (Silva & Henry, 2013). However, although the availability of food resources can directly control invertebrate fauna, physical factors such as depth, current and transparency also cause indirect effects by influencing the macrophytes distribution and abundance and the substrate characteristics (Weatherhead & James, 2001). Also working in the Pedra Branca lake, but analyzing the effect of induced drought on Cladocera in 2005, Debastiani-Júnior & Nogueira (2015) related the decrease of pH and dissolved oxygen values during the depletion event with an intense respiration and decomposition of organic matter originated from the exposition to the air of macrophytes in the littoral zone; in sequence, this dead biomass rehydrates, dissolves and releases dissolved ions, increasing the conductivity.

The higher values of diversity found in the end of the induced drought and after the filling emphasize the hydrological disturbance effect on this fauna, with reduction of dominant taxa such as *Caladomyia* that presented a strong density reduction throughout the management, while *Dicrotendipes* and *Thienemanniella* increased in density. After filling, the values of richness and density did not return to pre-management values, favoring diversity and evenness, with a distribution of abundance among Chironomidae genera and none expressing dominance. These temporal changes caused in the studied lake by the reservoir operational management could be viewed in the ordination analysis results (PCO), highlighting the strong effect of the management on the structure of the associated fauna. Our results resemble those obtained by Rader *et al.* (2007) for environments historically regulated by dams that also found a low Chironomidae resistance to hydrological disturbances.

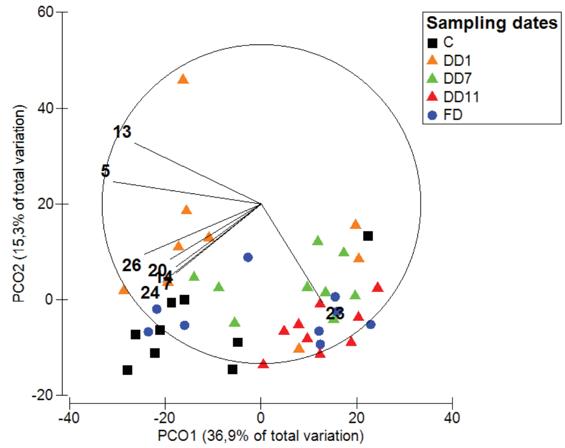

Figure 5. Results of the Principal Coordinates Analysis (PCO) showing the ordination of Chironomidae density data, in the five dates (C = control; DD = 1st, 7th and 11th days of the drought disturbance; FD = on the 49th day of the flood disturbance; nine replicates per date) during the management of Salto Grande reservoir, Paranapanema River. The vectors indicate the Chironomidae taxa that presented correlation > 0.6 with the ordination. Taxa: 5- *Caladomyia*, 7- *Dicrotendipes*, 13- *Parachironomus longistilus*, 14- *Polypedilum* sp3, 20- *Corynoneura*, 23- *Thienemanniella*, 24- *Ablabesmyia*, 26- *Labrundinia* sp5. *Resultados da Análise de Componentes Principais (PCO) mostrando a ordenação dos dados de densidade de Chironomidae, nas cinco datas (C = controle; DD = 1º, 7º e 11º dias da perturbação de seca; FD = no 49º dia da perturbação de cheia; nove réplicas por data) durante o manejo do reservatório Salto Grande, Rio Paranapanema. Os vetores indicam os táxons de Chironomidae que apresentaram correlação > 0.6 com a ordenação. Táxons: 5-* Caladomyia*, 7-* Dicrotendipes*, 13-* Parachironomus longistilus*, 14-* Polypedilum *sp3, 20-* Corynoneura*, 23-* Thienemanniella*, 24-* Ablabesmyia*, 26-* Labrundinia *sp5.*

Most taxa presented low density, being *Caladomyia* dominant in the studied lake. This genus is classified as collector-filterer (Berg, 1995; Coffman & Ferrington, 1996; Silva *et al.*, 2015), being found in shallow environments with substrate rich in fine particulate organic matter (Trivinho-Strixino & Strixino, 1991) and is adapted to the meso-habitat created by *E. densa* dominance (Ogbeibu, 2001; Penczac *et al.*, 2006). However, when the environmental conditions deteriorated, the density of this taxon was immediately impaired, indicating that variations in density may be attributed to changes in food availability.

The three subfamilies had their occurrence altered by the drought disturbance, but Chironominae, which included most of the taxa present in *E. densa* and the most expressive ones in density, was more sensitive. The two Chironominae genera suppressed by the drought disturbance responded differently to the flood disturbance, with *Caladomyia* at the management end representing only 1/10 of the initial density and *Dicrotendipes* returning to the values of the control. The recovery of *Dicrotendipes* may be related to its higher resistance to degraded environments, such as reservoirs (Floss *et al.*, 2012), mainly associated with submerged vegetation, rocks, logs and seaweed carpets (Epler, 1988), being one of the most abundant genera in submerged macrophytes (Copeland *et al.*, 2012) and eutrophic systems dominated by macrophytes (Kaczorowska & Suchora, 2014). The third Chironominae taxa in abundance was *Parachironomus longistilus*, which is known as a predator species tolerant to a wide range of environmental variations (Penczack *et al.*, 2006).

The predominance of Chironominae larva in abundance and richness is due, in part, to its detritivorous-herbivorous feeding habit (Berg, 1995; Dvořák, 1996), being collectors and scrapers favored by the large availability of organic matter and periphyton in macrophytes. The submerged macrophyte acts as a filter, retaining detritus and favoring the development of collecting organisms, such as Chironominae (Dornfeld & Fonsneca-Gessner, 2005; Peiró *et al.*, 2015), which act as main converters of organic matter of low energy value in living protein (Trivinho-Strixino, 2011).

The two Orthocladiinae genera suppressed by the drought disturbance, *Cricotopus* and *Thienemanniella*, also responded differently to the reservoir management, the first being strongly suppressed on all management dates and the second only on the first day of the drought disturbance. According to Simião-Ferreira *et al.* (2009), *Thienemanniella* is usually considered resistant to organic pollution, increasing in downstream sites where organic effluents are released.

The only Tanypodinae taxa suppressed by management (*Labrundinia* sp9) is known for both predator and omnivore feeding habit (Trivinho-Strixino, 2011). According to Dornfeld & Fonseca-Gessner (2005), the first instars are detritivores, but from the second instar they replace their food with larvae of Chironomidae, Oligochaeta and small crustaceans.

The observed changes in the Chironomidae composition seem to be indicative of changes in the lake stability. The drought disturbance altered the environmental conditions of the lake and added greater variability to the aquatic system, causing effects on diversity and stability of the Chironomidae fauna, through temporal changes in the structure (richness, density and dominance) related to peculiar adaptive characteristics of each taxon. Characteristics related to physiological adaptations to desiccation and food resources availability may have been the fundamental factors for some taxa being impaired (with density reduction or disappearance) and others favored (density increase or emergence) at certain moments of the reservoir management. With the environment modification caused by induced drought, most taxa reduced in density or disappeared, indicating low resistance. During the management, a successional process was initiated and some taxa were replaced by more tolerant ones (with high resistance) to the new habitat conditions.

Thus, the disturbance caused by the hydrological management induced in the Salto Grande reservoir attributed new conditions to the studied phytophilous fauna, disrupting the dominance patterns and favoring uncompetitive and rare taxa. The disturbances caused by water level variations influenced the environmental variables and biota, causing changes in the species composition and, possibly, with implications in the lake stability. The changes in water level caused by the reservoir management had direct implications on the taxonomic composition and, consequently, the trophic structure and stability of the aquatic system, with changes in the richness, density and diversity of the Chironomidae assemblage.

In the Pedra Branca lake, the changes in community attributes difffered between studies developed in 2005 with Cladocera (Debastiani-Júnior & Nogueira, 2015), and developed in 2011 with zooplankton (Portinho & Nogueira, 2017) and with Chironomidae assemblages (present study), although the changes in limnological variables due to the reservoir management were similar. Thus, this artificial drawdown over a short time frame not only affected directly physical processes and water quality, but also had different impact depending on the aquatic biota studied. All these results support the need for more research to achieve an equilibrium between the control of the macrophytes cover, in relation to the extent, frequency and duration of the drawdown management, and the maintenance of the biota structure.

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