Chironomidae feeding habits in different habitats from a Neotropical floodplain: exploring patterns in aquatic food webs

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Abstract

Ecological studies on food webs have considerably increased in recent decades, especially in aquatic communities. Because Chironomidae family are highly specious, occurring in almost all aquatic habitats is considered organisms-key to initiate studies on ecological relationships and trophic webs. We tested the hypothesis that the diversity of the morphospecies diet reflects differences on both the food items available among habitats and the preferences of larval feeding. We analyzed the gut content of the seven most abundant Chironomidae morphospecies of the different habitats from the Upper Paraná River. We categorized the food items found into algae, fungal spores, fragments of plants, algae and animal fragments and sponge spicules. We observed the algae predominance in the gut content of morphospecies from lakes. Considering the different regions from each lake, we registered the highest food abundance in the littoral regions in relation to the central regions. From the variety of feeding habits (number of item kinds), we classified Chironomus strenzkei, Tanytarsus sp.1, Procladius sp.1 as generalist morphospecies. We found a nested pattern between food items and Chironomidae morphospecies, where some items were common to all taxa (e.g., Bacillariophyceae algae, especially), while others were found in specific morphospecies (e.g., animals fragments found in *Procladius* sp.1). The algae represented the most percentage of gut contents of Chironomidae larvae. This was especially true for the individuals from littoral regions, which is probably due to the major densities of algae associated to macrophytes, which are abundant in these regions. Therefore, the feeding behavior of these morphospecies was generalist and not selective, depending only of the available resources.

Keywords: lakes, food networks, aquatic invertebrate, food resources, Upper Paraná River.

Hábitos alimentares de Chironomidae em diferentes habitats de uma planície de inundação Neotropical: explorando padrões em redes alimentares aquáticas

Resumo

Estudos sobre redes alimentares têm aumentado consideravelmente nas últimas décadas em pesquisas de ecologia, principalmente em comunidades aquáticas. Em função Família Chironomidae ser altamente especiosa, ocorrendo em quase todos os hábitats aquáticos, é considerada como organismos-chave para estudos preliminares sobre as relações ecológicas como redes tróficas. Nós testamos a hipótese de que a diversidade de dietas das morfoespécies reflete diferenças tanto na disponibilidade dos itens alimentares entre os hábitats analisados, quanto preferencias alimentares das larvas. Nós analisamos o conteúdo digestivo das sete morfoespécies mais abundantes de diferentes habitats da planície de inundação do alto rio Paraná. Nós categorizamos os itens alimentares encontrados como algas, esporos de fungos, fragmentos vegetais, fragmentos de algas ou de animais e espículas de esponjas. Nós observamos a predominância de algas no conteúdo digestivo das morfoespécies lacustres. Considerando as diferentes regiões de cada lagoa, nós registramos as maiores abundâncias de alimentos nas regiões litorâneas, quando comparadas com as regiões centrais. A partir da variedade de hábitos alimentares (número de tipos de itens), classificamos Chironomus strenzkei, Tanytarsus sp.1 e Procladius sp.1 como morfoespécies generalistas. Nós encontramos um padrão aninhado entre os itens alimentares e as morfoespécies de Chironomidae, onde alguns itens foram comuns a todos os táxons (por exemplo, algas da Classe Bacillariophyceae), enquanto outros foram encontrados em morfoespécies mais especificas (por exemplo, fragmentos de animais encontrados em *Procladius* sp.1). As algas representaram a maior porcentagem do conteúdo digestivo das larvas de Chironomidae. Este fato foi especialmente verdadeiro para os indivíduos das

regiões litorâneas, o qual é devido, provavelmente, pelas maiores densidades de algas associadas à macrófitas, que são abundantes nessas regiões. Portanto, o comportamento alimentar dessas morfoespécies foi generalista e não seletivo, dependendo apenas dos recursos disponíveis.

Palavras-chave: lagoas, redes alimentares, invertebrados aquáticos, recursos alimentares, alto rio Paraná.

1. Introduction

In ecology, food webs remain a current issue for research (Ballantyne, 2004). Quantifications of interaction structure have increasingly been used to examine the success of, for instance, the habitat restoration, the biological control of pests, and the biodiversity conservation (Memmott, 2009). Thereby, studies regarding to biotic interactions allow an adequate strategies planning for the management of natural resources. Analysis of food webs structure has recently stimulated a revival of 'descriptive' observation of interactions in the context of natural communities. The approach of food webs can provide an integrated view of ecosystem, and shares both organizational and ecological functions, which are not found with community analysis (Bluthgen, 2010).

The understanding about species diet provides significant information to analyze the ecological role of species in any ecosystem (e.g., interactions between species and their environment; the life history strategies determining their ecological roles or yet, to determine the structure of communities). In this sense, the resource partitioning amongst closely related species as a structuring force for communities has been a central theme in the development of modern ecology (Tokeshi, 1995; Pulliam, 2000; Dole-Olivier et al., 2009). Since the earliest ecological debates, studies on interspecific interactions have caused interest between scientists – see Paine (1974), for his pioneer study about the species relationships on the intertidal community structure. However, there is a lack on the cohesion on the different approaches, which promotes a great difficult in this research field (Ballantyne, 2004). Just recently, with the advent of new computational methods, studies about the pattern distribution between resource and consumer have lately gained popularity – see Patterson and Atmar (1986), Bascompte et al. (2003), Almeida Neto et al. (2008), Thébault and Fontaine (2010) to studies about methods to measurement the ecological interactions.

Benthic invertebrates are functionally important for food webs, composing the basal resources that are transferred to higher trophic levels (Cummins, 1973; Sanseverino and Nessimian, 2008). In Neotropical floodplains, the benthic community is represented predominantly by Chironomidae larvae (Higuti and Takeda, 2002; Higuti, 2004), which play an important role in food webs of freshwater ecosystems, representing the major link between producers and consumers (Tokeshi, 1995; Walther et al., 2006).

According to Rosin et al. (2009), during the historical formation of their life cycles, aquatic species developed strategies that depend on the natural flow regime. Consequently, likewise that many other aquatic communities from floodplains, both the distribution of

Chironomidae, as the adaptation strategies and feeding habits of the larvae are drive by hydrological dynamics. Rosin and Takeda (2007) found that in the Upper Paraná River floodplain, temporal variations of this community are directly linked to the hydro-sedimentological regime. Moreover, Ragonha et al. (2013) discussed the importance of different habitats providing differences in Chironomidae communities, and concluded the presence of macrophyte on the littoral zones increased both the abundance and richness of morphospecies.

Studies about Chironomidae feeding habits indicated the importance of quality and quantity of the available food resources (e.g., algae, detritus, plant fragments, decomposing wood, fungi and invertebrates) that are used by the species in different habitat types (Henriques-Oliveira et al., 2003; Sanseverino and Nessimian, 2008). Consequently, Chironomidae diet studies are essential for a better understanding of how these insect explore its habitats (Ingvason et al., 2004; Walther et al., 2006; Mokany et al., 2008). Therefore, we aimed to analyze the Chironomidae diet in different habitats from floodplain environments, based on the hypothesis that the diversity of the morphospecies diet reflects differences on both the food items available between the habitats and the preferences of larval feeding. According to our hypothesis, we expected that (i) there are differences in the amount and type of food items ingested between Chironomidae morphospecies (ii) there is an increasing of food availabilities from central to littoral regions. Moreover, considering the availability of food items and the preferences of Chironomidae feeding, we expected to found a nested pattern of the food items found among Chironomidae morphospecies, where some items (e.g., those more abundant) will be common to all taxa, while others will be consumed by a few morphospecies. In this scenario, when the preferred resources are scarce, the diets of the most selective individuals become a proper subset of the diet of the next more opportunistic individuals, leading to nestedness.

2. Material and Methods

2.1. Study area

The study area is located at lower Ivinhema River portion (22° 47' 59.64" S; 53° 32' 21.3" W), near of the confluence with Paraná River, whose is one of the main tributaries in region, named as the Upper Paraná River Floodplain. This floodplain is located between the reservoirs of Porto Primavera and Itaipu, a stretch that encompass 230 km (Stevaux et al., 2012; Figure 1). The sampling area exhibits a complex hydrological cycle, with several different environments (Thomaz et al., 2004; Bovo-Scomparin and Train, 2008), as connected and isolated floodplain lakes, channels and rivers.

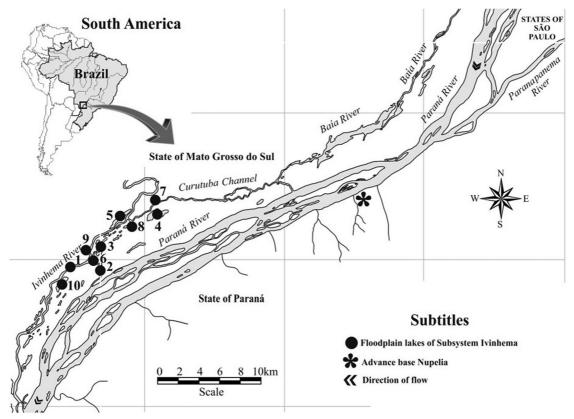


Figure 1. Study area with sampling stations site in the Ivinhema River State Park-MS. (1) IR- Ivinhema River; (2) IC – Ipoitã channel; Connected floodplain lakes: (3) PA - Patos; (4) SU - Sumida; (5) FR - Finado Raimundo; (6) BI - Boca do Ipoitã; and Isolated floodplain lakes: (7) CE - Cervo; (8) JA - Jacaré; (9) ZP - Zé do Paco; (10) VE - Ventura.

2.2. Field samplings and laboratory procedures

The study was carried out quarterly from February 2000 to May 2001. Three samples of sediment were taken at each site with a modified Peterson grab (0.0189 m² area). Soda water was added to the sample to prevent regurgitation of gut contents (Davies and McCauley, 1970). Approximately one hour later, the sediment was washed under running water using sieves with 2.0, 1.0 and 0.2 mm mesh sizes. The larvae retained by the first two sieves were sorted out and fixed in 80% alcohol. The sediment retained in the last sieve was stored in polyethylene pots containing 80% alcohol for subsequent laboratory screening.

Larvae previously identified to subfamily or tribe level were mounted on slides for morphospecies identification, following Trivinho-Strixino (2011), and analysis of the gut content. We assigned the composition and relative abundance of food items for each individual by the area occupied by each item. Subsequently the average was calculated according to the number of individuals analyzed in accordance with Nessimian and Sanseverino (1999).

The gut content of 30 morphospecies (from 3,508 individuals, 40% of the total) was identified and summarized 12,398 items analyzed. However, for constructing the food web were selected the seven most

abundant morphospecies. The food items were categorized as animal fragments, algae and plants fragments, fungal spores, sponge spicules and many algae. Despite the sponge spicules not being considered a food item, we not removed from the analysis because the spicules found in the studied lakes (with high organic matter contents), probably drifted from upstream areas, where there are appropriated conditions for sponge occurrences. Therefore, the presence of this item it is an indication of animals that fed on organic substrates, which we determined as shredders (Figure 2).

Diatoms were identified using Krammer and Lange-Bertalot's (1991), Lange-Bertalot et al. (1996), and euglenoids using Tell and Conforti (1986).

2.3. Statistical analysis

We performed analysis of variance (Anova) to test the differences between food items and habitats (regions into the lakes) and lakes, considering the significance for p<0.05. We also assess the distribution and abundance of the food item most representative (algae). Thus, we performed Anova between the algae density and both habitat and lakes. The analysis of variance and graphs of abundance and whiskers-plot were implemented in Statitica 7.0 software (Statsoft, 2005).

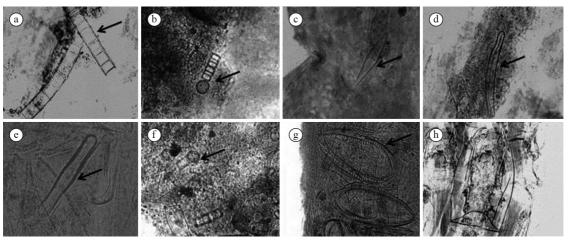


Figure 2. Food items in the gut contents of Chironomidae larvae: (a) Aulacoseira ambigua; (b) Aulacoseira alpigena (indicated by arrow); (c) Gomphonema gracile (indicated by arrow); (d) Eunotia bidens (indicated by arrow); (e) Pinnularia divergens (indicated by arrow); (f) fungal spores (indicated by arrow); (g) Surirella elegans and Surirella linearis (indicated by arrow); (h) animals fragments (cephalic capsules of Tanypodinae in the no gut contents of Procladius sp.1).

2.4. Food web analysis

In food webs, structural patterns of trophic interactions among species have been studied using network approaches, in which nodes represent species within a community and links among them depict their interactions (Dunne, 2006). Therefore, in order to verify whether the Chironomidae communities follow a nested pattern according to their food networks and if there are generalists or specialists among larvae we calculate nestedness analysis. This individual-resource network is defined as an incidence matrix R describing trophic interactions between individuals (represented in rows) and resources (in columns), where an element r_{ij} of the matrix is 1 if the consumption of resource j by individual i was recorded and zero otherwise (Bascompte et al., 2003).

The nestedness analysis measures thus the topological pattern in which interactions involving species with few connections represent a subset of interactions involving highly connected species. The "Nestedness metric based on overlap and decreased fill" - NODF index (Almeida-Neto et al., 2008) was used to compute the degree of nestedness of individual-resource networks. This metric has conceptual advantages when compared with other metrics and seems to be less prone to type-I statistical error, consistently rejecting nestedness for random networks (Almeida-Neto et al., 2008). The significance of NODF was estimated with a Monte Carlo procedure with 1,000 randomizations, using null model Ce, in which the interaction probability between the seven morphospecies and all food items is proportional to the total number of interactions. NODF will tend to 100 for highly nested matrices and tend to zero when individuals show other nonrandom patterns of resource use (Almeida-Neto et al., 2008). However, here we normalized the values to range from 0 (non-nested) to 1 (perfectly nested) to facilitate comparisons among measures. Because recent studies

have reported differences in the behaviour of different nestedness metrics (Ulrich et al., 2009; Joppa et al., 2010), we also report the results using matrix temperature, T, a more traditional measure of nestedness (Atmar and Patterson, 1993).

To determine amplitudes in the diet of the species, we used a metric named Relative Degree – RD. The RD metric measures the proportion of edges related with a vertex and considers total of edges in the graph that could relate to this vertex. The analysis was performed under the ANINHADO 3.0 software (Guimarães Junior and Guimarães, 2006) and the graphs of food web were plotted by a 2-mode network, using the Program for Large Network Analysis – Pajek 4.01 (Mrvar and Batagelj, 2014).

3. Results

3.1. Food items

Algae were the most abundant food items, mainly in the Patos, Cervo and Boca do Ipoitã (Figure 3a) and the only significant item among sample localities (Figure 3b). In addition, we verified that littoral regions of all environments presented higher densities of food items in relation to the central regions. (Figure 3c).

Patos, Cervo and Boca do Ipoitã floodplain lakes were statistically different to others (p < 0.05), and showed the highest algae densities (Figure 4a, b). In the same way of the aforementioned, littoral habitats showed higher values of algae than central region in all environments (Figure 4c).

3.2. Food webs

We observed significant differences on the Chironomidae diet. Through the metric T^{10} , we found a nestedness design between morphospecies and food items (P(T < 28,63) = 4.23 and -0.5 [-3.94]). In the same way,

the NODF index was also significant (T = 49.05 with p < 0.001). The analysis showed that all categorical food item (fungal spores, algae, plant and animal fragments and sponge spicules) were consumed by at least one morphospecies, resulting in a nested pattern. Specialist species (able to feeding only of specific items) composed

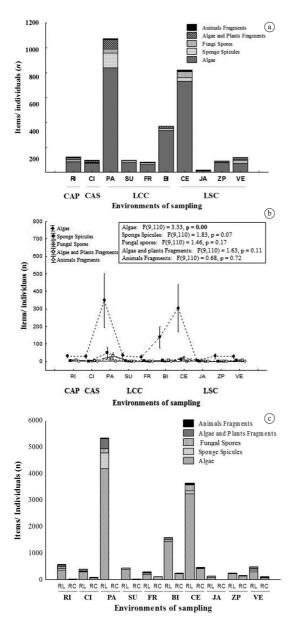


Figure 3. (a) Average number of total food items /individuals in the environments of sampling; (b) Analisys of variance (ANOVA) between the items /individuals and the environments of sampling n= number total of individuals (items); (c) Number of total food items /individuals in the different regions (RL and RC). RI - Ivinhema River; CI - Ipoitā channel; PA - Patos; SU- Sumida; FR - Finado Raimundo; BI - Boca do Ipoitā; CE - Cervo; JA - Jacaré; ZP - Zé do Paco; VE - Ventura; LCC - connected lakes; LSC - isolated lakes; RL - littoral region and RC - central region.

a subset of the generalist ones (those able to feeding on many food items) (Figure 5)).

Chironomus strenzkei contributed with higher values of Relative Degree (RD = 0.70), and may be considered a species with greater diet amplitude, with 70% of overall food items found in the gut contents. On the other hand, *Polypedilum* sp.2 presented the lower food amplitude among the taxa (RD = 0.29) with only 29% of food items registered (Figure 6).

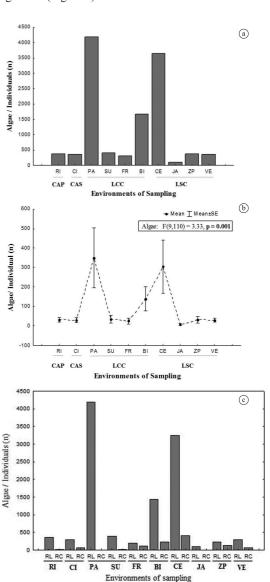


Figure 4. (a) Average number of algae in the environments of sampling and environment types; (b) Analysis of variance (ANOVA) between the algae /individuals and the environments of sampling, n= number total of individuals (algae); (c) Number of total algae/individuals in the different regions (RL and RC). RI - Ivinhema River; CI - Ipoitã channel; PA- Patos; SU- Sumida; FR - Finado Raimundo; BI - Boca do Ipoitã; CE - Cervo; JA - Jacaré; ZP - Zé do Paco; VE - Ventura; LCC - connected lakes; LSC - isolated lakes; RL - littoral region and RC - central region.

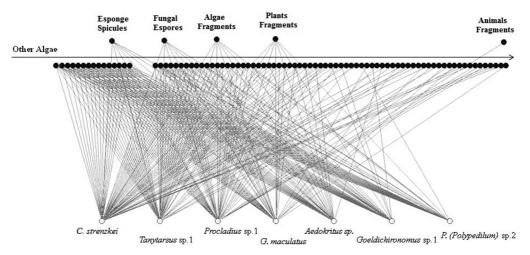


Figure 5. Trophic interaction net of Chironomidae morphotypes (silver circles) and food resources (black circles).

Foods Item and Chironomidae							
A. ambigua - BP	1	Pinnularia divergens - BP	25	Frustulia rhomboides - BP	49	Fragilaria capuccina - BP	73
A. ambigua var. spiralis - BP	2	Trachelomonas sp.1- EP	26	Gomphonema augur - BP	50	Fragilaria lata - BP	74
A. granulata - BP	3	Aulacoseira alpigena - BP	27	Gomphonema sp.3 - BP	51	Fragilaria pinnata - BP	75
Cymbella sp.1 - BP	4	Cyclotella sp.2 - BP	28	Gomphonema truncatum - BP	52	Fragilaria quadrata - BP	76
Eunotia inflata - BP	5	Acnanthes sp.1 - BP	29	Pinnularia subcaptata - BP	53	Gomphonema acuminatum - BP	77
Eunotia sp. 1 - BP	6	Eunotia bidens - BP	30	Stenopterobia capitata - BP	54	Gomphonema sp.1 - BP	78
Eunotia sp. 4 - BP	7	Eunotia papilio - BP	31	Surirella sp.2 - BP	55	Gomphonema sp.4 - BP	79
Fragilaria sp.1 - BP	8	Aulacoseira sp - BP	32	Synedra goulardii - BP	56	Luticola multica - BP	80
Gomphonema gracile - BP	9	Encyonema sp.1 - BP	33	Cyclotella meneghiniana - BP	57	Nitzchia sp BP	81
Gomphonema parvulum - BP	10	Eunotia formica - BP	34	Acnanthes minutissima - BP	58	Pinnularia neomajor - BP	82
Gomphonema sp.2 - BP	11	Navicula sp.1 - BP	35	Acnanthes sp.2 - BP	59	Pinnularia transversa - BP	83
Navicula cf. constans - BP	12	Surirella elegans - BP	36	Amphora sp BP	60	Surirella sp.3 - BP	84
Pinnularia cf. polyonca - BP	13	Surirella linearis - BP	37	Cymbella diminuta - BP	61	Trachelomonas oblonga - EP	85
Pinnularia sp.1 - BP	14	Surirella sp.1 - BP	38	Cymbella sp.2 - BP	62	Trachelomonas rugulosa - EP	86
Trachelomonas sp.2 - EP	15	Carpatograma cruscicula - BP	39	Encyonema selesianum - BP	63	Trachelomonas scupta - EP	87
Sponge spicules	16	Encyonema mesianum - BP	40	Eunotia arcus - BP	64	Trachelomonas sp.3- EP	88
Fungal Spores	17	Eunotia bilunaris - BP	41	Eunotia elegans - BP	65	Animals fragments	89
Algae fragments	18	Eunotia diodon - BP	42	Eunotia indica - BP	66	Chironomus strenzei sp.1 - CH	90
Plant fragments	19	Eunotia proverrypta - BP	43	Eunotia jemtlandica - BP	67	Tanytarsus sp.1 - CH	91
Caloneis sp.1 - BP	20	Eunotia rabenhorstii - BP	44	Eunotia lineolata - BP	68	Procladius sp.1 - CH	92
Eunotia flexuosa - BP	21	Eunotia serra - BP	45	Eunotia pectinalis - BP	69	Goeldichironomus maculatus - CH	93
Eunotia sp.2 - BP	22	Eunotia sp. 3 - BP	46	Eunotia pectinalis - BP	70	Aedokritus sp - CH	94
Pinnularia sp.2 - BP	23	Eunotia sp. 5 - BP	47	Eunotia trigibba - BP	71	Goeldichironomus sp.1 - CH	95
Cyclotella sp.1 - BP	24	Fragilariforma javanicum - BP	48	Eunotia trioton - BP	72	Polypedilum (Polypedilum) sp.2 - CH	96

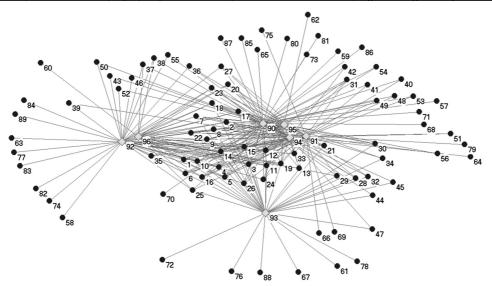


Figure 6. Food network by Chironomidae morphotypes (*silver diamonds*) and food items (*black circles*). Below the food network are the names the items and Chironomidae larvae. Codes: **BP** = Bacillariophyceae; **EP** = Euglenophyceae; **CH** = Chironomidae larvae.

4. Discussion

The differences in Chironomidae gut content reflect directly differences on the availability of food resources in environment, corroborating to our initial hypothesis. The influence of the habitat reflect the complexity of effects on invertebrates and the multiplicity of alternative strategies developed by invertebrates to adapt to the environment (Lamouroux et al., 2004). Consequently, differences in the abundance and type of food items in the diet of morphospecies may be a result of their higher adaptability to the different habitat types. All morphospecies have fed on at least some of those categorical items, supporting our prediction that these species are abundant and generalists in their diet. In this case, the availability of the item in the environment seems to be more important than the preferences for a specific food, unlike that we expected.

The analysis of gut content of larvae indicated the greater influence of different habitats in the quantities of food items ingested by the Chironomidae morphospecies and algae as the most abundant item. The environments from the Upper Paraná River floodplain are very shallow, represented by many floodplain lakes showing a euphotic zone that reaches the bottom. This wide euphotic zone enables the development of several algae in the sediment, which increase the resources throughout the food web (Train and Rodrigues, 2004; Bovo-Scomparin and Train, 2008). In our analysis, we verified that Chironomidae morphospecies used this food item as their main feeding resource, since it was most recorded in the gut content of individuals, which inhabit these floodplain lakes mainly in the littoral regions.

The importance of littoral zones of lakes as habitat for many species of invertebrates and vertebrates has been widely explored (see Weatherhead and James, 2001; Winfield, 2004). These zones provide heterogeneous areas with a varying degree of structural complexity forming a mosaic of different microhabitats (Chick and Mclvor, 1994). In our study, corroborating with the above observations, the largest diversity of food items was observed in the morphospecies from littoral zones. From these results, we can suppose the major influence of macrophytes stands, which could increase the habitat complexity of the littoral zone. The influence of the habitat diversities reflects the complexity of effects on invertebrates and the multiplicity of alternative strategies developed by invertebrates to adapt to the environment (Lamouroux et al., 2004). The analysis of the gut content of larvae indicated the greater availability of food resources in the littoral region of lakes. However, besides the larger quantities of organic detritus originated from littoral regions, the diet of Chironomidae was basically composed of algae.

The great algae abundance in the Chironomidae gut content can be explained not merely by higher availability of this resource in aquatic environments, but mainly due to the adaptations, life cycle, body morphologies (sizes, shapes and structures) among Chironomidae and algae in aquatic environments. Many of the algae found in the digestive content of larvae may have been originated from the Epipelon region (especially diatoms;

see Poulíčková et al., 2008 to definition of Epipelon) and sinking phytoplankton, and because of slow water flow, would have been suffering from sedimentation. Diatoms such as *Cyclotella meneghiniana, Fragilaria capuccina, Nitzchia* spp. and euglenoids such as *Trachelomonas oblonga, T. rugulosa* and *T. scupta* were only present in the digestive contents of *Chironomus strenzkei*. Train and Rodrigues (2004) reported the occurrence of the genus *Trachelomonas* especially in biotopes rich in organic matter or lentic habitats and frequently in isolated lakes of the Paraná River.

According to Rodrigues and Bicudo (2004) it is common to find periphytic diatoms attached to macrophytes (epiphyton) in floodplain lakes, such as: Achnanthidium minutissimum, Aulacoseira granulata, A. ambigua, Cyclotella meneghiniana, Frustulia rhomboides, Gomphonema gracile, G.parvulum, G. augur, G. truncatum, Navicula ef. constans, Pinnularia divergens and Surirella linearis. These taxa were common among food items of Chironomidae morphospecies. The abundance of the meroplanktonic diatom Aulacoseira granulata in the diet of several taxa is in accordance with Bovo-Scomparin and Train (2008) who stated that this is an abundant species in the phytoplankton of lakes associated with Ivinhema River. The wind perturbs the sediment more easily in the low water period and favors the development of this species, which occurs in high density both in the surface water and in the sediment, which was confirmed by the large number of filaments found in the Chironomidae gut content.

There were some peculiarities as animal remains found in the stomach content of *Procladius* sp.1. Galizzi et al. (2012) registered that *Procladius* sp. fed primarily on larger proportions of animal tissues (mainly Oligochaeta). Moreover, Henriques-Oliveira et al. (2003) found a large amount of algae in the gut content of the predators as *Procladius* sp. and also plant fragments, as well as silt and pollen. From this wide dietary variety we can suggest that this morphospecies is opportunistic and omnivore.

We showed that the trophic interaction displayed a nestedness pattern in the Chironomidae diet, reflecting in their niches. The abundance and diversity of consumed items allowed the coexistence of these morphospecies in the same environments, sharing the same niche, corroborating the results found by Galizzi et al. (2012). Therefore, habitats that promote the diversity of these resources (e.g., littoral zones) will facilitate the coexistence of these morphospecies and increasing the local Chironomidae diversity. The discovery of distributional patterns in environments such as floodplain lakes are of great importance for the maintenance and preservation of many species and among them, benthic invertebrates.

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