



Effects of a native and a non-native macrophyte species of Hydrocharitaceae on Chironomidae and Oligochaeta assemblages structure

Rômulo Diego de Lima Behrend^{1*}, Mariana Carolina Teixeira¹, Sue Ellen Prata Fernandes¹, Janieli Carvalho Camargo¹, Gisele Cristina Rosin¹ and Alice Michiyo Takeda²

¹Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Centro de Ciências Biológicas, Universidade Estadual de Maringá, Av. Colombo, 5790, 87020-900, Maringá, Paraná, Brazil. ²Universidade Estadual de Maringá, Maringá, Paraná, Brazil.

*Author for correspondence. E-mail: romulobehrend@yahoo.com.br

ABSTRACT. This study investigated the structure of the Oligochaeta and Chironomidae assemblages associated with monospecific stands of two submerged macrophyte species: *Egeria najas* and *Hydrilla verticillata*. Samplings were carried out in Leopoldo Backwater and Paraná river, in August 2008. To assess the structure of Oligochaeta and Chironomidae assemblage in each macrophyte we calculated: species density, richness, diversity, and evenness. A detrended correspondence analysis (DCA) was used to summarize Oligochaeta and Chironomidae assemblages composition. The highest values of species density and richness for the two groups were recorded in *H. verticillata*. Although there were no significant differences in density, richness and Shannon diversity, the assemblage composition of these groups was significantly different between plant species. These results suggest that despite being a recent colonizer in the upper Paraná river habitats, the non-native species *H. verticillata* seems to provide favorable conditions for the establishment of native assemblages of Chironomidae and Oligochaeta. Moreover, differences in the species composition of Oligochaeta and Chironomidae arose from peculiar characteristics of each plant, as attached microorganisms and organic matter, so that other factors, rather than plant architecture can also influence the assemblage of these groups.

Keywords: upper Paraná river, submerged macrophytes, *Hydrilla verticillata*, *Egeria najas*, invasion, Naididae.

Efeitos de uma espécie de macrófita nativa e uma invasora de Hydrocharitaceae sobre a estrutura das assembleias de Chironomidae e Oligochaeta

RESUMO. Este estudo objetivou investigar a estrutura da assembleia de Oligochaeta e Chironomidae em associação com bancos puros de duas espécies de macrófitas submersas: *Hydrilla verticillata* e *Egeria najas*. As coletas foram realizadas no ressaco do Leopoldo e no rio Paraná, em agosto de 2008. Para avaliar a estrutura da assembleia de Oligochaeta e Chironomidae em cada macrófita foram calculados: densidade, riqueza, diversidade de Shannon e equitabilidade. Uma análise de correspondência destendenciada (DCA) foi usada para sumarizar a composição da assembleia de Oligochaeta e Chironomidae. Os maiores valores de densidade e riqueza para os dois grupos foram registrados na *H. verticillata*. Embora não houvesse nenhuma diferença significativa na densidade, riqueza e diversidade de Shannon, a composição da assembleia desses grupos foi significativamente diferente entre as macrófitas. Esses resultados sugerem que apesar de ser uma colonizadora recente dos habitats do alto rio Paraná, *H. verticillata* parece prover condições favoráveis para o estabelecimento das assembleias de Oligochaeta e Chironomidae. Além disso, diferenças na composição de espécies desses grupos ocorreram devido às características peculiares de cada planta, como micro-organismos e matéria orgânica aderidos, de forma que outros fatores, em vez de arquitetura da planta, podem também influenciar a assembleia desses grupos.

Palavras-chave: alto rio Paraná, macrófitas submersas, *Hydrilla verticillata*, *Egeria najas*, invasão, Naididae.

Introduction

Aquatic macrophytes assemblages play important roles in freshwater environments (PELICICE et al., 2005; THOMAZ et al., 2008), since they affect resources partitioning (MCCOY; BELL, 1991; CAMPEAU et al., 1994), promote changes in biotic

interactions (BATZER; RESH, 1991; ZIMMER et al., 2000; FINKE; DENNO, 2003) and increase the structuring of aquatic habitats, by providing places of shelter, feeding and reproduction for several organisms (THOMAZ; BINI, 1998).

The habitat heterogeneity provided by aquatic macrophytes, mainly the submerged ones, is

considered a relevant factor influencing the diversity of the invertebrates' community (DOUGLAS; LAKE, 1994; COOPER et al., 1997; TANIGUCHI et al., 2003). The architecture of aquatic macrophytes is essential for detritus retention (ROOKE, 1984) and epiphytic algae growth (DUDLEY, 1988), leading to a direct influence on food availability for invertebrates (TANIGUCHI et al., 2003). Moreover, the plants structure influences the colonization by those organisms, with more intense colonization in the plants that show higher structural complexity (JACKSON, 1997; CHERUVELIL et al., 2002; DIBBLE et al., 2006).

In this way, distinct aquatic macrophyte communities will sustain different invertebrates communities (THORP et al., 1997; MELO et al., 2002; TAKEDA et al., 2003). Thus, if plants are similar in architecture, probably they are perceived in a similar fashion (DIBBLE et al., 2006) and colonized by organisms of comparable size (MORSE et al., 1985; TANIGUCHI; TOKESHI, 2004), as Oligochaeta and Chironomidae. However, the habitat selection process is not well understood, and probably involve several mechanisms, since simpler ones, as the presence or absence of predators (RESETARITS, 2005) and resources availability (DE HAAS, 2006) to more complex ones, as physical and/or chemical barriers that prevent colonization (DE HAAS, 2006).

In this study, we selected two macrophytes species based on similar architecture and physical complexity (MORMUL et al., 2010a). *Hydrilla verticillata* and *E. najas* present quite similar architectures (leaf edge, texture and shape of leaf and stem). They are rooted and submersed, canopy forming, with long slender stems, leaves in whorls at nodes (3–8 in *H. verticillata* and 5 per node in *E. najas*) (MORMUL et al., 2010a). Another characteristic of the leaves are: up to 25 mm long and 2.5 mm wide in *E. najas*, and up to 20 mm long and 4 mm wide in *H. verticillata* (COOK; URMIL-KÖNIG, 1984).

Among macroinvertebrate inhabiting aquatic macrophytes, Oligochaeta and Chironomidae groups are prominent by presenting wide distribution and abundance in inland aquatic environments (TAKEDA et al., 2003). Chironomidae larvae is a quite diverse group in macrophytes (BALCI; KENNEDY 2003), with great feeding plasticity, and survival ability under several environmental conditions. On the other hand, most of Oligochaeta individuals associated to macrophytes are opportunistic colonizer, since they are benefited by the accumulation of sediment and algae attached to the substrate (TAKEDA et al., 2003; CARVALHO; UIEDA, 2004).

This study examined the attributes of Oligochaeta and Chironomidae assemblage structure in association with monospecific stands of two macrophyte species: *Egeria najas* and *Hydrilla verticillata*. The hypothesis was

that there is no difference in Chironomidae and Oligochaeta species density, richness, diversity and evenness due to similar architecture of the two plant species. Nevertheless, we also hypothesized that there is difference in Chironomidae and Oligochaeta species composition, due to peculiar characteristics of each plant, since attached algae assemblage differ significantly between *H. verticillata* and *E. najas* (MORMUL et al., 2010b), and may affect the macroinvertebrate community.

Material and methods

Study area and macrophyte species

This study was carried out in Leopoldo Backwater and Paraná river. Leopoldo Backwater is a water body permanently connected to upper Paraná river through an opening with 15 m. It presents a surface area about three hectares, mean depth of three meters, and a perimeter of approximately 2,000 m. The studied stretch of the Paraná river was located in the entry of Leopoldo Backwater. The Paraná river is the main active fluvial channel.

Six samples of two species of submerged aquatic macrophytes (*Egeria najas* and *Hydrilla verticillata*) were taken in the entry of Leopoldo Backwater, in August 2008. It is important to point out that the macrophyte *Egeria najas* was collected inside of the backwater (entry), while *Hydrilla verticillata* was collected in stands located in the Paraná river, next to the entry of Leopoldo Backwater. We collected *H. verticillata* in Paraná river, due to the absence of this species inside of Leopoldo Backwater.

Concomitantly to macrophyte collections we obtained the following environmental variables: temperature and dissolved oxygen (YSI-550A), pH (Digimed DM 2P), conductivity (Digimed DM-3P), turbidity (Quimis – Q-179), and dissolved inorganic carbon.

Sampling

In an attempt to reduce the variation caused by the plant age, all the samples were collected at depths from 1.0 to 1.5 m, within the edge of the stand, avoiding apparently young or senescing plants. Since the samples were collected close to the surface, we assumed that all specimens had similar time to be colonized by algae and invertebrates. In addition, the strategy of getting only the upper 10 cm of each plant, assisted to reduce additional variation due to water quality.

In laboratory, the macrophytes were carefully washed for the removal of Chironomidae and Oligochaeta individuals. These individuals were

identified to the lowest possible taxonomic level with optical microscope, according to specialized bibliography (Chironomidae: TRIVINHO-STRIXINO; STRIXINO, 1995; COFFMAN; FERRINGTON, 1996; Oligochaeta: RIGHI, 1984; BRINKHURST; MARCHESE, 1991).

In order to determine the macrophytes areas, 10 apical portions of approximately 10 cm from each species were scanned, with attention not to allow twisted or folded leaves, and the surface areas were estimated by images analysis software of Image-Pro Express version 4.5.1.3 (Media Cybernetics, Inc.). After this, the portions were dried at 90°C for 24 hours, and weighed. The dry weight and the obtained areas (times two, considering both sides of plants) were used to generate a model for each species, by simple linear regressions, to determine surface area from the dry weight. With the estimated area, we calculated the organisms' densities.

Data analysis

To assess the structure of Oligochaeta and Chironomidae assemblage in each macrophyte, we calculated: species density (ind.m⁻²), richness (S), Shannon diversity (H'), and evenness (E). In order to test the differences between the mean values of species density, richness, diversity and evenness between the macrophyte species, *T* test was applied. Previously, we tested the assumption of homoscedasticity using the Levene's test.

Detrended correspondence analysis (DCA) was employed to summarize biological data (HILL; GAUCH, 1980). DCA is a multivariate ordination technique used to explore any underlying spatial gradient in species composition. This analysis allowed the visualization of the changes in Oligochaeta and Chironomidae assemblage according to the particularity of each macrophyte. To assess whether the composition of Oligochaeta and Chironomidae assemblages differed between the two plant species, we applied a *T* test to the scores from the first two DCA axes.

Species richness, Shannon diversity, evenness and DCA were computed using the software PC-ORD 4.0 (MCCUNE; MEFFORD, 1999). *T* test was performed using the software Statistica 7.0. The statistical significance level adopted was *p* < 0.05.

Results

Physicochemical and plants characteristics

The values of limnological variables presented a slight variation between the macrophyte stands, except

for CO₂ total and turbidity (Table 1). The latter was higher in *Egeria najas* stands, because this plant was collected in the entry of the backwater (place with more turbid water), while *Hydrilla verticillata* was collected in stands in the Paraná river, which presents clear water. Plants area ranged from 105 to 292 cm² per sample. Smaller areas were recorded for *E. najas* petioles, while larger ones were measured in *H. verticillata*.

Table 1. Mean (± Standard deviation) values of physicochemical variables measured in the stands of *Hydrilla verticillata* and *Egeria najas*.

Environmental variables	<i>H. verticillata</i>	<i>E. najas</i>
pH	6.88 (± 0.07)	6.49 (± 0.08)
Water temperature (°C)	22.85 (± 0.04)	23.33 (± 0.14)
Dissolved Oxygen %	112.50 (± 8.41)	163.27 (± 13.98)
Dissolved Oxygen (mg L ⁻¹)	9.47 (± 1.05)	14.77 (± 0.42)
Turbidity (NTU)	0.02 (± 0.001)	0.60 (± 0.06)
Conductivity (µS cm ⁻²)	56.30 (± 0.52)	61.63 (± 4.30)
CO ₂ total (µmol L ⁻¹)	504.80 (± 36.47)	765.03 (± 55.68)

Structure of Oligochaeta and Chironomidae assemblage in aquatic macrophytes

In this study, we recorded nine species of Oligochaeta, and 15 Chironomidae taxa, totaling 13,192 individuals. Concerning the Oligochaeta assemblage, all taxa from this group belongs to Naididae family. *Allonais paraguayensis* and *Stylaria lacustris* were only recorded in *H. verticillata*, whereas *P. americana* was exclusive for *Egeria najas*. There was no significant difference between macrophytes, considering Oligochaeta density (*t* = -2.13, *p* = 0.10). The highest values of mean density of Oligochaeta were recorded in *H. verticillata*. *Dero* (*Dero*) *digitata*, *Slavina evelinae* and *Chaetogaster diastrophus* presented the greatest values of mean density (Figure 1).

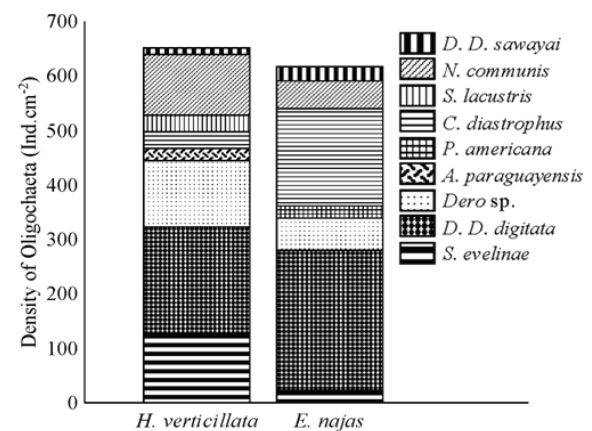


Figure 1. Mean density of Oligochaeta in distinct submerged macrophytes.

In relation to the individuals of Chironomidae family, 15 taxa were identified. *Chironomini* sp., *Pseudochironomini* sp., and *Chironomus* sp. were only

recorded in *H. verticillata*, while *Endotribelos* sp. and *Thienemanniella* sp. were only verified at *E. najas*.

No significant difference was verified between the macrophytes, considering the density of Chironomidae ($t = 1.65$; $p = 0.17$). The greatest values of mean density were registered in *H. verticillata*. *Rheotanytarsus* sp., *Cricotopus* sp. and *Onconeura* sp. presented the highest values of mean density in *H. verticillata*, while in *E. najas* the values of mean density among the taxa were similar, with predominance of *Onconeura* (Figure 2).

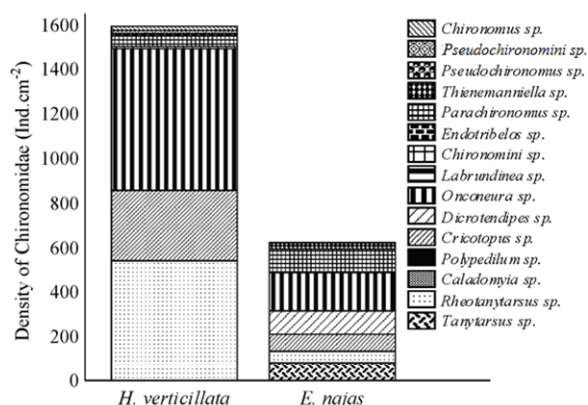


Figure 2. Mean density of Chironomidae in different submerged macrophytes.

There was no significant difference in species richness between macrophytes (Oligochaeta: $t = -0.31$, $p = 0.76$; Chironomidae: $t = 0.55$; $p = 0.60$). But, higher values of species richness of Oligochaeta and Chironomidae were observed in *H. verticillata* (Figure 3); with eight Oligochaeta species and eleven Chironomidae taxa recorded in *H. verticillata*; and seven Oligochaeta species and nine Chironomidae taxa registered at *E. najas*.

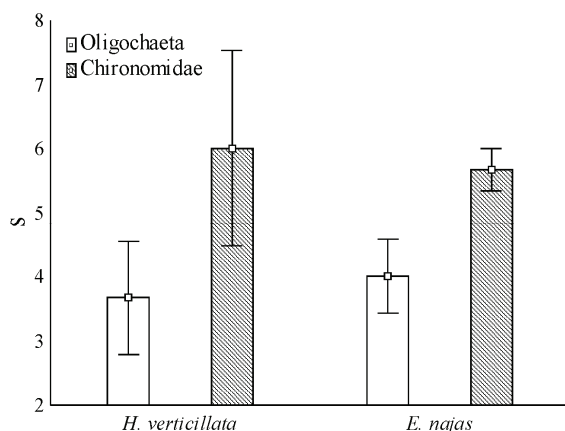


Figure 3. Mean value and standard error of species richness of Oligochaeta and taxa richness of Chironomidae in distinct submerged macrophytes.

In regard to diversity and evenness of Oligochaeta species in macrophytes, the highest values of these attributes were recorded in *H. verticillata* (Figures 4A, and B), unlike the observed for Chironomidae that presented higher values at *E. najas*. There was no significant differences in diversity and evenness of Oligochaeta between the aquatic macrophytes (H' : $t = -0.05$, $p = 0.95$; E : $t = 0.14$; $p = 0.89$), as well as in diversity of Chironomidae ($t = -2.63$, $p = 0.06$) (Figures 4A and B).

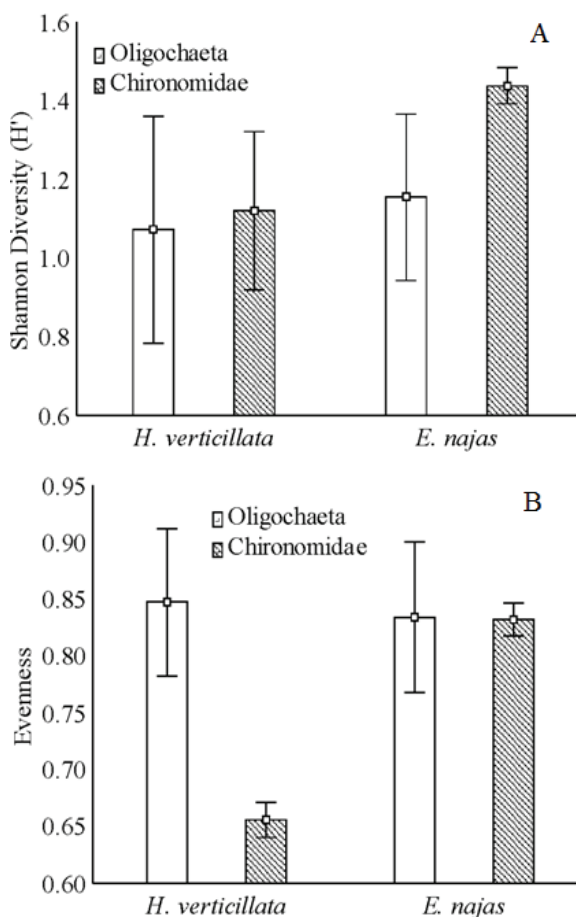


Figure 4. Mean value and standard error of diversity (A) and evenness (B) from Oligochaeta and Chironomidae assemblages in distinct macrophytes.

The DCA showed two distinct groups of samples regarding Oligochaeta species composition and Chironomidae taxa composition (Oligochaeta: axis 1 = 0.43; axis 2 = 0.10; Chironomidae: axis 1 = 0.60; axis 2 = 0.14) (Figure 5A and B). *T* test evidenced significant differences in composition of Oligochaeta and Chironomidae assemblages between macrophytes, using axis 1 from DCA (Oligochaeta: $t = 2.13$; $p < 0.05$; Chironomidae: $t = -4.21$; $p < 0.01$), but there was no significant difference in axis 2 (Oligochaeta: $t = -0.91$; $p = 0.38$; Chironomidae: $t = -1.17$; $p = 0.26$).

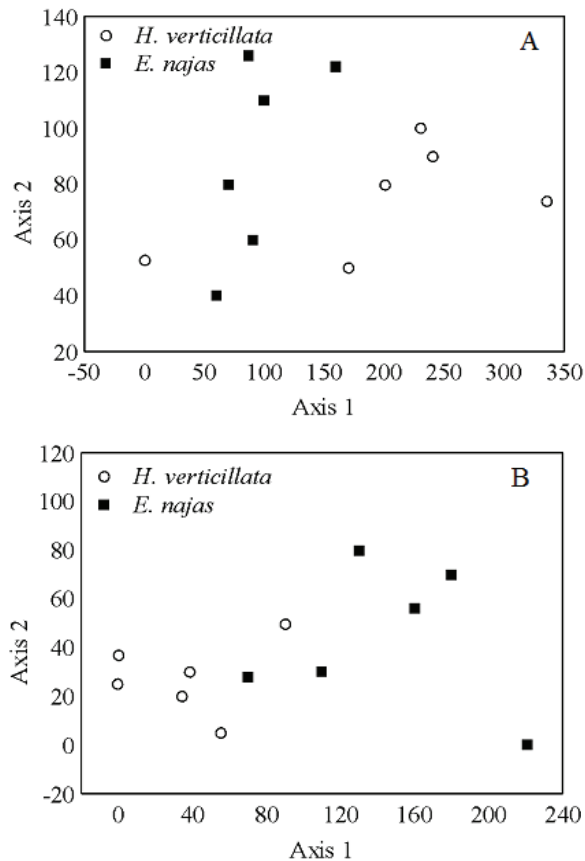


Figure 5. Ordination of DCA scores of Oligochaeta (A) and Chironomidae (B) assemblages.

Discussion

Our results showed that *H. verticillata* sustain similar Oligochaeta and Chironomidae densities, richness, and Shannon diversity compared to *E. najas*, but species composition (as shown by DCA axis 1) differed between the assemblages that had colonized both macrophyte species. These findings are in agreement with those from Theel et al. (2008) and Mormul et al. (2010a), who compared a monospecific stand of *H. verticillata* with a diverse one, and showed that there were no differences between invertebrate density and richness when analyzed separately, but the overall assemblage composition was different. These results were related to differences in plant macrophyte complexities, since there was no difference in abiotic characteristics between both stands of macrophytes (THEEL et al., 2008).

In this study, we recorded higher values of density, richness, and evenness of species of Oligochaeta in *H. verticillata*, whereas greater diversity values were verified in *E. najas*, indicating that Oligochaeta species are similarly distributed in both macrophytes, but begin to predominate at non-native species. The dominance of species from Naididae family in this study corroborates the results found by Takeda et al.

(2003). According to Carvalho and Uieda (2004), naidids are opportunist colonizers, since they get benefit from the backlog of sediment and algae attached to substrates (e.g. epilithon and periphyton). Moreover, this family is an important drift component of rivers, unlike other families, which are endobenthic and subterranean, and present resistance to hydraulic disturbance.

Another trait from this family is the fact of sexual and asexual reproduction occurs simultaneously or succeeds each other in their population, depending on environmental conditions. In Naididae, for example during favorable environmental conditions, the asexual reproduction is common, but when the conditions are unfavorable, the sexual reproduction takes place, mainly during high water and environments with variable temperature (LODEN, 1981). The proportion of these two types of reproduction controls the productivity and survival rates of the species (LODEN, 1981). Such aspects supposedly might play a key role on the colonization of Oligochaeta communities in submerged aquatic macrophytes from large rivers.

In relation to the Chironomidae assemblage, higher values of density and richness were recorded in *H. verticillata*. This group compounds a significant portion of insect fauna in many aquatic macrophytes (PEETS et al., 1994; BALCI; KENNEDY 2003). The dominance of the genera *Rheotanytarsus*, *Cricotopus* and *Onconeura* in *H. verticillata*, explains the lower values of diversity and evenness in this plant, since this predominance reflects the opportunism presented by these species in this macrophyte, which begins to spread rapidly in the Paraná river. Although this paper presents a preliminary study (six samples of each macrophyte), the invasion of Paraná river by *H. verticillata* might favor the presence of opportunists Chironomidae species, which take benefit of the fast increase in density and biomass of this plant.

The species and morphological architecture of aquatic macrophytes constitute in two major determinant factors on the abundance and taxonomic richness of associated fauna (TRIVINHO-STRIXINO; STRIXINO, 1991). In general, plants with finely dissected leaves maintain larger populations of macroinvertebrates than the plant with broader, undissected leaves (JEFFRIES, 1993; CHERUVELIL et al., 2000). This pattern probably occurs because finely dissected leaves provide more habitats for colonization, epiphyton biomass for grazing macroinvertebrates, or additional complexity that offers better refuge from predators. However, in our study, the macrophyte morphology did not explain the variations in density and richness of Chironomidae and Oligochaeta, due to the similarity in the architecture of these macrophytes. The variable with this task seems to be the sampled area, which was higher in *H. verticillata*.

Regarding species composition, we registered differences between the Oligochaeta and Chironomidae assemblages that colonized both macrophytes species, supporting our hypothesis. Meantime, due to the similar architecture, differences in Oligochaeta and Chironomidae assemblage composition may be associated to other reasons. According to Taniguchi et al. (2003), many other factors which are different among plant species, as posture and pattern of undulatory movement in water currents, rates of leaf growth and senescence, release of allelopathic and other chemical substances, may affect the richness and abundance of associated invertebrate taxa. Moreover, macrophyte species may also differ regarding the attached microorganisms and organic matter (DA ROCHA et al., 2006), which make up important food resources for these groups. Mormul et al. (2010b), for example, pointed that *H. verticillata* and *E. najas* collected in the upper Paraná river differ significantly considering attached algae assemblages. Changes in attached microorganisms and organic matter have an effect on invertebrates (LODGE, 1986) and thus, could explain differences between Oligochaeta and Chironomidae assemblages in this study. However, because our data represent only patches of small sized representative from two habitats in the floodplain, larger sample sizes and further data from other habitats are necessary to confirm this difference in species composition at larger scales.

Conclusion

These results suggest that despite being a recent colonizer of the upper Paraná river habitats, the non-native species *H. verticillata* seems to provide favorable conditions for the establishment of native Chironomidae and Oligochaeta assemblages, since we recorded higher values of species richness and density at this plant. In this preliminary study, we found the highest values of density and richness of Oligochaeta and Chironomidae in *Hydrilla verticillata*. We suggest new attempts to verify these trends in the future, because this macrophyte species is spreading quickly in the upper Paraná river floodplain, resulting in probable adaptations of these organisms to the new environmental conditions. Concerning the composition of Oligochaeta and Chironomidae assemblages, this attribute was different due to peculiar characteristics of each plant, as attached microorganisms and organic matter, so that other factors, besides the plant architecture can also influence the assemblage of these groups.

Acknowledgements

The authors would like to thank the financial support from the Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais (PEA) /

Universidade Estadual de Maringá for the discipline 'Ecologia de Zoobentos' (Zoobenthos Ecology); the professors Alice Michiyo Takeda and Sidinei Magela Thomaz, by encouraging the authors to publish this study; the CAPES / CNPq by the scholarship for the students and two anonymous reviewers whose suggestions improved the quality of this manuscript.

References

- BALCI, P.; KENNEDY, J. H. Comparison of Chironomids and other macroinvertebrates associated with *Myriophyllum spicatum* and *Heteranthera dubia*. **Journal of Freshwater Ecology**, v. 18, n. 2, p. 235-247, 2003.
- BATZER, D. P.; RESH, V. H. Trophic interactions among a beetle predator, a chironomid grazer, and periphyton in a seasonal wetland. **Oikos**, v. 60, n. 2, p. 251-257, 1991.
- BRINKHURST, R. O.; MARCHESE, M. R. **Guia para la identificación de oligoquetos acuáticos continentales de Sud y Centro America**. Santo Tomé: Asociacion de Ciencias Naturales del Litoral. 1991.
- CAMPEAU, S.; MURKIN, H. R.; TITMAN, R. D. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. **Canadian Journal of Zoology**, v. 51, n. 3, p. 681-692, 1994.
- CARVALHO, E. M.; UIEDA, V. S. Colonização por macroinvertebrados bentônicos em substrato artificial e natural em um riacho da serra de Itatinga, São Paulo, Brasil. **Revista Brasileira de Zoologia**, v. 21, n. 2, p. 287-293, 2004.
- CHERUVELIL, K. S.; SORANNO, P. A.; SERBIN, R. D. Macroinvertebrates associated with submerged macrophytes: sample size and power to detect effects. **Hydrobiologia**, v. 441, p. 133-139, 2000.
- CHERUVELIL, K. S.; SORANNO, P. A.; MADSEN, J. D.; ROBERSON, M. J. Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. **Journal of the North American Benthological Society**, v. 21, n. 1, p. 261-277, 2002.
- COFFMAN, W. P.; FERRINGTON, L. C. Chironomidae. In: MERRIT, R. W.; CUMMINS, K. W. (Ed.). **An introduction to the aquatic insect of North America**. Dubuque: Kendall Hunt Publish Co., 1996. p. 635-754.
- COOK, C. D. K.; URMI-KÖNIG, K. A revision of the genus *Egeria* (Hydrocharitaceae). **Aquatic Botany**, v. 19, n. 1-2 p. 73-96, 1984.
- COOPER, S. D.; BARMUTA, L.; SARNELLEK, K.; DIEHL, S. Quantifying spatial heterogeneity in streams. **Journal of the North American Benthological Society**, v. 16, n. 1, p. 174-188, 1997.
- DA ROCHA, C. M. C.; VENEKEY, V.; BEZERRA, T. N. C.; SOUZA, J. R. B. Phytal marine nematode assemblages and their relation with the macrophytes structural complexity in a Brazilian tropical rocky beach. **Hydrobiologia**, v. 553, n. 1, p. 219-230, 2006.

- DE HAAS, E. K. Habitat selection by chironomid larvae: fast growth requires fast food. **Journal of Animal Ecology**, v. 75, n. 1, p. 148-155, 2006.
- DIBBLE, E. D.; THOMAZ, S. M.; PADIAL, A. A. Spatial complexity measured at a multi-scale in three aquatic plant species. **Journal of Freshwater Ecology**, v. 21, n. 2, p. 239-247, 2006.
- DOUGLAS, M.; LAKE, P. S. Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship. **Oikos**, v. 69, n. 3, p. 387-396, 1994.
- DUDLEY, T. L. The role of plant complexity and epiphyton in colonization of macrophytes by stream insects. **Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie**, v. 23, n. 1, p. 1153-1158, 1988.
- FINKE, D. L.; DENNO, R. F. Intra-guild predation relaxes natural enemy impacts on herbivore populations. **Ecological Entomology**, v. 28, n. 1, p. 67-73, 2003.
- HILL, M. O.; GAUCH, H. G. Detrended correspondence analysis: an improved ordination technique. **Vegetatio**, v. 42, n. 1, p. 47-58, 1980.
- JACKSON, M. J. **Sampling methods for studying macroinvertebrates in the littoral vegetation of shallow lakes**. Norwich: Broads Authority, 1997. (Broads Authority Research Series - BARS).
- JEFFRIES, M. Invertebrate colonization of artificial pondweeds of differing fractal dimension. **Oikos**, v. 67, n. 1, p. 142-148, 1993.
- LODEN, M. S. Reproductive ecology of Naididae (Oligochaeta). **Hydrobiologia**, v. 83, n. 1, p. 115-123, 1981.
- LODGE, D. M. Selective grazing on periphyton – a determinant of fresh-water gastropod microdistributions. **Freshwater Biology**, v. 16, n. 6, p. 831-841, 1986.
- MCCOY, E. D.; BELL, S. S. Habitat structure: the evolution and diversification of a complex topic. In: BELL, S. S.; MCCOY, E. D.; MUSHINSKY, H. R. (Ed.). **Habitat structure: the physical arrangement of objects in space**. New York: Chapman and Hall, 1991. p. 3-27.
- MCCUNE, B.; MEFFORD, M. J. **PC-ORD: Multivariate Analysis of Ecological Data**. Version 4. Gleneden Beach: MjM Software Design, 1999.
- MELO, S. M.; TAKEDA, A. M.; MONKOLSKI, A. Seasonal dynamics of *Callibaetis willineri* (Ephemeroptera, Baetidae) associated with *Eichornia azurea* (Pontederiaceae) in Guaraná lake of the upper Paraná river, Brazil. **Hydrobiologia**, v. 470, n. 1-3, p. 57-62, 2002.
- MORMUL, R. P.; THOMAZ, S. M.; HIGUTI, J.; MARTENS, K. Ostracod (*Crustacea*) colonization of a native and a non-native macrophyte species of *Hydrocharitaceae* in the upper Paraná floodplain (Brazil): an experimental evaluation. **Hydrobiologia**, v. 644, n. 1, p. 185-193, 2010a.
- MORMUL, R. P.; THOMAZ, S. M.; SILVEIRA, M. J.; RODRIGUES, L. Epiphyton or macrophyte: which primary producer attracts the snail *Hebetancylus moricandi*? **American Malacological Bulletin**, v. 28, n. 1-2, p. 127-133, 2010b.
- MORSE, D. R.; LAWTON, J. H.; DODSON, M. M.; WILLIAMSON, M. H. Fractal dimension of vegetation and the distribution of arthropod body lengths. **Nature**, v. 314, n. 1, p. 731-733, 1985.
- PELICICE, F. M.; AGOSTINHO, A. A.; THOMAZ, S. M. Fish assemblages associated with *Egeria* in a tropical reservoir: investigating the effects of plant biomass and diel period. **Acta Oecologica**, v. 27, n. 1, p. 9-16, 2005.
- PEETS, R.; MILLER, A. C.; BECKETT, D. C. **Effects of three species of aquatic plants on macroinvertebrates in Lake Seminole, Georgia**. Vicksburg: U.S. Army Corps of Engineers Waterway Experiment Station, 1994. (Technical Report A-94-5).
- RESETARITS, W. J. J. Habitat selection behaviour links local and regional scales in aquatic systems. **Ecology Letters**, v. 8, n. 5, p. 480-486, 2005.
- RIGHI, G. Oligochaeta. In: SCHADEN, R. (Ed.). **Manual de identificação de invertebrados límicos do Brasil**. Brasília: CNPq, 1984. p. 1-48.
- ROOKE, J. B. The invertebrate fauna of four macrophytes in a lotic system. **Freshwater Biology**, v. 14, n. 5, p. 507-513, 1984.
- TAKEDA, A. M.; SOUZA-FRANCO, G. M.; MELO, S. M.; MONKOLSKI, A. Invertebrados associados a macrófitas aquáticas da planície de inundação do alto rio Paraná (Brazil). In: THOMAZ, S. M.; BINI, L. M. (Ed.). **Ecologia e Manejo de Macrófitas Aquáticas**. Maringá: Eduem, 2003. p. 243-260.
- TANIGUCHI, H.; TOKESHI, M. Effects of habitat complexity on benthic assemblages in a variable environment. **Freshwater Biology**, v. 49, n. 9, p. 1164-1178, 2004.
- TANIGUCHI, H.; TAKANO, S.; TOKESHI, M. Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. **Freshwater Biology**, v. 48, n. 4, p. 718-728, 2003.
- THEEL, H. J.; DIBBLE, E. D.; MADSEN, J. D. Differential influence of a monotypic and diverse native aquatic plant bed on a macroinvertebrate assemblage; an experimental implication of exotic plant induced habitat. **Hydrobiologia**, v. 600, n. 1, p. 77-87, 2008.
- THOMAZ, S. M.; BINI, L. M. Ecologia e manejo de macrófitas aquáticas em reservatórios. **Acta Limnologia Brasiliensia**, v. 10, n. 1, p. 103-116, 1998.
- THOMAZ, S. M.; DIBBLE, E.; EVANGELISTA, L. R.; HIGUTI, J.; BINI, L. M. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. **Freshwater Biology**, v. 53, n. 2, p. 358-367, 2008.
- THORP, A. G.; JONES, R. C.; KELSO, D. P. A comparison of water-column macroinvertebrate communities in beds of different submersed aquatic vegetation in the tidal freshwater Potomac river. **Estuaries**, v. 20, n. 1, p. 86-95, 1997.
- TRIVINHO-STRIXINO, S.; STRIXINO, G. Estrutura da comunidade de insetos aquáticos associados a *Pontederia lanceolata* Nuttall. **Revista Brasileira de Biologia**, v. 53, n. 1, p. 103-111, 1991.
- TRIVINHO-STRIXINO, S.; STRIXINO, G. **Larvas de Chironomidae (Diptera) do Estado de São Paulo: guia**

de identificação e diagnose dos gêneros. São Carlos: PPG-ERN/UFSCar, 1995.

ZIMMER, K. D.; HANSON, M. A.; BUTLER, M. G. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. **Canadian Journal of Zoology**, v. 57, n. 1, p. 76-85, 2000.

Received on August 10, 2010.

Accepted on November 23, 2010.

License information: This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.