

## Benthic distribution in small tropical lakes: the presence of macrophytes matters

ERIKA MAYUMI SHIMABUKURO<sup>1\*</sup> & RAOUL HENRY<sup>2</sup>

<sup>1</sup>*Centro de Ciências da Natureza, UFSCar, Campus Lagoa do Sino, Buri, São Paulo, Brazil.*

<sup>2</sup>*Department of Zoology, Institute of Biosciences, Campus of Botucatu, State University of São Paulo, UNESP, Brazil*

**Abstract:** The objective of this study was to compare the structure of macroinvertebrate communities in two lakes, one with and another without macrophytes (M+ and M-, respectively). Due to the high concentration of macrophytes into the eastern portion of the M+, we expected: (i) spatial heterogeneity of environmental variables and spatial variation of benthic composition in this lake, comparing to M-, and (ii) higher richness into the macrophytal portion (eastern portion of M+), comparing to the free macrophyte portion (western portion of M+), and also a higher richness in M+ in relation to the M-. The study was conducted in two lakes marginal to a river in Southeastern Brazil. Sampling was performed in two periods in ten sites within each lake. Three replicate samples of sediment were collected with a Van Veen grab in each site and period. Abiotic variables of water and sediment were measured at each sampling site. Macrophytes clearly determined two compartments in M+. The taxa richness was higher in the eastern portion of the M+, where the macrophytes were concentrated, and even the western portion of M+ presented higher richness than M-. *Chironomus paragigas* Reiss 1974 (Chironomidae) predominated in M-, a homogeneous environment. In contrast, several other taxa, such as *Cryptochironomus*, *Cladopelma*, *Asheum*, *Dicrotendipes*, *Procladius* occurred exclusively in the lake with macrophytes, a fragmented and heterogeneous environment. Therefore, in this study macrophytes presence induced spatial heterogeneity, reflecting in benthic macroinvertebrates' richness and distribution.

**Key words:** Aquatic plants, chironomidae, diversity, macroinvertebrates, organic matter, pond, spatial variation.

### Introduction

Benthic macroinvertebrate distribution does not follow random patterns in natural conditions (Thrush 1991). The community structure is affected by the high spatial heterogeneity produced mainly by the water flow into lotic ecosystems (Davy-Bowker *et al.* 2006; Mathers *et al.* 2014; Vanotte *et al.* 1980) and the horizontal gradient, from pelagic to littoral zones, in lentic water bodies (Trigal-Dominguez *et al.* 2009).

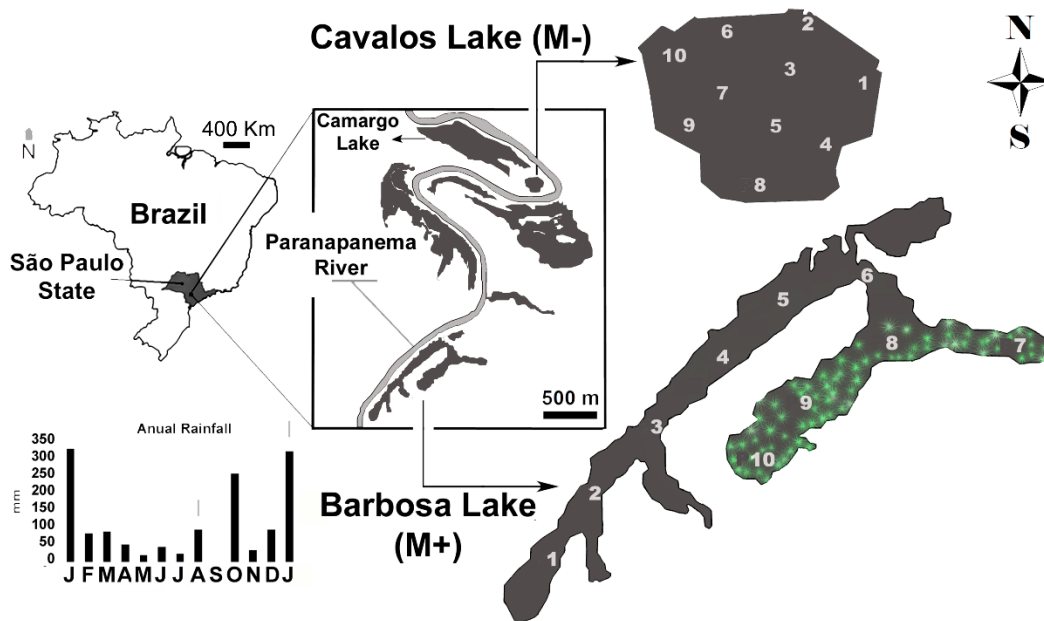
Aquatic macrophytes contribute significantly to a great diversity of organisms found in the marginal

region of lentic environments (Merritt & Cummins 1996; Ward 1992). Several studies have focused on the interaction of macrophytes with other aquatic organisms, particularly due to their importance as habitat, shelter, food source and nursery (Cremona *et al.* 2008; Silva & Henry 2013; Tarkowska-Kukuryk 2014; Tessier *et al.* 2004; Thomaz & Cunha 2010). However, the importance of macrophytes for benthic organisms, especially benthic macroinvertebrates, has been historically neglected (Kornijów *et al.* 1990; McLachlan 1969; Palmer *et al.* 2000; Schramm & Jirka, 1989).

Macrophytes can contribute to increase the

---

\*Corresponding Author; e-mail: erika.msh@gmail.com



**Fig. 1.** A. Study area, B. M- (Cavalos Lake), top, and M+ (Barbosa Lake), bottom, both with ten sampling sites each (1–10), the macrophyte zone (M+(+)) is highlighted in green. C. Rainfall data.

spatial complexity in benthic compartment, changing sediment characteristics by providing additional substrate, such as root masses and decaying plant material, and consequently are responsible for altering habitat conditions for benthic fauna (Schramm & Jirka 1989). Regarding the macrophytal influence over aquatic ecosystem, these aquatic plants can lead to a decrease in turbidity (Petticrew & Kalff 1992) and an increase in the environmental stability (Madsen *et al.* 2001; Sand-Jensen 1998). Macrophytes are frequently the main source of organic matter in lentic environments, supplying as much as around 100 t of dry weight/ha/year in the Amazon (Piedade *et al.* 1991). Also, they are responsible for the release of a great pool of nutrients after decomposition, because they are key components of pasture and detritus food chains and affect the metabolic process of the entire ecosystem (Bianchini Jr. & Cunha-Santino 2016; Enríquez *et al.* 1993; Esteves 1998; Wetzel 1990).

The contribution of vegetal sources to macroinvertebrates feeding have already been investigated in several studies (Boyero *et al.* 2011; Earle *et al.* 2013; Graça *et al.* 2001), and macrophytes may represent the most important basal resource in lakes, as live (Elger & Lemoine 2005; Jacobsen & Sand-Jensen 1995) or decaying (James *et al.* 2000; Kornijow *et al.* 1990) material. The importance of this food item to macroinvertebrates has also been confirmed by stable

isotope analysis (Cremona *et al.* 2009). Therefore, the presence of macrophytes in lakes can provide a great amount of resources to sustain complex food webs and long food chains (Pace *et al.* 2016; Ziegler *et al.* 2015).

Considering that these plants are important sources of sedimentary organic matter into lakes, increasing niches, resources and spatial heterogeneity, the aim of this study was to compare the structure of benthic macroinvertebrate communities in two tropical marginal lakes, one with and another without aquatic macrophytes. We expect to find a higher number of taxa in the lake with macrophytes when compared to the other lake. In addition, we expect a higher spatial variation in abiotic conditions (spatial heterogeneity) and consequently, a variation in benthic community composition and richness into the lake with macrophytes, due to the irregular distribution of macrophytes stands in this lake.

## Material and methods

### Study Area

The area selected for study is the mouth zone of the Paranapanema River, one of the main tributaries of the Paraná River, in the Jurumirim Reservoir (São Paulo State, Brazil) (Fig. 1). This region has a great diversity of aquatic environments, formed by the

main river channel and a series of lakes and ponds with varied degrees of connection to the river. This region is an artificial wetland, according to Junk *et al.* (2014), and hydrological connectivity does not follow the peculiar dynamics of floodplains because flooding is also affected by the reservoir operation (Henry 2005). Sampling was performed in the dry and rainy seasons in August 2011 and January 2012, respectively.

Cavalos Lake (denominate as M-) (23°29'12.81"S and 48°37'02.34"W) is an isolated ecosystem but connects to the Paranapanema River during episodes of extreme flood, such as observed in 1997 and 2004 (Panarelli *et al.* 2008). It is perennial, fed by rain and underground flow from the river. During this study, the intense precipitation of January 2012 did not contribute to connect the lake to the river, but led to its association with nearby Camargo Lake, which is permanently connected to the Paranapanema River by a channel (Fig. 1). M- is circular and surrounded by *Echinochloa polystachya* (Kunth) Hitchcock, an invasive grass.

Barbosa Lake (M+) (23°30'13.11"S and 48°37'45.17"W) is elongated and branched. Its surrounding vegetation is composed also by *Echinochloa polystachya* (Kunth) Hitchcock. This lake presents floating macrophytes (*Eichhornia azurea* Kunth and *Salvinia auriculata* Aublet) and rooted ones (*Myriophyllum aquaticum* (Vell.) Verdc.), especially concentrated in the eastern portion of the lake (M+(+), sampling sites 7–10, while the initial portion (M+(-), sampling sites 1–6 does not present a significant amount of macrophytes (Fig. 1).

#### *Abiotic variables*

We measured the following variables at 10 cm from the bottom at each sampling site: water temperature (Thermistor Toho Dentram ET-3); dissolved oxygen (Winkler method- Golterman *et al.* 1978), pH (Micronal B-380) and electrical conductivity (Hatch model 2511, corrected data for 25 °C according to Golterman *et al.* 1978). Water transparency was measured with a Secchi disk.

For granulometric analysis sediment samples were dried in stove (100 °C) for 24 hours, processed with NaOH (0.1 N) and washed into a sieve (53 µm) to remove silt and clay attached to larger particles. After dried, all weigh-standardized sediment samples were submitted to a mechanic agitator which sorted the sediment according to particles size (VCS- very coarse sand; CS- coarse sand, MS-

medium sand, FS- fine sand, VFS- very fine sand, SC- silt and clay), following the Wentworth's scale (Suguio 1973) and the organic matter was estimated by sediment burning in a muffle at 550 °C for 1 h.

#### *Benthic Macroinvertebrates*

Sediment samples were collected with a Van Veen grab (area: 0.064 m<sup>2</sup>) at ten equidistant sites spread over each lake. At each site, three samples were collected for the analysis of benthic macroinvertebrates with one additional sample for particle size and organic matter analysis. The samples were fixed in 4% formaldehyde and after transferred to 70% ethanol. In the laboratory, the organisms were sorted in sieves (250 µm mesh), identified and counted in stereoscopic and optical microscopes.

The benthic macroinvertebrate groups were identified at the lowest taxonomic level possible according to the literature (Brinkhurst & Marchese 1991; Merritt & Cummins 1996; Mugnai *et al.* 2010; Trivinho-Strixino 2011). The taxa density of each sample was expressed in ind.m<sup>-2</sup>.

#### *Data analysis*

Shapiro-Wilk test was used to verify data normality. Data was not transformed. Comparative tests (variance analysis- ANOVA for parametric data and Kruskal-Wallis test for nonparametric data) were used to detect significant abiotic (physical and chemical variables of water and sediment characteristics) and biotic (richness of benthic macroinvertebrates) variation inside each lake and between lakes (M+ and M-). In order to test if abiotic conditions and richness also differ between macrophytal portion and free-macrophyte portion of M+, we analyzed the lake as two different compartments: M+(-) = the western portion, free from macrophytes, and M+(+) = the eastern portion, densely covered by macrophytes. After the significant differences had been pointed out by ANOVA, homogenous groups were identified using the Tukey HSD test ( $P < 0.05$ ), and the Kruskal-Wallis analysis by means of multiple comparison test ( $P < 0.05$ ).

In order to assess homogeneity or heterogeneity within lakes a spatial ordination of environmental variables was carried out using Principal Component Analysis (PCA).

The similarity of spatial variation in community composition was identified by cluster analysis

**Table 1.** Abiotic factors that significantly changed among M-, M+(-) and M+(+) (M-: lake without macrophytes; M+(-): sites outside macrophyte's zone in M+; M+(+): sites within macrophytes' zone in M+). Superscript letters indicate homogeneity by HSD Tukey or by multiple comparison of means tests ( $P < 0.05$ ). Data represented by mean  $\pm$  standard deviation.

Abiotic variables	M-	M+(-)	M+(+)	P
Transparency	133.65 $\pm$ 26.02 <sup>a</sup>	96.25 $\pm$ 20.79 <sup>b</sup>	120.94 $\pm$ 12.11 <sup>a</sup>	0.001
Depth	1.91 $\pm$ 0.38 <sup>a</sup>	2.85 $\pm$ 0.77 <sup>b</sup>	2.63 $\pm$ 1.14 <sup>b</sup>	0.001
Dissolved Oxygen	4.61 $\pm$ 1.70 <sup>a</sup>	3.27 $\pm$ 2.20 <sup>b</sup>	3.89 $\pm$ 1.93 <sup>ab</sup>	0.03
Conductivity	83.63 $\pm$ 20.84 <sup>a</sup>	68.77 $\pm$ 23.91 <sup>b</sup>	67.67 $\pm$ 25.87 <sup>b</sup>	0.01
Organic Matter	7.64 $\pm$ 4.77 <sup>a</sup>	8.8 $\pm$ 4.15 <sup>a</sup>	18.18 $\pm$ 7.45 <sup>b</sup>	0.001
Very Coarse Sand	0.95 $\pm$ 0.79 <sup>a</sup>	0.13 $\pm$ 0.21 <sup>b</sup>	0.13 $\pm$ 0.24 <sup>b</sup>	0.001
Coarse Sand	0.98 $\pm$ 0.85 <sup>a</sup>	0.25 $\pm$ 0.29 <sup>b</sup>	0.13 $\pm$ 0.10 <sup>b</sup>	0.001
Medium Sand	3.57 $\pm$ 2.5 <sup>a</sup>	0.76 $\pm$ 0.85 <sup>b</sup>	0.21 $\pm$ 0.17 <sup>b</sup>	0.001
Fine Sand	39.60 $\pm$ 16.34 <sup>a</sup>	10.55 $\pm$ 14.88 <sup>ab</sup>	0.45 $\pm$ 0.48 <sup>b</sup>	0.001
Very Fine Sand	20.12 $\pm$ 6.76 <sup>a</sup>	19.34 $\pm$ 11.98 <sup>a</sup>	1.85 $\pm$ 2.54 <sup>b</sup>	0.001
Silt and Clay	34.78 $\pm$ 19.29 <sup>a</sup>	69.72 $\pm$ 25.41 <sup>ab</sup>	97.24 $\pm$ 3.11 <sup>b</sup>	0.001

using the City-block (Manhattan) distance index and the Ward method for sites and sampling periods (Kindt & Coe 2005).

To show the influence of environmental variables on benthic macroinvertebrates, the community was associated with the abiotic variables through Redundancy Analysis (RDA). RDA is a constrained ordination that investigates how much of the variation in one set of data explains the variation in the set of data, a multivariate analysis that is analog to simple linear regression.

ANOVA and associated respective tests (Shapiro-Wilk, Tukey) and cluster and linear regression analyses were performed using the Statistic 6.0 software (Statsoft 2002). PCA and RDA were carried out using the free distribution software R (2012), with the Vegan package version 2.2 (Oksanen *et al.* 2014).

## Results

### *Abiotic variables within lakes*

In M-, only depth and transparency significantly changed among sites (Fig. 2A-B). The depth showed a tendency of increase from S1 to S10, while transparency was higher in central portion of the lake (S5 and S7). Water temperature ( $H = 1.31$ ;  $P = 0.1$ ), dissolved oxygen ( $H = 3.02$ ,  $P = 0.96$ ), pH ( $H = 8.66$ ,  $P = 0.47$ ), electrical conductivity ( $H = 3.04$ ,  $P = 0.96$ ), organic matter content in the sediment ( $H = 12.71$ ,  $P = 0.18$ ), and sediment granulometry (VCS:  $H = 0.95$ ,  $P = 0.79$ ; CS: 0.98,  $P$

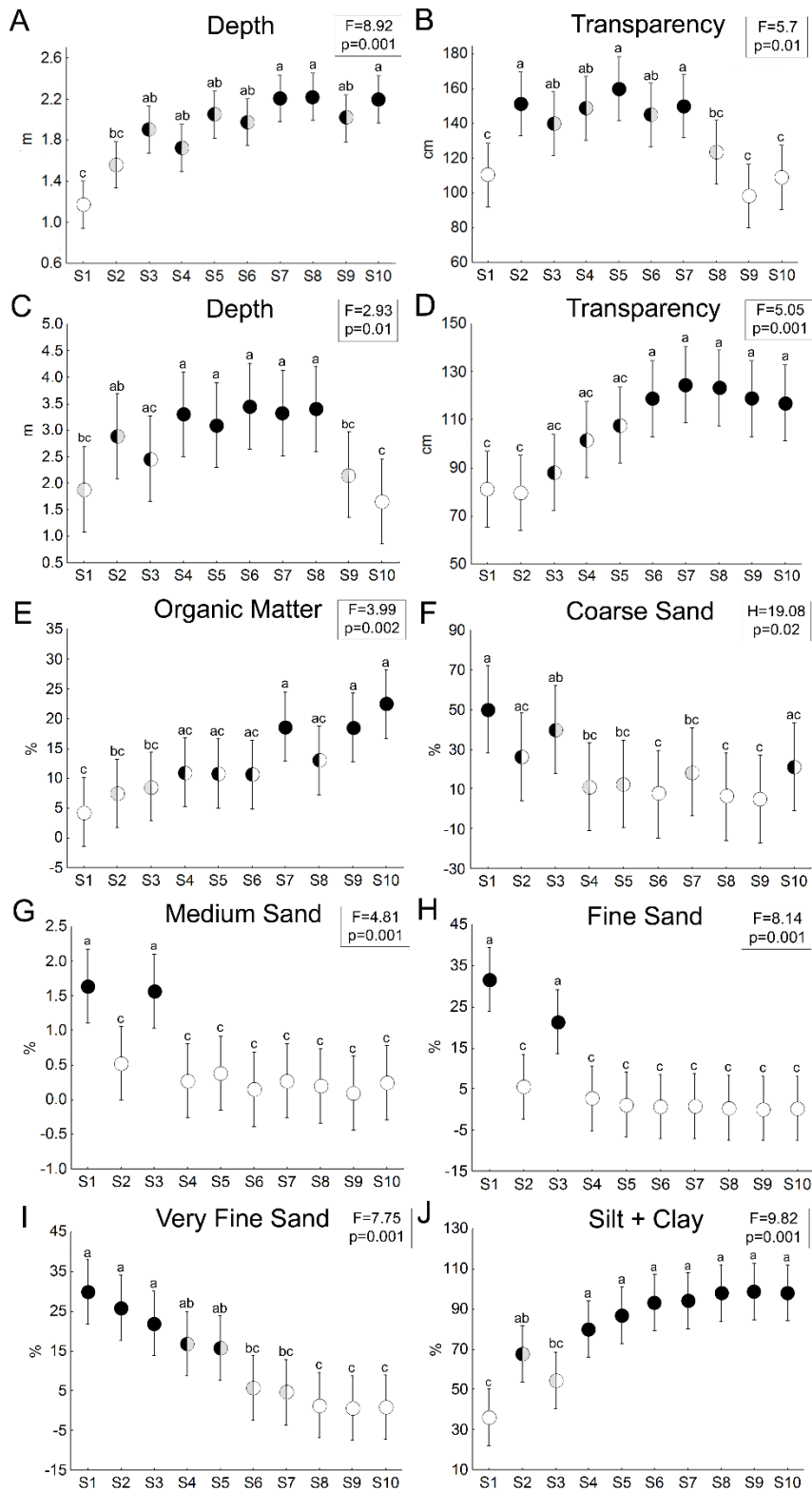
= 0.84; MS:  $H = 3.57$ ,  $P = 2.50$ ; FS:  $F = 1.32$ ,  $P = 0.27$ ; VFS:  $F = 1.34$ ,  $P = 0.26$ ; SC:  $F = 9.96$ ,  $P = 0.35$ ) did not varied significantly among sites in M-.

In M+, depth and transparency of water were significantly different among sites. In addition, all sediment characteristics measured, except for VCS ( $H = 9.51$ ,  $P = 0.39$ ), significantly varied among sites (Fig. 2C-J) However, temperature ( $H = 4.76$ ,  $P = 0.85$ ), dissolved oxygen ( $F = 0.73$ ,  $P = 0.68$ ), pH ( $H = 4.87$ ,  $P = 0.85$ ) and conductivity ( $H = 0.06$ ,  $P = 0.96$ ) did not varied in this lake.

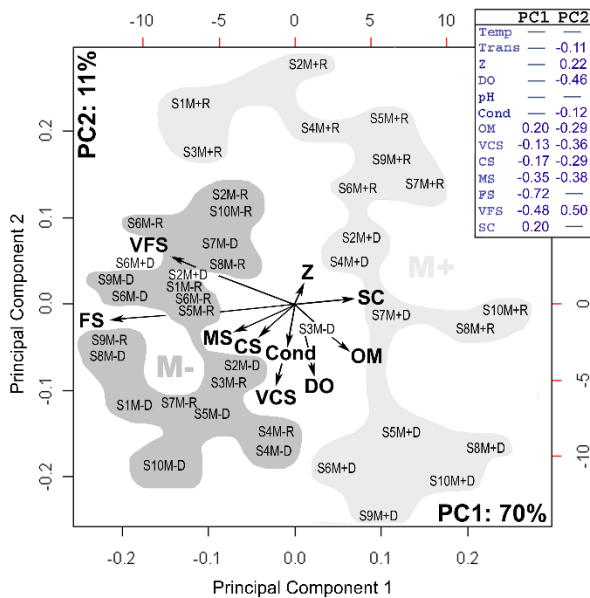
Except for the depth, all the other variables that significantly changed among sites within M+ have showed a tendency of variation in this lake. In general, transparency increased from S1 to S10 (Fig. 2D); organic matter content in the sediment was higher in the final sites, especially S7, S9 and S10 (Fig. 2E); all sand categories occurred in higher proportions in the initial sites, especially S1 to S3 (Fig. 2F-I); contrary to silt and clay proportion that was notably higher from S6 to S10 (Fig. 2J).

### *Abiotic variables between lakes*

Except for water temperature ( $H = 0.79$ ,  $P = 0.67$ ) and pH ( $H = 1.26$ ,  $P = 0.53$ ), all variables measured significantly differed among the three situations observed (M-, M+ without macrophytes and M+ with macrophytes) (Table 1). Transparency was lowest in the western portion of M+, where macrophytes were scarcely present ( $F = 20.9$ ,  $P = 0.001$ ). High transparency was observed in M+(+). Depth was lowest at M- ( $F = 14.53$ ,  $P = 0.001$ ). Dissolved oxygen was highest at M- and lowest at



**Fig. 2.** Spatial variation of abiotic variables within both lakes, compared by means of ANOVA (F) or Kruskal-Wallis (H) tests and respective significance test (P) at 0.05 level. Superscript letters plus gray-scale patterns indicate homogeneous groups evidenced by HSD Tukey or by multiple comparisons of means ( $P < 0.05$ ). A,B.: M-. C-J.: M+. S1-S10: Sampling sites.



**Fig. 3.** Principal component analysis of the abiotic factors for both lakes (M- and M+). Key: S1–S10: Sampling sites. D: Dry season, R: Rainy season. Table, scores (loadings) of variables that significantly explain the observed spatial and temporal variations.

M+(-) ( $F = 3.7$ ,  $P = 0.03$ ). Conductivity was highest at M-, and it did not differ significantly between M+(-) and M+(+) ( $F = 4.43$ ,  $P = 0.01$ ). Organic matter content in the sediment was higher at M+, where macrophytes predominated ( $F = 23.5$ ,  $P = 0.001$ ). VCS, CS, MS and FS percentages were higher in M- and did not differ between M+(+) and M+(-) ( $F = 19.48$ ,  $P = 0.001$ ;  $F = 15.97$ ,  $P = 0.001$ ;  $F = 27.64$ ,  $P = 0.001$ ;  $H = 52.9$ ,  $P = 0.001$ , respectively); VFS percentage was lower at M+(+) ( $F = 30.79$ ,  $P = 0.001$ ) and SC percentage was highest at M+(+), intermediate in M+(-) and lowest at M- ( $H = 48.5$ ,  $P = 0.001$ ) (Table 1).

According to the PCA, a clear difference was observed between the lakes determined by spatial and temporal variations in the physical and chemical variables of the water and sediment characteristics (Fig. 3). Sediment characteristics were the most important variables to distinguish M- and M+. The latter presented fine sand, silt and clay, and organic matter, while M- sediment had all the other coarser categories of sand. Oxygen was an important factor to differentiate M+ between the rainy and dry seasons, since its concentration was very low in the rainy season. Water and sediment characteristics were very similar among sites and between seasons in M-, suggesting a spatial and

temporal homogeneity. The greatest similarity was, therefore, observed among M- sites, when compared to M+ (Fig. 3).

### Benthic macroinvertebrates

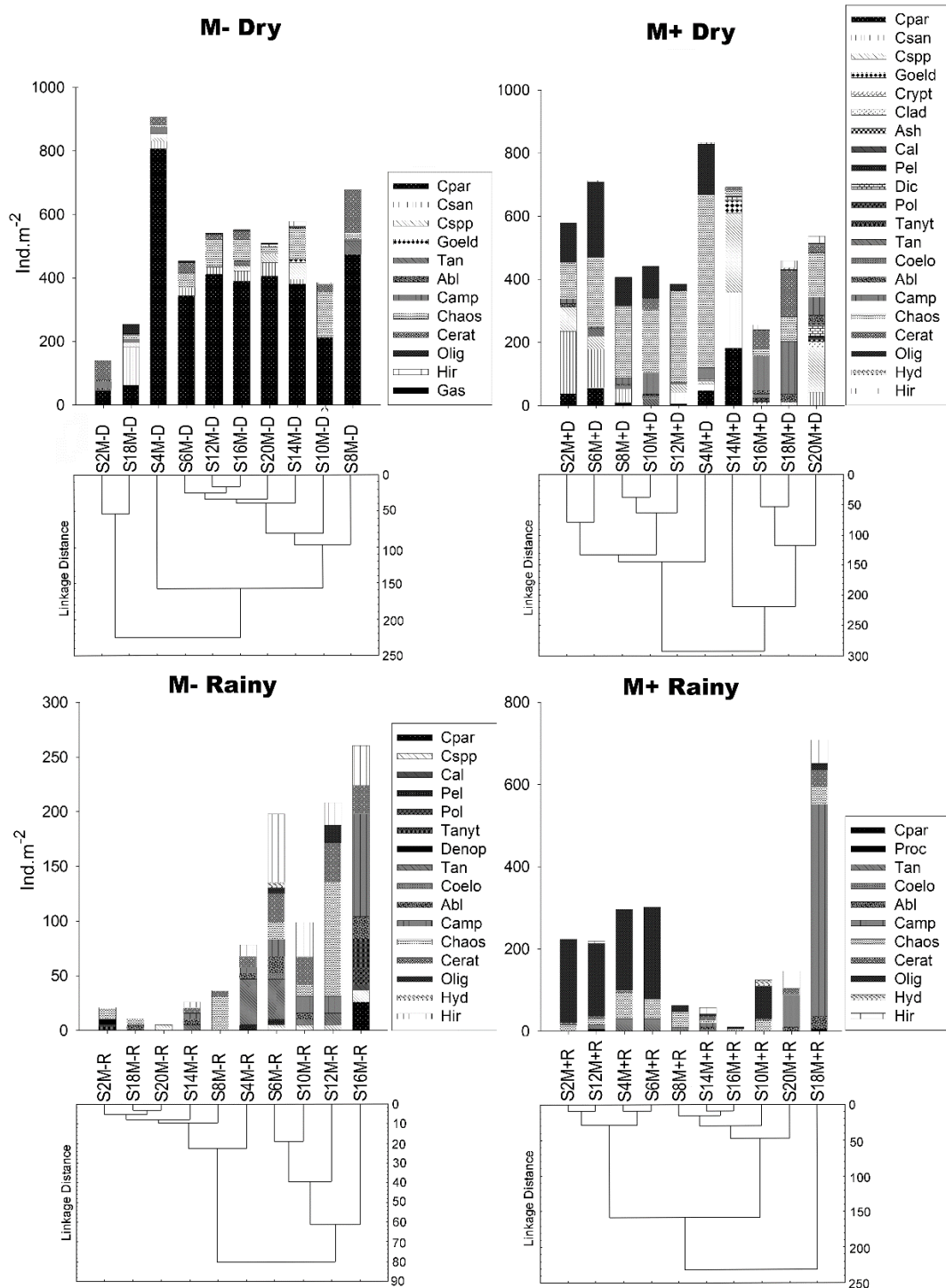
Higher taxa richness was obtained for M+, especially where macrophytes were abundant (Fig. 4-5); significant difference of richness between M- and M+(+) was observed, while M+(-) presented intermediate values of richness and did not differ significantly from M- and M+(+) (Fig. 5).

Cluster analysis of macroinvertebrate community highlighted the compositional differences within M+ with the formation of two distinct groups, one at the macrophyte region, M+(+), and another outside this zone, in M+(-) (Fig. 4). The distinction between these two regions in M+ was maintained for both seasons (Fig. 4). A great homogeneity between sites in M- was evidenced by cluster analysis, in the dry season (Fig. 4). However, during the rainy season taxa richness increased in M- and the homogeneity among sites was attenuated (Fig. 4).

*Chironomus parvigigas* (Reiss 1974) was abundant during the dry season in M- and contributed to the homogeneity observed in the community structure (Fig. 4). In the rainy season, the population decreased significantly in both lakes. *Chironomus sancticarioli* (Strixino & Strixino 1981) was also abundant in the dry season in M-, and it predominated in M+(-). In addition to *C. sancticarioli*, three other *Chironomus* species (*Chironomus* spp) were found in great densities in M+ (Fig. 4).

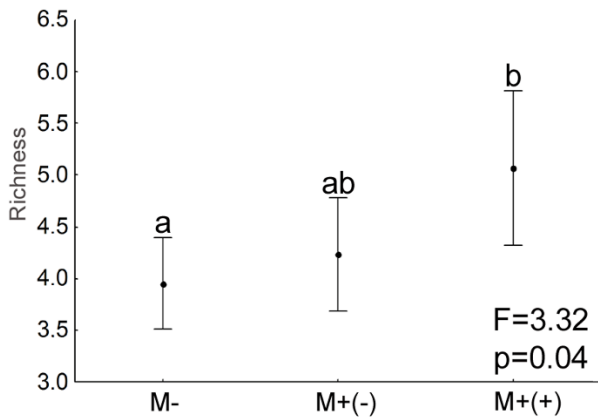
*Campsurus* (Ephemeroptera) and *Chaoborus* (Chaoboridae) were the most abundant organisms in M+. High density of *Campsurus* were observed in the macrophyte zone, while *Chaoborus* and *Oligochaeta* predominated in M+(-) (Fig. 4). *Cryptochironomus*, *Cladopelma*, *Asheum*, *Dicortendipes* and *Procladius* were observed only in macrophytal zone of M+ (Fig. 4).

According to the RDA, different abiotic variables were responsible for the observed distribution of benthic macroinvertebrates (Fig. 6). *Campsurus*, *Asheum*, *Cryptochironomus*, *Pelomus*, *Polypedilum* and *Dicortendipes* were positively correlated with organic matter content in the sediment, silt and clay percentage, and the water temperature, which were notably higher into the macrophytal portion of M+. *Chaoborus* and *Oligochaeta* were positively influenced by pH and depth in M+(-). Depth also contributed for the high

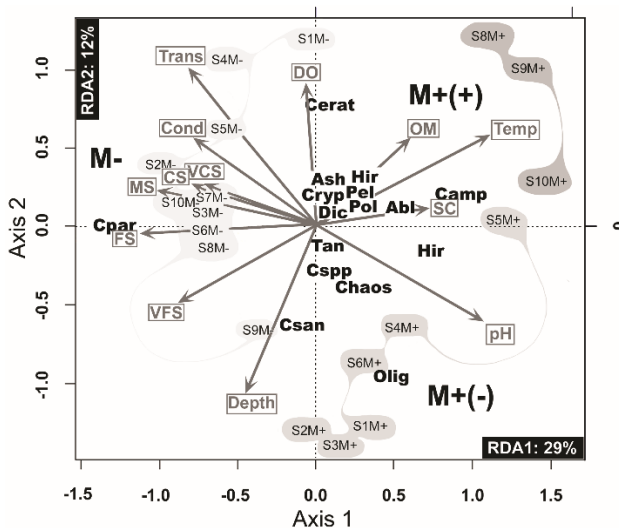


**Fig. 4.** Spatial and temporal variation in benthic macroinvertebrate density (ind.m<sup>-2</sup>) and richness (values above the bars) and similar site groupings considering benthic macroinvertebrate density according to the cluster analysis. Cpar: *Chironomus parvigigas*, Csan: *Chironomus sancticaroli*, Cspp: *Chironomus* spp, Goeld: *Goeldichironomus* sp., Crypt: *Cryptochironomus* sp., Clad: *Cladopelma* sp., Ash: *Asheum* sp., Cal: *Caladomyia* sp., Pel: *Pelomus* sp., Dic: *Dicotendipes* sp., Pol: *Polypedilum* sp., Denop: *Denopelopia* sp., Tanyt: *Tanytarsus* sp., Tan: *Tanypus* sp., Coelo: *Coelotanypus* sp., Abl: *Ablabesmyia* sp., Proc: *Procladius* sp., Camp: *Campsurus* sp., Chaos: *Chaoborus* sp., Cerat: Ceratopogonidae, Olig: Oligochaeta, Hyd: Hydracarina, Hir: Hirudinea, Gas: Gastropoda.





**Fig. 5.** Richness variation between M- and M+ (sites outside macrophyte's zone: M+(-) and sites within macrophytes' zone: M+(+)), compared by means of ANOVA (F). Superscript letters indicate homogeneity by HSD Tukey ( $P < 0.05$ ).



**Fig. 6.** Biplot of redundancy analysis between benthic macroinvertebrates and the environmental variables in M- and M+ (sites outside macrophyte's zone: M+(-) and sites within macrophytes' zone: M+(+)).

abundance of *C. sancticaroli* in M-. The dominance of *C. paragigas* in M- was conditioned mainly by the high percentage of sand (from fine to very coarse sand) and low quantity of silt, clay and organic matter in the sediment (Fig. 6).

## Discussion

In a small spatial scale, environmental factors are the main controlling variables of aquatic

organism distribution (Árva *et al.* 2015; Johnson & Geodkoop 2002). As expected in the present study, the benthic fauna distribution profile was distinct in each lake and was determined mainly by sediment composition, especially by organic matter content, which differed from site to site mainly as a result of the presence of macrophytes.

In M-, most of the environmental variables did not change among sites, revealing a highly homogeneous condition inside this lake. In contrast, in M+, significant changes in abiotic variables were evidenced, especially for sediment characteristics. We attribute these differences to the macrophytes presence in eastern portion of the lake.

In general, the western portion of the lake (S1–S6) presented higher percentage of sand (coarse and fine particles) and lower percentage of organic matter content, while the eastern portion (S7–S10) presented high concentration of silt and clay and organic matter content. The high concentration of organic matter in the sediment from M+, especially in the eastern portion (M+(+)), is consequence of the natural macrophyte senescence in this part of the lake. After completing their life cycle, these plants make up an organic pool at the bottom of the lake (Camargo & Esteves 1995; Junk & Piedade 1993). In addition, the dense macrophytes stands concentrated in one branch of the lake provide high stability to this region, preventing water movement and the suspension of particulate material from the sediment (Esteves 1998; Madsen *et al.* 2001). Therefore, the stability ensured by the macrophytes in the eastern portion of M+ led also to the high transparency of water in this region and, consequently, the percentage of silt and clay (easily suspended material) into the sediment was significantly higher when compared to M+(-).

As expected, richness differed between lakes, especially when comparing the benthic fauna in macrophytal portion of M+ with M-. A significant higher richness of benthic macroinvertebrates was observed at M+, at the eastern region, where macrophytes were abundant. Macrophytes are the main contributors to the organic matter in lakes, and this type of detritus is one of the most important for the energy flow and the stability of aquatic ecosystems (Wetzel 1990). Dense macrophyte stands have been associated with a high number of available niches and a great food resource supply for benthic invertebrates (Tolonen *et al.* 2003). Also, as the main basal resource in aquatic ecosystems (Elger & Lemoine 2005; Jacobsen & Sand-Jensen 1995; James *et al.* 2000;



Kornijów *et al.* 1990), the presence of macrophytes in lakes may determine food chains length and the complexity of food webs (Pace *et al.* 2016; Ziegler *et al.* 2015).

The compositional analysis clustered together sites within the influence zone of macrophytes, evidencing the high community similarity among them. In contrast, another group of sites have been formed outside the influence zone of macrophytes in M+. In wide water bodies the effects of macrophytes on water and sediment quality are restricted to the sites where the plants occur (Carpenter & Greenlee 1981; Carpenter & Lodge 1986). The modifications caused by the macrophytes in the present study (especially the increase of organic matter in the sediment and water transparency) were limited to the eastern portion of the lake, and the elongated shape of the lake favoured the spatial changes in benthic fauna distribution. Thus, the irregular shoreline of M+ and the aggregation of macrophytes in this lake also contribute to the spatial heterogeneity.

In M-, few spatial variations of abiotic variables were observed and low concentration of organic matter in the sediment was verified. With respect to benthic macroinvertebrates, the lowest richness and the predominance of *C. paragigas* was verified when the ecosystem was isolated (dry season). The dominance of *C. paragigas* in the M- sediment may have been due to its great competitive capacity (De Hass *et al.* 2006; Reiss 1974). The quantity of organic matter in the sediment from M- is low and may limit the development of other detritivorous organisms of low efficiency of consumption or assimilation, resulting in the *C. paragigas* dominance. The opportunist habit (De Hass *et al.* 2006) and the low or reduced fish potential predation in this lake (Carvalho *et al.* 2005) may also have contributed to the prevalence of *C. paragigas*.

During the rainy season, the connection between M- and a marginal lake (Camargo Lake) promoted modifications in the physical and chemical conditions of the water (for example, increased dissolved oxygen) in M-. The connection between aquatic ecosystems favours the transference of particulate and dissolved materials, such as organic matter, and organisms (Bornette *et al.* 1998; Casanova *et al.* 2009; Granado & Henry 2008; Thomaz *et al.* 2007). This exchange between ecosystems led to a deep change in benthic fauna of M-, increasing richness and attenuating structural homogeneity.

Oligochaeta and *Chaoborus* predominated into the deeper region of M+, where dissolved oxygen, temperature, transparency and organic matter content in the sediment were low. A good adaptation to low oxygen content, low temperature and low water transparency has already been observed for *Chaoborus* and Oligochaeta species (LaRow 1970; Liljendahl-Nurminen *et al.* 2002; Ohtaka 2001; Volpers & Neumann 2005). In such conditions, *Chaoborus* can migrate vertically and capture oxygen and Oligochaeta reduce the metabolism to extreme levels (Knudsen & Larsson 2009; LaRow 1970). In the present study, these environmental factors contributed to the occurrence of these taxa at the M+(-).

A high *Campsurus* sp. abundance was found in the final compartment of M+. The high biomass of Ephemeroptera, in comparison to other macroinvertebrates (Benke & Jacobi 1986; Brittain & Sartori 2003; Fisher & Gray 1983), suggests the availability of a great energetic potential in this zone of the lake (Gregg & Rose 1985). The high secondary production of this genus seems to be related to high deposition rates of fine particles (Nolte 1988). Thus, organic matter and fine particles deposited in the eastern portion of the lake favoured the individuals from this genus.

We found a strong relation between macroinvertebrate richness in sediment and macrophyte presence. Chironomidae richness, for example, was highest in the macrophyte zone. Despite the low densities of *Cryptochironomus*, *Cladopelma*, *Asheum*, *Dicrotendipes* and *Procladius*, they were exclusively found in this compartment of the lake. These macroinvertebrates were associated with high concentrations of organic matter, their main food item (Trivinho-Strixino 2011). In addition, for most of Chironominae subfamily, such as these taxa favored in macro-phytal region, the organic matter is also necessary to build tubes used as habitats (Chaloner & Wotton 1996; Hirabayashi & Wotton 1999). Thus, macrophytes can also promote an increase in habitat complexity at the bottom of lakes leading to a diverse benthic community.

The contribution of aquatic macrophytes to the bottom compartment of lacustrine environments is related to the availability of food resources to detritivorous macroinvertebrates inhabiting the sediment. The high availability of basal resources, such as organic matter for the detritivorous food webs, provides enough energy stock to support a complex net of organisms, favoring the coexistence

of species by limiting competition (Correa *et al.* 2011; Kneitel & Chase 2004; Ross 1986; Schoener 1974), and enabling high abundance (Ogbeibu 2001) and biomass (Gregg & Rose 1985) of macroinvertebrates.

## Conclusions

In the present study, the presence of macrophytes caused important modifications in limnological and bottom characteristics of a small lake, and the occurrence of many benthic taxa was influenced by these conditions. Macrophytes contributed to increase water transparency, organic matter content and the amount of silt and clay in the sediment, consequently richness was higher in the region with macrophytes, where many Chironomidae taxa were found exclusively, and organisms with the largest biomass (*Campsurus* sp.) were densely found. The irregular distribution of macrophyte stands in M+ contributed for the high spatial heterogeneity observed, in contrast to the notable homogeneity depicted by M- lake. We conclude that macrophytes contributed effectively to increase the quality of the bottom habitat, resulting in an increase in richness and a reduction in dominance in benthic taxa.

## Acknowledgements

The authors thank CAPES- Coordenação de Aperfeiçoamento de Pessoal de Nível superior- for financial support to this study. We also thank Hamilton Antônio Rodrigues, Joaquim Nunes da Costa, Lucio Miguel de Oliveira, Gilmar Perbiche Neves and Larissa Cunha for field helping.

## References

- Árva, D., M. Tóth, H. S. Horváth, A. N. Sándor & A. Specziár. 2015. The relative importance of spatial and environmental processes in distribution of benthic chironomid larvae within a large and shallow lake. *Hydrobiologia* **742**: 249–266.
- Benke, A. C. & D. I. Jacobi. 1986. Growth rates of mayflies in a subtropical river and their implications for secondary production. *Journal of North American Benthological Society* **5**: 107–114.
- Bianchini Jr., I. & M. B. Cunha-Santino. 2016. CH<sub>4</sub> and CO<sub>2</sub> from decomposition of *Salvinia auriculata* Aublet, a macrophyte with high invasive potential. *Wetlands* **36**: 557–564.
- Bornette, G., C. Amoros & N. Lamouroux. 1998. Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology* **39**: 267–283.
- Boyero, L., R. G. Pearson, D. Dudgeon, M. A. S. Graca, M. O. Gessner, *et al.* 2011. Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. *Ecology* **92**: 1839–1848.
- Brinkhurst, R. O. & M. R. Marchese. 1991. *Guia Para la Identificación de Oligoquetos Acuáticos Continentales de sur y Centroamérica*. Asociación Ciencias Naturales del Litoral. J. Maciá, San Tome, Argentina.
- Brittain, J. E. E. & M. Sartori. 2003. Ephemeroptera (Mayflies). pp. 373–380. *In*: V. H. Resh & R. T. Cardé (eds.) *Encyclopedia of Insects*. Academic Press, Amsterdam.
- Camargo, A. F. M. & F. A. Esteves. 1995. Biomass and productivity of aquatic macrophytes in Brazilian lacustrine ecosystems. pp. 137–149. *In*: J. G. Tundisi, C. E. M. Bicudo & T. Matsumura-Tundisi (eds.) *Limnology in Brazil*. ABC/SBL, Rio de Janeiro.
- Carpenter, S. R. & J. K. Greenlee. 1981. Lake deoxygenation after herbicide use: A simulation model analysis. *Aquatic Botany* **11**: 173–186.
- Carpenter, S. R. & D. M. Lodge. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany* **26**: 341–370.
- Carvalho, E. D., L. R. Marcus, F. Foresti & V. F. B. Silva. 2005. Fish assemblage attributes in a small oxbow lake (Upper Paraná River Basin, São Paulo State, Brazil): species composition, diversity and ontogenetic stage. *Acta Limnologica Brasiliensia* **17**: 45–56.
- Casanova, S. M. C., E. A. Panarelli & R. Henry. 2009. Rotifer abundance, biomass, and secondary production after the recovery of hydrologic connectivity between a river and two marginal lakes (São Paulo, Brazil). *Limnologica* **39**: 292–301.
- Chaloner, D. T. & R. S. Wotton. 1996. Tube building by larvae of 3 species of midge (Diptera: Chironomidae). *Journal of North American Benthological Society* **15**: 300–307.
- Correa, C. E., M. P. Albrecht & N. S. Hahn. 2011. Patterns of niche breadth and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin. *Neotropical Ichthyology* **9**: 637–646.
- Cremona, F., D. Planas & M. Lucotte. 2008. Biomass and composition of macroinvertebrate communities associated with different types of macrophyte architectures and habitats in a large fluvial lake. *Archiv für Hydrobiologie* **171**: 119–130.
- Cremona, S., S. Hamelin, D. Planas & M. Lucotte. 2009. Sources of organic matter and methylmercury in littoral macroinvertebrates: a stable isotope approach. *Biogeochemistry* **94**: 81–94.
- Davy-Bowker, J., W. Sweeting, N. Wright, R. T. Clarke & S. Arnott. 2006. The distribution of benthic and

- hyporheic macroinvertebrates from the head and tails of riffles. *Hydrobiologia* **563**: 109–123.
- De Haas, E. M., C. Wagner, A. A. Koelmans, M. H. S. Kraak & W. Admiraal. 2006. Habitat selection by chironomid larvae: fast growth requires fast food. *Journal of Animal Ecology* **75**: 148–155.
- Earle, W. R. Mangan, M. O'Brien & J. R. Baars. 2013. Biology of *Polypedilum* sp. (Diptera Chironomidae), a promising candidate agent for the biological control of the aquatic weed *Lagarosiphon major* (Hydrocharitaceae) in Ireland. *Biocontrol Science and Technology* **23**: 1265–1283.
- Elger, A. & D. Lemoine. 2005. Determinants of macrophyte palatability to the pond snail *Lymnaea stagnalis*. *Freshwater Biology* **50**: 86–95.
- Enríquez, S., C. M. Duarte & K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* **94**: 457–471.
- Esteves, F. A. 1998. *Fundamentos de Limnologia*. Inter-ciência, Rio de Janeiro.
- Fisher, S. G. & L. J. Gray. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* **64**: 1217–1224.
- Golterman, H. L., R. S. Clymo & M. A. M. Ohnstad. 1978. *Methods for Physical and Chemical Analysis of Freshwaters*. Blackwell Scientific Publications, Oxford.
- Graça, M. A. S., S. C. Cressa, M. O. Gessner, M. J. Feio, K. A. Callies & C. Barrios. 2001. Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. *Freshwater Biology* **46**: 947–957.
- Granado, D. C. & R. Henry. 2008. The influence of the hydrologic pulse on the water physical and chemical variables of lateral lakes with different connection levels to Paranapanema River in the mouth zone at Jurumirim Reservoir (São Paulo, Brazil). *Acta Limnologica Brasiliensia* **20**: 265–275.
- Gregg, W. W. & F. L. Rose. 1985. Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia* **128**: 45–56.
- Henry, R. 2005. The connectivity of the Paranapanema river with two lateral lakes in its mouth zone into the Jurumirim reservoir. *Acta Limnologica Brasiliensia* **17**: 57–69.
- Hirabayashi, K. & R. S. Wotton. 1999. Organic matter processing by chironomid larvae (Diptera: Chironomidae). *Hydrobiologia* **382**: 151–159.
- Jacobsen, D. & K. Sand-Jensen. 1995. Variability of invertebrate herbivory on the submerged macrophyte *Potamogeton perfoliatus*. *Freshwater Biology* **34**: 357–365.
- James, M. R., I. Hawes, M. Weatherhead, C. Stanger & M. Gibbs. 2000. Carbon flow in the littoral food web of an oligotrophic lake. *Hydrobiologia* **441**: 93–106.
- Johnson, R. K. & W. Goedkoop. 2002. Littoral macroinvertebrate communities: spatial scale and ecological relationships. *Freshwater Biology* **47**: 1840–1854.
- Junk, W. J. & M. T. F. Piedade. 1993. Biomass and primary-production of herbaceous plant communities in the Amazon floodplain. *Hydrobiologia* **263**: 155–162.
- Junk, W. J., M. T. F. Piedade, R. Lourival, F. Whittmann, P. Kandus, et al. 2014. Brazilian wetlands: their definition, delineation, and classification for research, sustainable management and protection. *Aquatic Conservation: Marine and Freshwater Ecosystems* **24**: 5–22.
- Kindt, R. & R. Coe. 2005. *Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies*. World Agroforestry Centre (ICRAF), Nairobi.
- Kneitel, J. M. & J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* **7**: 69–80.
- Knudsen, F. R. & P. Larsson. 2009. Discriminating the diel vertical migration of fish and *Chaoborus flavicans* in a lake using a dual-frequency echo sounder. *Aquatic Living Resources* **22**: 1–8.
- Kornijów, R., R. D. Gulati & E. V. Donk. 1990. Hydrophyte-macroinvertebrate interactions in Zwemlust, a lake undergoing biomanipulation. *Hydrobiologia* **200/201**: 467–474.
- LaRow, E. J. 1970. The effect of oxygen tension on the vertical migration of *Chaoborus* larvae. *Limnology and Oceanography* **15**: 357–362.
- Liljendahl-Nurminen, A., J. Horppila, P. Eloranta, T. Marinen & L. Uusitalo. 2002. The seasonal dynamics and distribution of *Chaoborus flavicans* larvae in adjacent lake basins of different morphometry and degree of eutrophication. *Freshwater Biology* **47**: 1283–1295.
- Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch & D. F. Westlake. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**: 71–84.
- Mathers, K. L., J. Millett, A. L. Robertson, R. Stubbington & P. J. Wood. 2014. Faunal response to benthic and hyporheic sedimentation varies with direction of vertical hydrological exchange. *Freshwater Biology* **59**: 2278–2289.
- McLachlan, A. J. 1969. The effect of aquatic macrophytes on the variety and abundance of benthic fauna in a newly created lake in the tropics (Lake Kariba). *Archiv Fur Hydrobiologie* **66**: 212–231.
- Merritt, R. W. & K. W. Cummins. 1996. *An Introduction*

- to the *Aquatic Insects of North America*. 3rd ed. Kendall/Hunt, Dubuque.
- Mugnai, R., J. L. Nessimian & D. F. Baptista. 2010. *Manual de Identificação de Macroinvertebrados Aquáticos do Estado do Rio de Janeiro*. [Identification Manual of Aquatic Macro-invertebrates from State of Rio de Janeiro]. 1st ed. Technical Book, Rio de Janeiro.
- Nolte, U. 1988. Small water colonization in pulse stable (várzea) and constant (terra firme) biotopes in the Neotropics. *Archiv fur Hydrobiologie* **113**: 541–550.
- Ogbeibu, A. E. 2001. Composition and diversity of Diptera in temporary pond in southern Nigeria. *Tropical Ecology* **42**: 259–268.
- Ohtaka, A. 2001. Oligochaetes in Lake Towada, Japan, an oligotrophic caldera. *Hydrobiologia* **436**: 83–92.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, et al. 2014. *Vegan: Community Ecology Package. R Package Version 2.2-0* [online document]. URL <http://CRAN.R-project.org/package=vegan> (accessed on 27 December 2014).
- Pace, R. L., J. M. Chambers & B. J. Robson. 2016. Potential of submerged macrophytes to support food webs in lowland agricultural streams. *Marine and Freshwater Research* **68**: 549–562.
- Palmer, M. A., A. P. Covich, S. Lake, P. Biro, J. J. Brooks, et al. 2000. Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes. *BioScience* **50**: 1062–1075.
- Panarelli, E. A., S. M. C. Casanova & R. Henry. 2008. The role of resting eggs in the recovery of zooplankton community in a marginal lake of the Paranapanema River (São Paulo, Brazil), after a long drought period. *Acta Limnologica Brasiliensia* **20**: 73–88.
- Petticrew, E. L. & J. Kalf. 1992. Water flow and clay retention in submerged macrophyte beds. *Canadian Journal of Fishery and Aquatic Sciences* **49**: 2483–2489.
- Piedade, M. T. F., W. J. Junk & S. P. Long. 1991. The productivity of the C<sub>4</sub> grass *Echinochloa polystachya* on the Amazon floodplain. *Ecology* **72**: 1456–1463.
- R Development Core Team. 2009. *A Language and Environment for Statistical Computing*. Vienna, Austria, R Foundation for Statistical Computing URL: <http://www.R-project.org> (accessed on: 15 April 2009).
- Reiss, F. 1974. Vier neue *Chironomus*-Arten (Chironomidae, Diptera) und ihre ökologische Bedeutung für die Benthosfauna zentralamazonischer Seen und Überschwemmungswälder. [Four new *Chironomus* species (Chironomidae, Diptera) and their ecological significance for the benthosfauna of Central-Amazonian lakes and floodplain forests]. *Amazoniana* **5**: 3–23.
- Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia* **1986**: 352–388.
- Sand-Jensen, K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshwater Biology* **39**: 663–679.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* **185**: 27–39.
- Schramm Jr., H. L. & K. J. Jirka. 1989. Effects of aquatic macrophytes on benthic macroinvertebrates in two Florida lakes. *Journal of Freshwater Ecology* **5**: 1–12.
- Silva, C. V. & R. Henry. 2013. Aquatic macroinvertebrates associated with *Eichhornia azurea* (Swartz) Kunth and relationships with abiotic factors in marginal lentic ecosystems (São Paulo, Brazil). *Brazilian Journal of Biology* **73**: 149–162.
- StatSoft, Inc. 2002. *Statistica (Data Analysis Software System)*, version 6.0. Statsoft Inc., Tulsa, OK, USA.
- Suguio, K. 1973. *Introdução à Sedimentologia*. Edgard Blucher, São Paulo.
- Tarkowska-Kukuryk, M. 2014. Spatial distribution of epiphytic chironomid larvae in a shallow macrophyte-dominated lake: effect of macrophyte species and food resources. *Limnology* **15**: 141–153.
- Tessier, C., A. Cattaneo, B. Pinel-Alloul, G. Galanti & G. Morabito. 2004. Biomass, composition and size structure of invertebrate communities associated to different types of aquatic vegetation during summer in Lago di Candia (Italy). *Journal of Limnology* **63**: 190–198.
- Thomaz, S. M. & E. R. Cunha. 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages composition and biodiversity. *Acta Limnologica Brasiliensia* **22**: 218–236.
- Thomaz, S. M., L. M. Bini & R. L. Bozelli. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* **579**: 1–13.
- Thrush, S. F. 1991. Spatial patterns in soft-bottom communities. *Trends in Ecology & Evolution* **6**: 75–79.
- Tolonen, K. T., H. Hämäläinen, I. J. Holopainen, K. Mikkonen & J. Karjalainen. 2003. Body size and substrate association of littoral insects in relation to vegetation structure. *Hydrobiologia* **499**: 179–190.
- Trigal-domínguez, C., C. Fernández-Aláez & F. García-Criado. 2009. Habitat selection and sampling design for ecological assessment of heterogeneous ponds using macroinvertebrates. *Aquatic Conservation* **19**: 786–796.
- Trivinho-Strixino, S. 2011. *Larvas de Chironomidae: guia de identificação*. EdUFSCar, São Carlos.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R.

- Sedell & C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fishery and Aquatic Science* **37**: 130–137.
- Volpers, M. & D. Neumann. 2005. Tolerance of two tubificid species (*Tubifex tubifex* and *Limnodrilus hoffmeisteri*) to hypoxic and sulfidic conditions in novel, long-term experiments. *Archiv für Hydrobiologie* **164**: 13–38.
- Ward, J. V. 1992. *Aquatic Insect Ecology*. Wiley & Sons. Inc., New York.
- Wetzel, R. G. 1990. Detritus, macrophytes and nutrient cycling in lakes. *Memorie dell'Istituto Italiano di Idrobiologia Dott Marco de Marchi* **47**: 233–249.
- Ziegler, J. P., C. T. Solomon, B. P. Finney & I. Gregory-Eaves. 2015. Macrophyte biomass predicts food chain length in shallow lakes. *Ecosphere* **6**: 1–16.

(Received on 16.08.2017 and accepted after revisions, on 27.03.2018)