



***Campsurus violaceus* (Ephemeroptera, Polymitarcyidae) in a subtropical reservoir: control factors and relationship with the macroinvertebrate community**

JUAN CLEMENTE*, ALEJANDRA KROGER, GUILLERMO GOYENOLA, FRANCO TEIXEIRA-DE-MELLO, SOLEDAD MARRONI, CLAUDIA FOSALBA, CARLOS IGLESIAS & NÉSTOR MAZZEO

Departamento de Ecología y Gestión Ambiental, Centro Universitario Regional del Este, Universidad de la República, Maldonado, Uruguay.

Corresponding author: checho@fcien.edu.uy

Abstract: *Campsurus violaceus* is a benthic species that play an important role in sediment bioturbation processes. We explored aspects of its basic biology and life-cycle in a subtropical lake (Laguna del Sauce, Uruguay). We elucidated the habitat preference of *C. violaceus* and evaluated if might foster a more diverse and abundant macroinvertebrate community. The population of *C. violaceus* showed univoltine behavior with nymphs all year around. The spatial distribution of *Campsurus* in the system was related with various sediment attributes, particularly granulometry. A clear positive relationship between abundance of *C. violaceus* and the associated macroinvertebrate community was found. This association could not be explained by the availability of basal resources, nor sediment preferences, but direct or indirect biotic interactions appeared to be important.

Key Words: eutrophic environment, population structure, biotic and abiotic interactions.

***Campsurus violaceus* (Ephemeroptera, Polymitarcyidae) en un reservorio subtropical: factores ambientales reguladores y su relación con la comunidad de macroinvertebrados.** *Campsurus violaceus* es una especie bentónica que desempeña un rol importante en los procesos de bioturbación de los sedimentos. Exploramos aspectos de su biología básica y ciclo de vida en un lago subtropical (Laguna del Sauce, Uruguay). Hemos analizado la preferencia de hábitat de *C. violaceus* y evaluamos si podría fomentar una comunidad de macroinvertebrados más diversa y abundante. La población de *C. violaceus* mostró un comportamiento univoltino con ninfas durante todo el año. La distribución espacial de *Campsurus* en el sistema se relacionó con varios atributos de sedimentos, particularmente granulometría y contenido de materia orgánica (aunque no en todos los períodos). Se encontró una clara relación positiva entre la abundancia de *C. violaceus* y la comunidad de macroinvertebrados asociada. Esta asociación no pudo explicarse por la disponibilidad de recursos basales, ni las preferencias de sedimentos, las interacciones bióticas directas o indirectas parecen jugar un rol relevante.

Palabras clave: ambiente eutrófico, estructura poblacional, interacciones bióticas y abióticas.

Introduction

Freshwater macroinvertebrate benthic community plays a key role in the matter and energy flows through the aquatic trophic webs (Benke et al. 1993). It constitutes a polyphyletic and diverse group, some of them live inside the sediment while

others inhabit its surface.

Campsurus is a species rich genus of mayflies in the Neotropic whose nymphs burrow tunnels, acting as bioturbators of soft silt or clay substrates (Callisto et al. 2001; Salles et al. 2010; Molineri & Salles 2013; Santos-Lima & Pamplin 2016). As

other species of the same genus, *Campsurus violaceus* may play an important role in the matter and energy exchanges between water column and sediments (Cummins et al. 2005; Leal et al. 2005, 2007). That is why the displacement and mixing of the sediment by *C. violaceus* cause a continuous vertical movement of particles in the surface layers of sediment (Moore 2006; Cuddington 2007). Moreover, *C. violaceus* bio-irrigates its U-shaped burrows by pumping in order to obtain oxygen and food, thereby modifying the redox conditions around the burrows and exporting pore-water solutes into the overlying water column (Leal et al. 2003, 2005, 2007). In consequence, the presence and activity of *C. violaceus* could modify directly the sediment structure and composition, the availability of resources, the degree of compartmentalization and habitat complexity (e.g. range of interstitial space sizes), and consequently the biotic interactions, and indirectly the macroinvertebrate composition and abundance (Weatherhead & James 2001; Kovalenko et al. 2012). Despite the potential ecological relevance of *C. violaceus*, the knowledge about its basic biology, spatial distribution, environmental preferences, and interactions with the benthic community, is scarce.

We explored aspects of basic biology, life-cycle and ecology of *C. violaceus* in a subtropical South American eutrophic lake, analyzing its spatial distribution in relation to environmental variables and evaluated if foster a more diverse and abundant macroinvertebrate community.

Material and methods

Study area: The study was performed in Laguna del Sauce (LSS) one of the largest (4.691 ha) shallow (Z_{\max} 5 m) systems, in Maldonado, Uruguay ($34^{\circ} 43' S$, $55^{\circ} 13' W$; Figure 1), composed by three interconnected lakes (del Sauce, de los Cisnes and del Potrero). It was dammed in 1947 and nowadays it is used for drinking water supply. Main tributaries are del Sauce and Pan de Azúcar streams (Figure 1). LSS has experienced a fast eutrophication due to non-point nutrient inputs from agriculture, livestock productions and gardens, inputs from urban areas without proper sewage waste treatments, as well as nutrient and algal biomass retention promoted by the dam (Mazzeo et al. 2010). The system shows a complex spatial pattern of eutrophication while del Potrero is dominated by submerged plants, del Sauce exhibit periodical algal and cyanobacterial blooms that cause severe interference with the drinking water supply system (Crisci 2006; Mazzeo et al. 2010). Aquatic plants are dominated by submerged species, mainly *Egeria densa*, *Ceratophyllum demersum*, *Potamogeton pectinatus* and *Cabomba caroliniana* (Crisci 2006). Phytoplankton blooms dominance varies among *Dolichospermum crassum*, *Aphanizomenon gracile*, *Cuspidothrix issatschenkoi* and *Cylindrospermopsis raciborskii* (González-Madina et al. 2018). During the study period total Phosphorous, total Nitrogen and algal biomass were $126 \mu\text{g-P/l}$, $800 \mu\text{g-N / L}$ and $80 \mu\text{g Chl-a / L}$ on average, respectively (Rodríguez-Fernández 2006; Mazzeo et al. 2010).

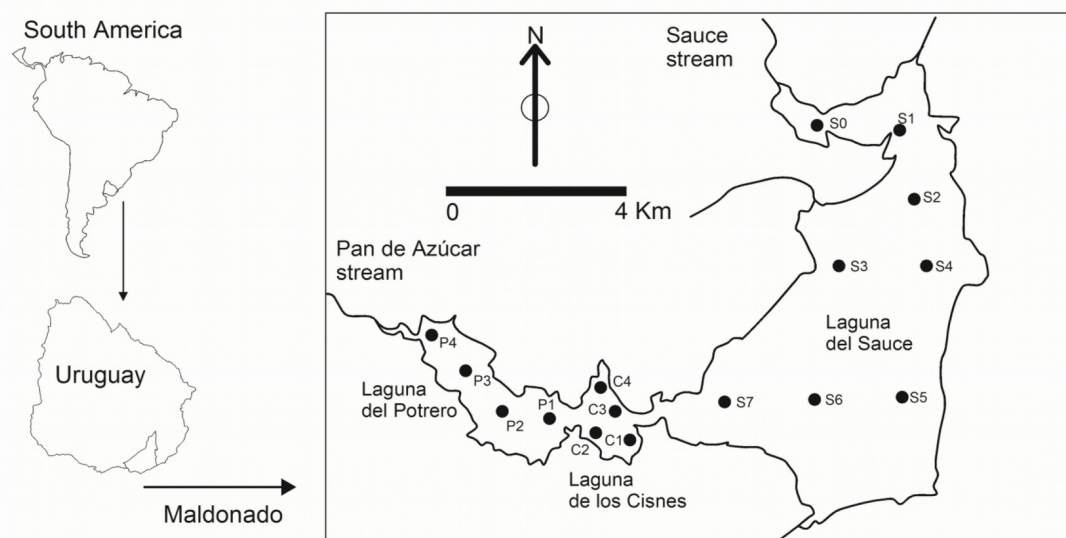


Figure 1. Geographical location of Laguna del Sauce system (LSS), Maldonado, Uruguay. Sampling sites are shown; **S** corresponds to del Sauce, **C** to de los Cisnes and **P** to del Potrero lakes, respectively.

Sampling procedures and analysis: We used a regular grid sampling following Håkanson & Jansson (1983). A total of 16 stations were visited four times, being two in winter (July 2003 and 2008) and two in summer (January 2004 and December 2008). At each of the 16 stations, six random samples of sediment were collected by scuba diving using a 50 cm long and 11 cm internal diameter corer. Three of the samples were frozen to analyze the granulometric characteristics of the sediment and to determine organic matter (OM %), total Phosphorus (TP $\mu\text{g-P} / \text{g DW}^{-1}$) and total Nitrogen (TN $\mu\text{g-N} / \text{g DW}^{-1}$) contents.

The organic matter was determined by loss of ignition at 450°C during 2 h (Håkanson & Jansson 1983), TP and TN were determined following Valderrama (1981). The granulometric characteristics of the sediment were determined by sieving 100 g sample sediment through different mesh sizes, 2000 and 1000 μm (coarse sand is retained), 500 and 250 μm (medium sand is retained), 125 μm (fine sand is retained) and 63 μm (silt and clay go through), according to Folk & Ward (1957). Simpson diversity index was used to quantify the diversity of grain size ($\lambda = \sum p_i^2$), where p_i is the proportional abundance of each grain class (the weight of each category divided by the total weight of the sample). Finally, presence or absence of submerged plants was recorded by a grapnel survey in each sampling point.

The top 15 cm of the other three sediment cores were sieved in the field with a 500 μm mesh size. The resultant samples were fixed with 70% ethanol for subsequent identification and quantification of macroinvertebrates in the laboratory. Taxonomic composition of organisms was determined to family level following the taxonomic references of Lopretto & Tell (1995), and Merritt & Cummings (1996). We measured the length and weight (oven-dried at 60°C for 48 h) of 320 *C. violaceus* nymphs (from the summer 2004 campaign), to the nearest mm and mg, respectively.

Statistical analyses: The main environmental variables were explored by multivariate methods (Principal Component Analysis, using Pearson correlation matrix), the following attributes were considered: granulometry (including grain diversity), organic matter and nutrient content of the sediment, presence or absence of submerged plants and water depth. The spatial patterns of *Campsurus* abundance and macroinvertebrate assemblage structure (composition and abundance) were studied by cluster analysis, using Bray-Curtis algorithm and

unweighted grouping method.

One-way analysis of variance (ANOVA) was performed to determine the statistical significance of *C. violaceus* differences in abundance among sampling stations. The data were square root transformed, checked for homogeneity of variances (Cochran's test), and visually inspected for normality of the distribution of the residuals. Spatial differences among sampling stations considering the macroinvertebrate composition and abundance were tested with analysis of similitude, specifically ANOSIM test (rA), considering the Bray-Curtis algorithm.

The correlations between *C. violaceus* abundance with sediment granulometry and organic matter, was tested by Spearman correlation (ρ); Legendre & Legendre 1998; Quinn & Keough 2002). Partial Mantel test was considered for testing the correlation composition and abundance of macroinvertebrates without *Campsurus* (matrix A) and environmental attributes and/or environmental features + *Campsurus* abundance (matrix B), controlling the effect of the spatial distance among sites (matrix C; Legendre & Legendre 1998; Oden & Sokal 1992). The algorithms considered were Bray-Curtis for matrix A, correlation for matrix B (environmental matrix or environmental matrix + *Campsurus* presence and abundance), and finally the geographical distance for matrix C. The permutation test was performed with 10000 iterations. All the statistical analyses were carried out using PAST software (Hammer et al. 2001).

The relationship between size and dry biomass of *C. violaceus* nymphs was adjusted to a linear regression over log-log data (Smock 1980). A length frequency histogram was made to evaluate the number of coexisting cohorts in summer-2004 and to discuss about life cycle and voltinity.

Results

Sediment: Sediment granulometry showed large differences between sites. In del Sauce lake a variation from coarse to fine sand from north to south arose clearly. Moreover a less pronounced decrease in particle size at greater depths was also evidenced, where the silt and clay percentage reached almost 50% (Table I). In del Potrero lake, the spatial heterogeneity was related to the granulometry, organic matter and nutrient content of the sediment. Contrarily, de los Cisnes lakes showed a greater spatial homogeneity, however, all the sampling stations recorded the highest diversity of grain size and also high amounts of organic matter and phosphorus and nitrogen (Table I).

Table II. Abundances (ind/m²) of *Campylopus* and macroinvertebrates families collected in Laguna del Sauce system (average of three replicates per station). The taxa richness of each station included the lowest taxonomic identification, in some cases genus or species.

WINTER 2003	S0	S1	S2	S3	S4	S5	S6	S7	C1	C2	C3	C4	P1	P2	P3	P4
<i>Campylopus violaceus</i>	1125	0	0	250	1333	1583	1583	0	42	583	83	0	625	292	42	83
Macroinvertebrates families																
<i>Caenidae</i>	83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	125
Ceratopogonidae	83	42	0	0	0	0	0	0	0	42	0	0	167	0	0	0
Chaoboridae	0	0	0	0	0	0	0	0	0	0	0	83	0	0	0	0
<i>Chironomidae</i>	3333	1083	458	2333	1250	2750	835	667	375	2375	2083	208	3083	875	333	917
<i>Tubificidae</i>	292	458	42	417	125	0	1417	250	292	83	83	667	292	125	717	750
Glossiphoniidae	83	333	583	292	1167	167	42	0	0	583	83	0	42	83	0	0
Richness	7	4	4	5	6	7	4	4	3	7	6	3	8	7	4	5
SUMMER 2004	S0	S1	S2	S3	S4	S5	S6	S7	C1	C2	C3	C4	P1	P2	P3	P4
<i>Campylopus violaceus</i>	292	0	208	167	0	792	417	0	125	417	875	667	625	375	1708	1083
Macroinvertebrates families																
<i>Caenidae</i>	0	0	0	0	0	0	0	0	0	0	0	0	208	42	83	0
Ceratopogonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42
Chaoboridae	0	0	0	0	0	0	0	0	0	0	0	83	0	0	42	0
<i>Chironomidae</i>	625	417	583	333	1292	417	167	417	458	708	583	500	1208	1125	792	2333
<i>Tubificidae</i>	83	0	0	0	0	958	0	83	0	0	125	42	42	0	583	83
Glossiphoniidae	167	42	83	208	208	0	0	0	125	42	375	0	42	42	542	167
Richness	4	3	5	3	5	4	2	3	2	5	5	4	7	5	6	7
SUMMER 2008	S0	S1	S2	S3	S4	S5	S6	S7	C1	C2	C3	C4	P1	P2	P3	P4
<i>Campylopus violaceus</i>	211	3791	316	105	1580	1580	105	2001	9056	211	1264	0	1685	737	105	2106
Macroinvertebrates families																
<i>Caenidae</i>	0	0	0	0	0	0	0	0	316	105	0	36750	105	0	105	0
Beatidae	0	0	0	0	0	0	0	0	0	0	211	2317	0	0	0	0
<i>Chironomidae</i>	2633	5160	3159	1264	5476	3686	1580	4949	9372	4949	3159	75395	3686	1580	1895	5792

Ceratoponidae	0	0	0	0	105	0	105	105	0	0	105	105	527	0	105	211
Chaobouridae	0	0	0	0	0	0	0	0	0	0	105	0	0	0	0	0
Gomphidae	0	0	0	0	0	0	0	0	0	0	0	105	0	0	0	0
Coenagrionidae	0	0	0	0	0	0	0	0	0	0	0	632	0	0	0	0
Leptoceridae	0	0	0	0	0	0	0	0	0	0	0	105	0	0	0	0
Hydroptilidae	0	0	0	0	0	0	0	0	0	0	0	105	0	0	0	0
Hydrobiidae	105	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phyisidae	0	0	0	0	0	0	0	0	0	105	0	0	0	0	0	0
Hyaellidae	0	0	0	0	0	0	0	0	0	105	0	9372	0	0	0	0
Tubificidae	105	316	0	105	0	2843	105	105	632	1369	421	0	0	316	0	105
Glossiphoniidae	1053	632	105	211	737	211	0	1474	527	1369	3370	1264	1264	421	737	211
Richness	3	3	5	3	5	4	2	3	3	5	5	4	7	5	7	7
WINTER 2008	S0	S1	S2	S3	S4	S5	S6	S7	C1	C2	C3	C4	P1	P2	P3	P4
<i>Campsurus violaceus</i>	105	211	1264	105	1264	211	1369	211	1895	1474	1158	2843	18217	22429	4001	0
Macroinvertebrates families																
Caenidae	0	0	0	0	0	0	0	0	0	0	105	0	0	0	0	1895
Beatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	105
Chironomidae	316	632	1053	842	2633	2106	842	8635	1580	2317	2843	3791	10004	7371	2106	11583
Ceratopogonidae	0	0	0	0	0	0	0	2843	0	211	211	105	316	105	105	105
Tubificidae	105	527	2001	1053	2001	2738	4001	1158	1790	737	421	1053	105	0	0	9688
Glossiphoniidae	105	105	0	0	737	421	211	421	421	737	1053	842	3475	1895	2843	0
Richness	7	4	4	6	6	7	4	4	3	7	6	2	7	7	4	6

Organic matter content varied between 1.3 to 33.5 % (Table I). A negative correlation was observed between grain size and organic matter content ($\rho = -0.44$, $p < 0.05$), regardless of the sampling period considered.

The percentages of organic matter, nitrogen and phosphorus content were strongly and positively correlated in winters (ρ OM- TN=0.81, ρ OM-TP=0.62 and ρ P-N=0.90, $p < 0.001$ in all cases) and summers (ρ OM-TN=0.73, ρ OM-TP=0.87 and ρ TP-TN=0.85, $p < 0.001$ in all cases). Considering the similar spatial gradient between nutrient and organic matter content and in order to simplify the statistical analysis, we performed the subsequent statistical relationships with macroinvertebrates, only considering organic matter content.

Macroinvertebrate community: Macroinvertebrate community included insects, bivalves, shrimps (Malacostraca), leeches (Hirudinea), oligochaets (Clitellata) and gastropods. Among insects, Ephemeroptera were represented by species of Caenidae, Baetidae and Polymitarcyidae families (Table II). The most representative species from the last family, in terms of abundance and spatial distribution, was *Campsurus violaceus*. The most abundant families of insects were Ceratopogonidae, Chaoboridae (*Chaoborus* spp.) and Chironomidae (Table II). Several genera of Chironomidae were collected: *Polypedilum*, *Chironomus* gr. *decorus*, *Chironomus* gr. *riparius*, *Dicrotendipes*, *Ablabesmyia* (only *annulata*), *Pentaneura*, *Coelotanypus*, *Djalmabatista* (mainly *pulcher*), and *Larsia*.

Bivalves were represented by the native *Diplodon parallelipedon* (Hyriidae), and the exotics *Corbicula fluminea* (Corbiculidae) and *Limnoperna fortunei* (Mytilidae). As a consequence of its low density, the area sampled was not enough for properly estimates of the abundance of bivalves and this group was, therefore, not considered in statistical analysis.

Among the Malacostraca, *Palaemonetes argentinus* (Decapoda, Palaemonidae) and *Hyalella curvispina* (Amphipoda, Hyalellidea), were collected. Finally, Planorbidae and Hydrobiidae families were the most representative snails, and in the case of Clitellata, were the subclasses Hirudinea and Oligochaeta (Table II).

The average abundance of macroinvertebrates (excluding *Campsurus*) per station was 2066 ind/m² in winter 2003, 1031 ind/m² in summer 2004, 6588 ind/m² in winter 2008 and 6319 ind/m² in summer

2008 (Fig. 2). The spatial pattern of mean macroinvertebrate abundance did not show temporal stability ($0.34 < \rho < 0.47$; $p < 0.01$).

The spatial heterogeneity of the community structure (in terms of species and abundance) was analyzed using all the replicates per station (Fig. 3). In winter 2003 and summer 2004, the differences among sampling stations composition and abundance were statistically significant (ANOSIM test $rA = 0.53$, $p < 0.001$ for 2003; $rA = 0.45$, $p < 0.001$ for 2004). The same pattern was observed in summer and winter 2008 ($rA = 0.31$, $p < 0.001$ and $rA = 0.28$, $p < 0.001$, respectively).

In winter 2003, a negative correlation between total macroinvertebrate abundance and the sediment size was recorded, ($\rho = -0.43$, $p < 0.01$). A positive correlation was confirmed during winter 2008, however the statistical relationship was not significant ($\rho = 0.24$, $p < 0.09$). The zones with highest organic matter content had in some periods the highest macroinvertebrates abundances, but the relationships were not significant ($\rho = 0.34$, $p < 0.09$, summer 2004).

Spatial and temporal distribution of *Campsurus violaceus*: *Campsurus violaceus* was present in all periods studied, but was absent in some replicates. Its maximum density was 14216 ind/m² and it was found in winter 2008. All sampled periods showed statistically significant differences among stations ($F_{(15,32)} = 11.9$, $p < 0.001$, $F_{(15,32)} = 7.3$, $p < 0.001$, $F_{(15,32)} = 7.4$, $p < 0.001$, $F_{(15,32)} = 6.9$, $p < 0.001$; winter 2003, summer 2004, summer and winter 2008, respectively; Fig. 4).

Size distribution of *C. violaceus* in summer 2004 showed a unimodal pattern (Fig. 5), it ranged from 4 to 22 mm. In this period, a clear linear relationship between the log-log dry weight and length of nymphs was observed ($R^2 = 0.90$, $p < 0.001$, $n = 320$, $a = -1.86$ and $b = 2.71$, Fig. 6).

Sediment grain size and organic matter content of the sediment showed a negative correlation with *C. violaceus* abundance in some periods, during winter 2003 with the silt-clay percentage ($\rho = -0.70$, $p < 0.001$) and with fine sand percentage ($\rho = -0.26$, $p < 0.08$) during winter 2008. Finally, during winter 2004 we observed a positive correlation between organic matter content and *C. violaceus* abundance ($\rho = 0.56$, $p < 0.001$).

***Campsurus violaceus* and macroinvertebrate community:** Samples with higher abundance of *C. violaceus* also had higher abundance of the others macroinvertebrates ($\rho = 0.66$, $p < 0.001$; $\rho = 0.40$,

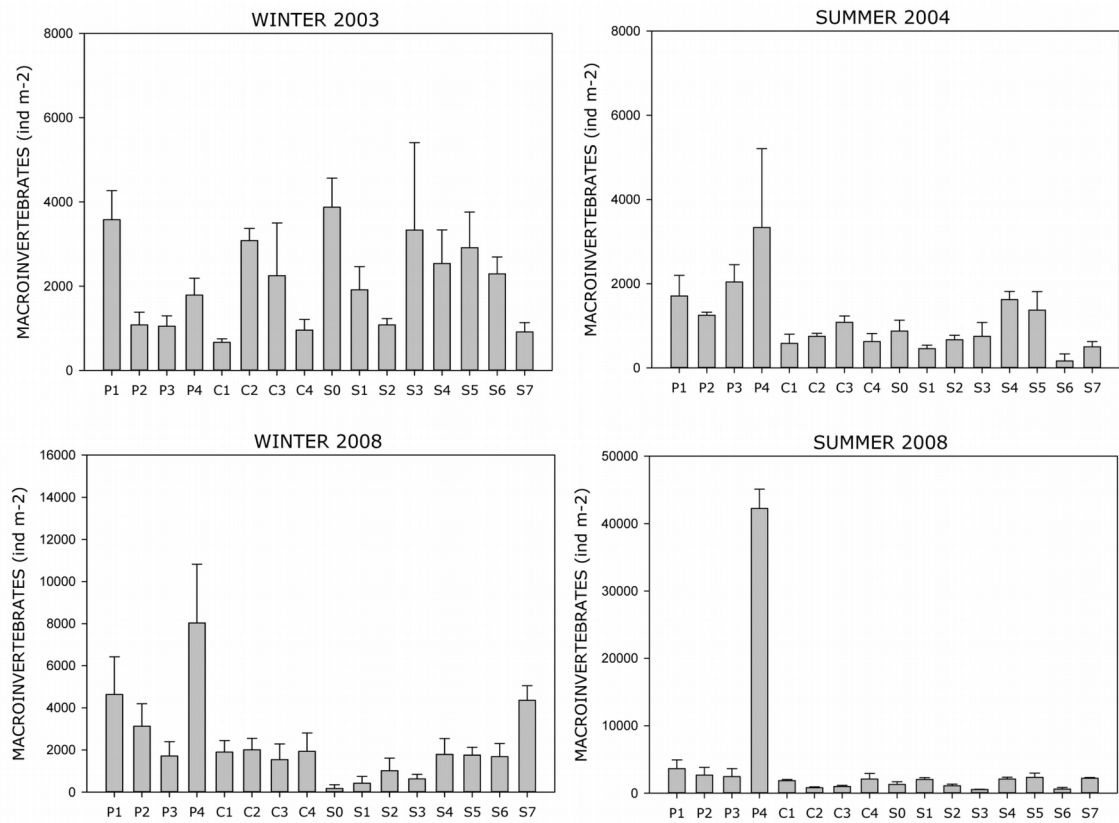


Figure 2. Macroinvertebrates abundances (ind/m² mean ± SE) in the different sampling sites and seasons at Laguna del Sauce system, Maldonado, Uruguay.

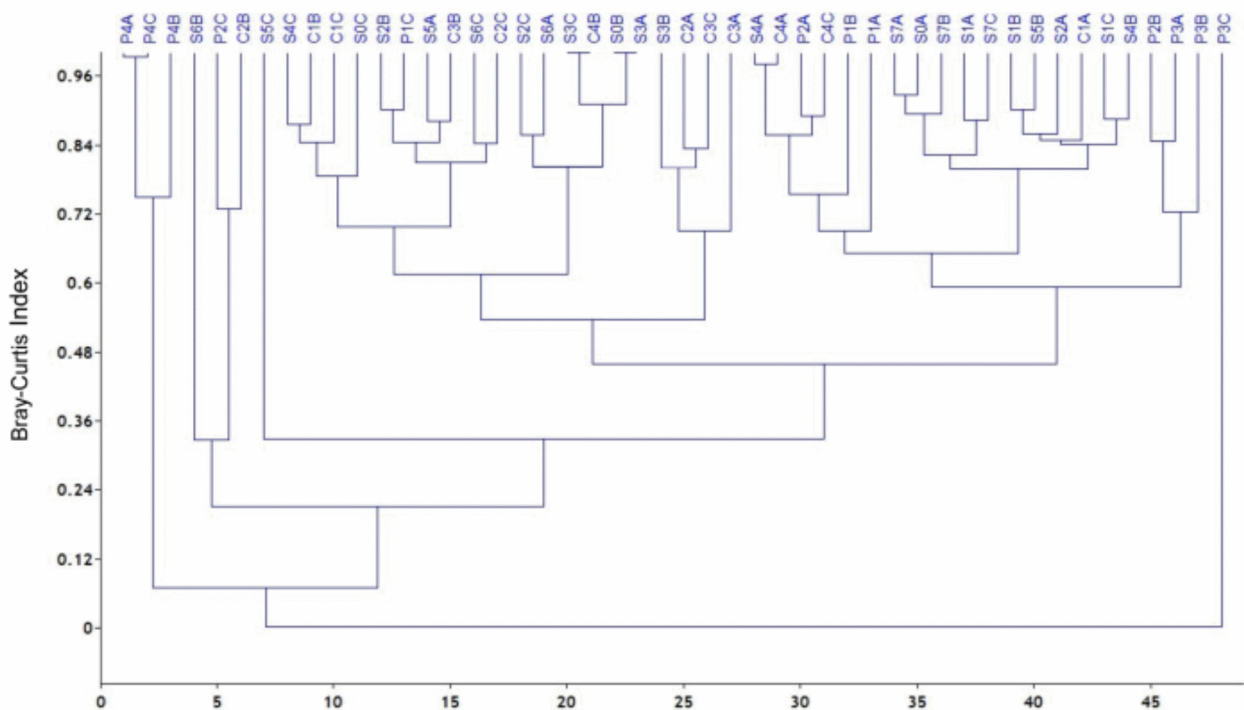


Figure 3. Similarities among sampling sites and replicates during winter 2003 and summer 2004 and summer and winter 2008 based on the composition and abundance of macroinvertebrate community (except *Campsurus*). The algorithm considered was Bray-Curtis and unweighted average for clustering. The co-phenetic correlation was 0.89.

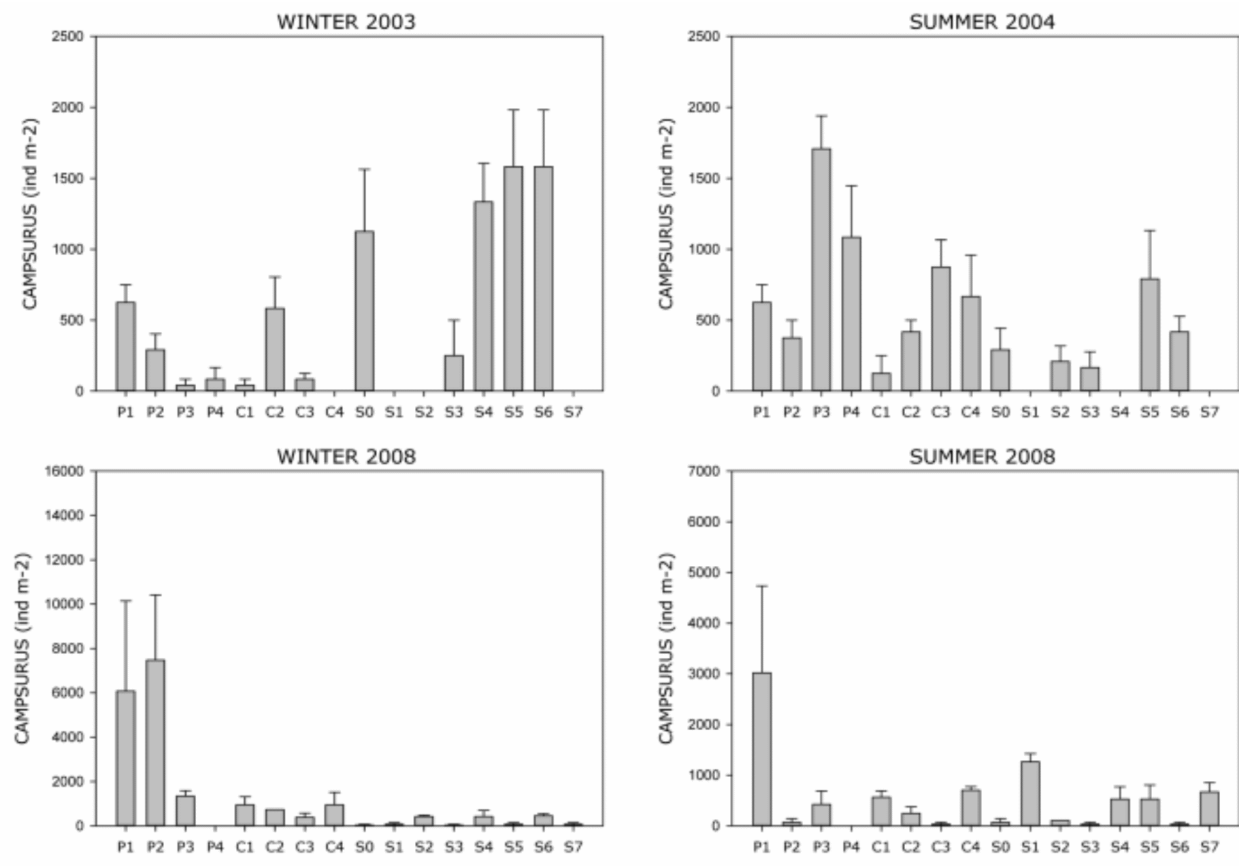


Figure 4. *Campsurus violaceus* abundance (ind/m², mean ± SE) in the different sampling sites and seasons at Laguna del Sauce system, Maldonado, Uruguay.

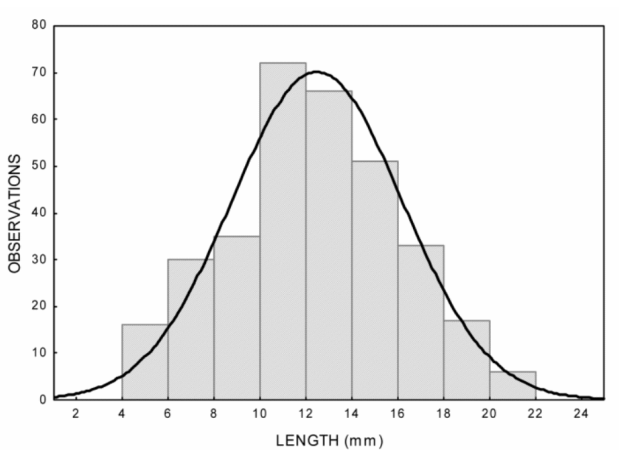


Figure 5. *Campsurus violaceus* nymphs' total length frequency distribution at Laguna del Sauce system, Maldonado, Uruguay. The histogram was constructed using 320 individuals collected in the different sampling sites during summer 2004.

$p < 0.01$; $\rho = 0.49$, $p < 0.001$; $\rho = 0.35$, $p < 0.05$, winter 2003, summer 2004, winter and summer 2008, respectively).

The partial Mantel test between macroinvertebrates (composition and abundance, excluding *Campsurus*,

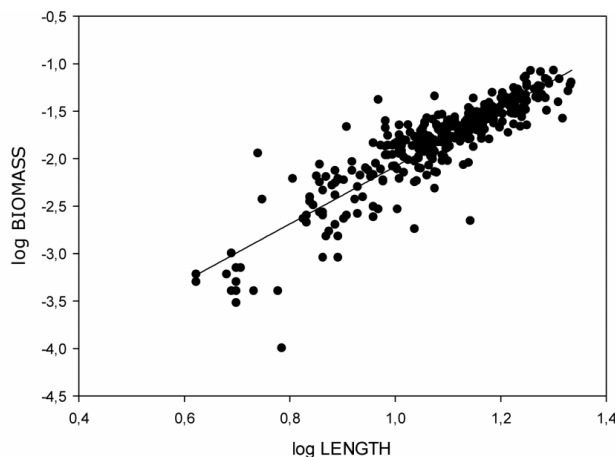


Figure 6. Linear regression of the log-transformed length and dry weight of *Campsurus violaceus* nymphs.

matrix A) versus environmental attributes (matrix B) were not significant for all the periods tested. However, the addition of *Campsurus* abundance to matrix B led to significant relationships for winter 2003 as well as summer and winter 2008 ($rM = 0.28$ $p < 0.05$, $rM = 0.79$ $p < 0.001$, $rM = 0.34$ $p < 0.05$, respectively). The spatial pattern of sampling

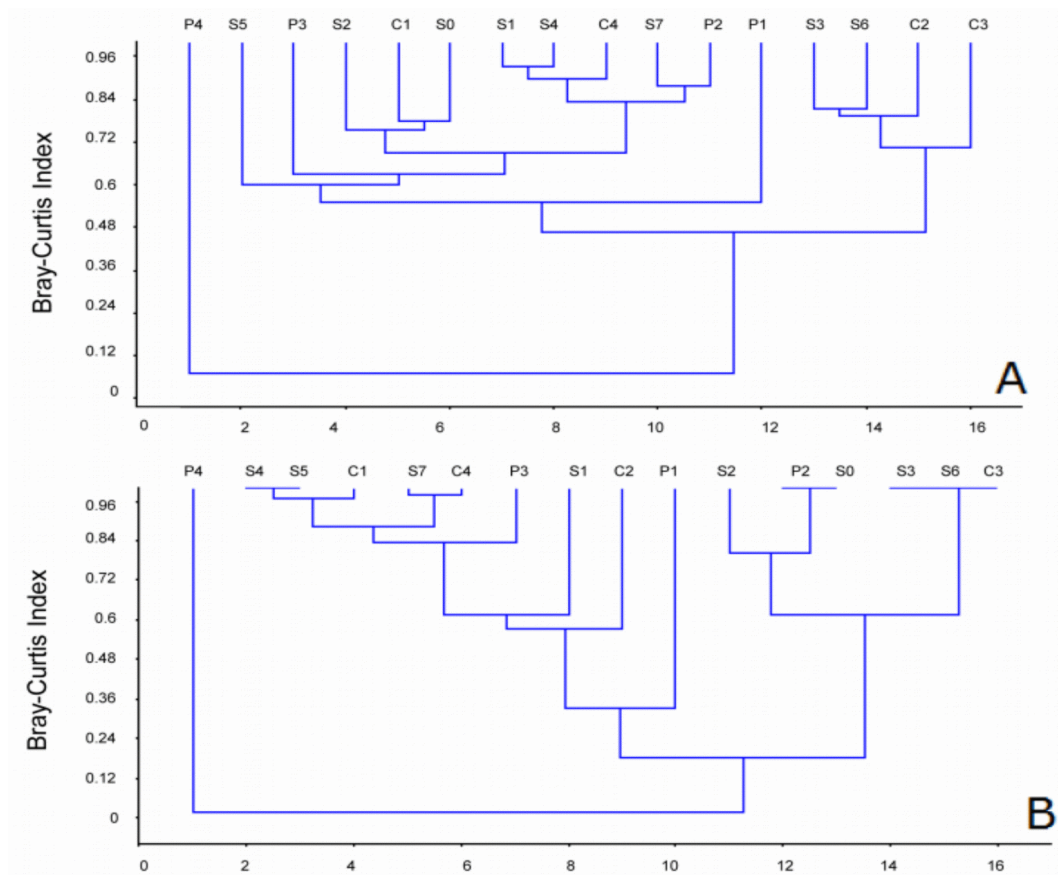


Figure 7. Similarities among sampling sites during summer 2008 based on A) the composition and abundance of macroinvertebrate community (except *Campsurus*) and B) abundance of *Campsurus*. The algorithm considered was Bray-Curtis and unweighted average for clustering. The partial Mantel test between both matrices considered was $rM: 0.56, p < 0.01$.

stations based on *C. violaceus* abundance was similar to the spatial structure based on macroinvertebrate composition and abundance, a statistically significant partial Mantel test were recorded for winter 2003 and summer and winter 2008 ($rM = 0.23, p < 0.05$; $rM = 0.56, p < 0.01$; $rM = 0.40, p < 0.01$, respectively; Figure 7). The significance of partial Mantel test was higher when including the replicates average per station; however, the analysis with all replicates did not modify the statistical significance of the relationship.

Discussion

Campsurus violaceus nymphs were present in LSS both in winter and summer, where no statistical difference in abundances attributable to seasonality arose. Its size distribution, particularly at the beginning of the summer, indicates that all the population sampled belonged to the same cohort. Campbell et al. (1990) observed univoltine cycles for the Ephemeroptera species from Australia, while Ferreira (1990), Jackson & Sweeney (1995), Salas &

Dudgeon (2003) and Santos-Lima & Pamplin (2016) found multivoltine regimes in warm regions. Takeda & Gryzbkowska (1997) found populations of univoltine or bivoltine regimes of *C. violaceus* in Paraná floodplain.

Campsurus violaceus spatial distribution was frequently related with granulometry and organic matter content of sediments in LSS. Molineri & Salles (2013) and Zilli (2012) found *C. violaceus* to be distributed on a wide spectrum of sediment and vegetal substrates (alive or dead). LSS is characterized by a particular large spatial pattern variation in sediment types, however, the zones with fine size grain did not have particularly high organic matter content, that otherwise is a typical pattern observed in lakes without important tributaries (Håkanson & Jansson 1983). This may have weakened the relationship to substrate type as, higher organic matter and nutrients can be retained, transformed and stored in sediments affecting the distribution and composition of *C. violaceus* and other macroinvertebrates. Additionally, sampling

sites with higher organic matter content (and also nutrients) did not exhibit an oxygen deficit at sediment-water interface, even at summer time, likely due to the intense mixing of the water column and the overall absence of extended stratification (Rodríguez-Fernández 2006), which could potentially indirectly prevented macroinvertebrates settlement.

Campsurus violaceus highest abundance was observed in del Potrero, a lake that exhibits also the higher spatial heterogeneity at LSS, principally due to the presence of submerged plants and less harsh wind conditions. The aquatic plants might act as substrate for the oviposition and offer refuge against fish predation (Diehl & Kornijów 1998; Thomaz et al 2008). Despite, submerged plants are not live consumed by *C. violaceus*, their presence could promote sediment and detritus settlement, increasing food availability.

A positive spatial distribution relationship between *C. violaceus* and the associated macroinvertebrate community, both regarding total abundance and community structure, were clearly evidenced. This may either reflect similar response to studied environmental gradients or as a consequence of biotic interactions between *C. violaceus* and the other macroinvertebrates which concurs with previous findings (Floater, 2001; Kovalenko et al., 2012). Accordingly, the partial Mantel test indicated that the main environmental patterns (granulometry, grain diversity, organic matter and nutrient content of the sediment, water column depth, presence or absence of submerged plants) did not explain macroinvertebrates distribution and community structure. Moreover, when including *C. violaceus* abundance to the analysis, then a significant relationship appeared supporting the idea that biotic interactions were of key importance structuring the associated macroinvertebrate community. Several factors may be involved and explain the observed structuring role. Firstly, *C. violaceus* increases the volume of sediment potentially to be colonized by macroinvertebrate leading to higher abundance per unit of sediment area (Kristensen et al., 2012), i.e bioturbation by *C. violaceus* may promote a higher depth of sediment colonization by increasing the oxygen availability in the sediment profile (Leal et al. 2005). Simultaneously, the feeding activity of *C. violaceus* can facilitate the occurrence macroinvertebrate detritivores that consume plant detritus or fecal pellets (i.e. *Chironomus gr. riparius* and *Chironomus gr. decorus*) generated by the

Ephemeroptera nymphs. However, also a strong predation pressure over macroinvertebrates might have conditioned the similar spatial pattern observed. Fish communities in LSS have high densities, especially species that fed on insects in the bottom (i.g. *Pimelodella australis*, *Rhamdia quelen*, *Bryconamericus iheringii*; Mazzeo et al. 2010). Therefore, similarities between *C. violaceus* spatial distribution and the pattern of abundance and composition of macroinvertebrates could reflect a strong spatial variability in fish predation pressure. Temperature and food has not been analyzed in our study, despite these could be other important factors affecting *C. violaceus* and others macroinvertebrates interactions and abundance (Benke, 1984; Zilli 2012) that should be further analyzed in future studies.

Acknowledgements

The authors are deeply grateful to the Puppo family, namely María, Carmen, Blanca and to the memory of Juan José, for their kind hospitality providing access to the reservoir through their farmland. The authors also thank OSE-UGD personnel at Laguna del Sauce water facility, specially to Gustavo Méndez and Juan José Lagomarsino. This work was supported by Programa de Desarrollo de las Ciencias Básicas (PEDECIBA), CSIC-UdelaR and Cooperation Program between OSE-UGD and UdelaR. C. Iglesias, N. Mazzeo, F. Teixeira de Mello and G. Goyenola were supported by Sistema Nacional de Investigadores (SNI-ANII).

Disclosure statement: No potential conflict of interest was reported by the authors.

References

- Benke, A.C. 1993. Concepts and patterns of invertebrate production in running water. **Verhandlungen des Internationalen Verein Limnologie**, 25: 15-38.
- Cadée, G.C. 2001. Sediment dynamics by bioturbating organisms. In: Reise K, editor. Ecological comparisons of sedimentary shores. **Ecological Studies**, 151: 128–148.
- Callisto, M., Moreno, P. & Barbosa, F.A.R. 2001. Habitat diversity and benthic functional trophic groups at Serra do Cipó. **Revista Brasileira de Biologia**, 61: 259–266.
- Campbell, J.I., Duncan, M. & Swadling, K. 1990. Life Histories of some Ephemeroptera from Victoria, Australia. Mayflies and Stoneflies. In: Campbell J, editor. **Mayflies and**

- stoneflies: life histories and biology.** Kluwer Academic Publishers. Dordrecht, 4p.
- Crisci, C. 2006. Principales factores que determinan el patrón espacial de la vegetación sumergida en Laguna del Potrero (Maldonado- Uruguay). **BSc. Thesis.** Universidad de la República. Montevideo, Uruguay.
- Cuddington, K. 2007. Ecosystem Engineering: utility, contention and progress. In: Cuddington K, Byers JE, Wilson WG, Hastings A, editors. **Ecosystem Engineering, Plants to Protists. Theoretical Ecology Series.** Elsevier. San Diego, California, 6p.
- Cummins, K.W., Merritt, R.W. & Andrade, P.C.N. 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. **Studies on Neotropical Fauna and Environment**, 40: 69-89.
- Diehl, S. & Kornijow, R. 1998. Influence of submerged macrophytes on trophic interactions among fish and macroinvertebrates. In: Jeppesen E, Sondergaard M, Sondergaard M, Christoffersen K, editors. **The Structuring Role of Submerged Macrophytes in Lakes.** Springer, New York, 23p.
- Dos Santos, D.A., Emmerich, D., Molineri, C., Nieto, C. & Domínguez, E. 2015. On the position of Uruguay in the South American biogeographical puzzle: insights from Ephemeroptera (Insecta). **Journal of Biogeography**, 43: 361-371.
- Ferreira, M.J.N. 1990. Estudo da fauna de Ephemeroptera do Córrego do Pedregulo-Pedregulo, SP. **MSc. Thesis.** Universidade de São Paulo. Riberão Preto, Brazil.
- Floater, G.J. 2001. Habitat complexity, spatial interference and “minimum risk distribution”: a framework for population stability. **Ecological Monographs**, 71: 447-468.
- Folk, R. & Ward, W. 1957. Brazos River Bar: a study on the significance of grain size parameters. **Journal of Sedimentary Petrology**, 27: 3–26.
- Graça, M., Rodrigues Capítulo, A., Ocon, C. & Gómez, N. 2002. In situ tests for water quality assessment: a case study in Pampean rivers. **Water Research**, 36: 4033-4040.
- González-Madina, L., Pacheco, J.P., Yema, L., Tezanos, P., Levrini, P., Clemente, J., Crisci, C., Lagomarsino, J.J., Méndez, G., Fosalba, C., Goyenola, G. & Mazzeo, N. 2018. Drivers of cyanobacteria dominance, composition and nitrogen fixing behavior in a shallow lake with alternative regimes in time and space, Laguna del Sauce (Maldonado, Uruguay). **Hydrobiologia**, 1-16.
- Håkanson, L. & Jansson, M. 1983. **Principles of Lake Sedimentology.** Springer-Verlag. Berlin: 316 p.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. **Palaeontologia Electronica** 4(1): 1-298.
- Harris, G., Batley, B., Jernakoff, P., Newell, B., Fox, D., Molloy, R., Parslow, J., Walker, S., Hall, D., Murray, D. & Skyring, G. 1996. **Port Phillip Bay Environmental Study. Final Report.** CSIRO. Canberra, Australia, 239 p.
- INUMET. 2016. **Climatological statistics. Montevideo (UR): Instituto Uruguayo de Meteorología.** World Wide Web electronic publication accessible at <http://www.meteorologia.com.uy/ServCli/estadisticasClimatologicas>. (Accessed 5/9/2016)
- Jackson, J. & Sweeney, B. 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. **Journal of the North American Benthological Society**, 14 (1): 115-130.
- Kovalenko, K.E., Thomaz, S.M. & Warfe, D.M. 2012. Habitat complexity: approaches and future directions. **Hydrobiologia**, 685: 1–17.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O. & Banta, G.T. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. **Marine Ecology Progress**, 446: 285–302.
- Leal, J.J.F., Esteves, F.A., Farjalla, V.F. & Enrich-Prast, A. 2003. Effect of *Campsurus notatus* on NH₄ DOC Fluxes, O₂ Uptake and Bacterioplankton Production in Experimental Microcosms with Sediment-Water Interface of an Amazonian Lake Impacted by Bauxite Tailings. **International Review of Hydrobiology**, 2:167–178.
- Leal, J.J.F., Enrich-Prast, A., Esteves, F.A., Bozelli, R. & Farjalla, V.F. 2005. Influence of *Campsurus notatus* bioturbation on oxygen profile and uptake in sediments of an Amazonian lake impacted by bauxite tailings. **Archive für Hydrobiologie**, 4:557–574.
- Leal, J.J.F., Furtado, A.L.S., Esteves, F.A., Bozelli, R.L. & Figueiredo-Barros, M.P. 2007. The

- role of *Campsurus notatus* (Ephemeroptera: Polymitarcyidae) bioturbation and sediment quality on potential gas fluxes in a tropical lake. **Hydrobiologia**, 586: 143-154.
- Legendre, P. & Legendre, L. 1998. **Numerical Ecology**. Elsevier Science. Amsterdam, 852 p.
- Lopretto, E.L. & Tell, G. 1995. **Ecosistemas de Aguas Continentales. Metodología para su estudio. (Vol. III)**. Ediciones Sur. La Plata, 1400 p.
- Mazzeo, N., García-Rodríguez, F., Rodríguez, A., Mendez, G., Iglesias, C. & Inda, H. 2010. Estado trófico de Laguna del Sauce. In: Steffen M, Inda H, editors. **Bases técnicas para el manejo integrado de Laguna del Sauce y cuenca asociada**. UDELAR-SARAS. Montevideo, 20p.
- Merritt, R. & Cummins, R. 1996. **An introduction to the aquatic insects of North America**. Kendall/Hunt Publishing. Dubuque, 862 p.
- Molineri, C. & Salles, F.F. 2013. Phylogeny and biogeography of the ephemeral *Campsurus Eaton* (Ephemeroptera, Polymitarcyidae). **Systematic Entomology**, 38: 265-277.
- Moore, J. 2006. Animal ecosystem engineers in streams. **Bioscience**, 56: 237-246.
- Plan Nacional de Aguas Síntesis. Ministerio de Vivienda Ordenamiento Territorial y Medio Ambiente**. 2016. MVOTMA, Montevideo, 76 p.
- Nolte, U.M., Oliveira, M. & Sturs, E. 1997. Seasonal, discharge driven patterns of mayfly assemblages in an intermittent neotropical stream. **Freshwater Biology**, 37: 333-343.
- Ocon, C.S. & Rodríguez Capítulo, A. 2004. Presence and abundance of Ephemeroptera and other sensitive macroinvertebrates in relation with habitat conditions in pampean streams (Buenos Aires, Argentina). **Archiv für Hydrobiologie**, 159(4): 473-487.
- Oden, N.L. & Sokal, R.R. 1992. An investigation of three-matrix permutation tests. **Journal of Classification**, 9: 275-290.
- Peel, M.C., Finlayson, B.L., McMahon, T.A. 2007. Updated world map of the Köppen-Geiger climate classification. **Hydrology and Earth System Sciences**, 11:1633-1644.
- Quinn, G. & Keough, M. 2002. **Experimental Design and Data Analysis for Biologists**. Cambridge University Press. New York, 537 p.
- Rodríguez-Fernández, A. 2006. Evolución del estado trófico de la Laguna del Sauce e importancia de la carga interna de nutrientes. **MSc. THESIS**. Universidad de la República. Montevideo, Uruguay.
- Salles, F.F., Nascimento, J.M.C., Massariol, F.C., Angeli, K.B., Silva, P.B., Rúdio, J.A. & Boldrini, R. 2010. Primeiro levantamento da fauna de Ephemeroptera (Insecta) do Espírito Santo, Sudeste do Brasil. **Biota Neotropica**, 10: 293-307.
- Salas, M. & Dudgeon, D. 2003. Life History, production dynamics and resource utilization of mayflies (Ephemeroptera) in two tropical Asian streams. **Freshwater Biology**, 48: 485-499.
- Santos-Lima, J.C.S. & Pamplin, P.A.Z. 2016. Life cycle and secondary production of two species of *Campsurus* (Ephemeroptera, Polymitarcyidae) in reservoirs of southeastern Brazil. **Studies on Neotropical Fauna and Environment**, 1-10.
- Scheffer, M. 1998. **Ecology of shallow lakes**. Chapman & Hall. London, 357 p
- Smock, L.A. 1980. Relationship between body size and biomass of aquatic insects. **Freshwater Biology**, 10:375-883.
- Takeda, A.M. & Grzybkowska, M. 1997. Seasonal dynamics and production of *Campsurus violaceus* nymphs (Ephemeroptera, Polymitarcyidae) of the Baía River, upper Paraná River floodplain, Brazil. **Hydrobiologia**, 356: 149-155.
- Thomaz, S.M., Dibble, E.D., Evangelista, L.R., Higuti, J. & Bini, L.M. 2008. Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. **Freshwater Biology**, 53:358-367.
- Valderrama, J.C. 1981. The simultaneous analysis of total N and P in natural waters. **Marine Chemistry**, 10:1009-1022.
- Webb, A. & Eyre, B. 2004. The effect of natural populations of the burrowing and grazing soldier crab (*Mictyris longicarpus*) on sediment irrigation, benthic metabolism and nitrogen fluxes. **Journal of Experimental Marine Biology and Ecology**, 309:1-19.
- Weatherhead, M. & James, R. 2001. Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. **Hydrobiologia**, 462:115-129.
- Wootton, J.T. 1994. The nature and consequences of

- indirect effects in ecological communities. **Annual Review of Ecology, Evolution, and Systematics**, 25:443-66.
- Zilli, F.L. 2010. Bentos en ambientes lentos con diferentes grado de conectividad en la llanura aluvial del río Paraná Medio. **Ph.D. Thesis**. Universidad Nacional de la Plata, Argentina.
- Zilli, F.L. 2012. Life history traits and secondary production of *Campsurus violaceus* (Ephemeroptera: Polymitarcyidae) in the Paraná River floodplain lakes, Argentina.
- Studies on Neotropical Fauna and Environment**, 47:61-71.
- Zuñiga de Cardoso, M., Rojas de Hernandez, A. & Mosquera de Aguilera, S. 1997. Biological Aspects of Ephemeroptera in Rivers of Southwestern Colombia (South America). In: Landolt, P. & Sartori, M., (Eds.) **Ephemeroptera & Plecoptera: Biology-Ecology-Systematics**. Mauron, Tinguely & Lachat. Fribourg, Switzerland, 268p.

Received: July 2018

Accepted: October 2018

Published: December 2018