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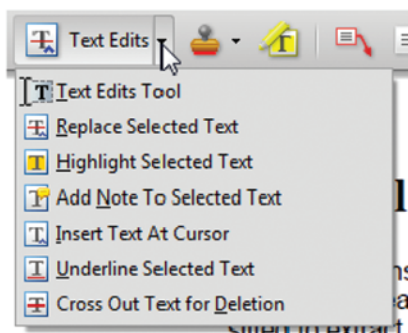
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## ORIGINAL ARTICLE

### Life history traits and secondary production of *Campsurus violaceus* (Ephemeroptera: Polymitarcyidae) in the Paraná River floodplain lakes, Argentina

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10 *Campsurus* nymphs are among the most abundant mayflies in neotropical aquatic habitats. The abundance patterns and secondary production of *Campsurus violaceus* were analyzed monthly from April 2005 to March 2006 in lakes with different degrees of connectivity in the floodplain of the Middle Paraná River. Significant differences were estimated for the abundance and secondary production of the species among the studied lakes. The patterns in the abundance of nymphs were correlated to substrate characteristics (type of substrate, content of detritus), water transparency, and conductivity of lakes and the variations in the life cycle were related to temperature. Degree of connectivity of lakes was the main factor in determining differences among populations, as it influenced local conditions, finally determining regional dissimilarities in abundance pattern and secondary production for the species.

15 Las ninfas de *Campsurus* se encuentran dentro de las efímeras más abundantes en ambientes acuáticos neotropicales. Se analizaron los patrones de abundancia y la producción secundaria de *Campsurus violaceus* en lagunas con diferente nivel de conectividad mensualmente entre Abril de 2005 y Marzo de 2006. Se estimaron diferencias significativas entre las lagunas estudiadas en la abundancia y producción secundaria de la especie. Los patrones de abundancia de ninfas se correlacionaron con las características del sustrato (tipo de sustrato, contenido de detrito), transparencia del agua y conductividad de las lagunas y las variaciones en el ciclo de vida se relacionaron con la temperatura. El nivel de conectividad fue el factor principal en determinar diferencias entre las poblaciones al influenciar las condiciones locales, determinando disimilitudes regionales en el patrón de abundancia y en la producción secundaria de la especie.

20 **Keywords:** secondary production; life history traits; *Campsurus violaceus*; floodplain lakes; Argentina

#### Introduction

25 In large neotropical rivers an increasing environmental heterogeneity has been shown in the cross-section from the main channel into the floodplain habitats (Marchese and Ezcurra de Drago 1992; Marchese et al. 2002, 2005; Ezcurra de Drago et al. 2004). In such systems the flood pulse, the change between flowing and stagnant conditions (Junk et al. 1989; Neiff 1990) and the degree of connectivity (Amoros and Roux 1988; Ward and Stanford 1995) determine habitat patchiness and ecological functions. The degree of connectivity of floodplain lakes determined by their type of connection and position in relation to active channels establishes diverse patches of available resources for invertebrates. In the Middle Paraná River floodplain, the varying inputs of river-borne matter determine habitat patchiness depending on lakes' location within the network and on their hydrological connection (Poi de Neiff et al. 1994; Drago et al. 2003; Wantzen et al. 2005).

30 Mayflies (Ephemeroptera) are an abundant and diverse component of freshwater systems in the Neotropics (Domínguez et al. 2006). Moreover, the nymphs of *Campsurus* are primary colonizers, behaving as r-strategists in environments with soft sediments and high concentration of suspended solids (Nolte 1987). The nymphs of *Campsurus violaceus* Needham and Murphy, 1924 are abundant in the benthic assemblages of the Paraná River floodplain habitats (Melo et al. 1993; Takeda and Gryzbkowska 1997; Ezcurra de Drago et al. 2007; Zilli 2010). In addition, a high contribution of biomass to the ecosystem was estimated for *Campsurus* emerging in the Orinoco River basin (Wantzen and Junk 2006).

35 Regardless of the importance of mayflies for aquatic habitats and food webs as they process basal resources that are transferred to the higher trophic levels (Beltzer 1991; Merritt et al. 2002; Cummins et al. 2005), little is known about their density, biomass, vol-  
40 tinism, duration of cohorts and secondary production  
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for floodplain habitats. Furthermore, there is no information concerning effects of degree of connectivity of floodplain habitats over the life history traits of *C. violaceus*. Therefore, the main aim of the present study was to analyze whether spatial heterogeneity due to degree of connectivity of floodplain lakes could determine dissimilarities in the abundance patterns and secondary production of *C. violaceus* in the Middle Paraná River floodplain.

## Materials and methods

### Study area

The sampling was conducted during a normal flooding regime in four lakes with different degrees of connectivity located on the Paraná River floodplain at the cross-section of Santa Fe city and Paraná city (31°40'–31°43' S and 60°33'–60°39' W) (Figure 1). The type of connectivity of floodplain lakes during the study

period was defined based on previous research on the Middle Paraná River (compiled in Paira and Drago 2007). On one extreme of the gradient, a superficially isolated lake (PI) was sampled. On the other side, a lake (PC) with an indirect but permanent connection to the main stem of the river through a channel (average depth of 7.8 m) was sampled. Lakes with temporal connection were directly (TCn) and indirectly (TCI) connected and had different quotients of connectivity (days connected/days isolated), in relation to their location within the floodplain. TCn was located 0.10 km from the main channel and had a quotient of connectivity of 14; TCI was located 2.12 km from the main channel and had a quotient of connectivity of 5. In each lake, three sampling stations were established.

There is a marked seasonality for the region with high temperatures from September to early May. The thermal regime of floodplain lakes is warm polymictic. The principal sources of autochthonous detritus are floating macrophytes, principally *Eichhornia* Kunth

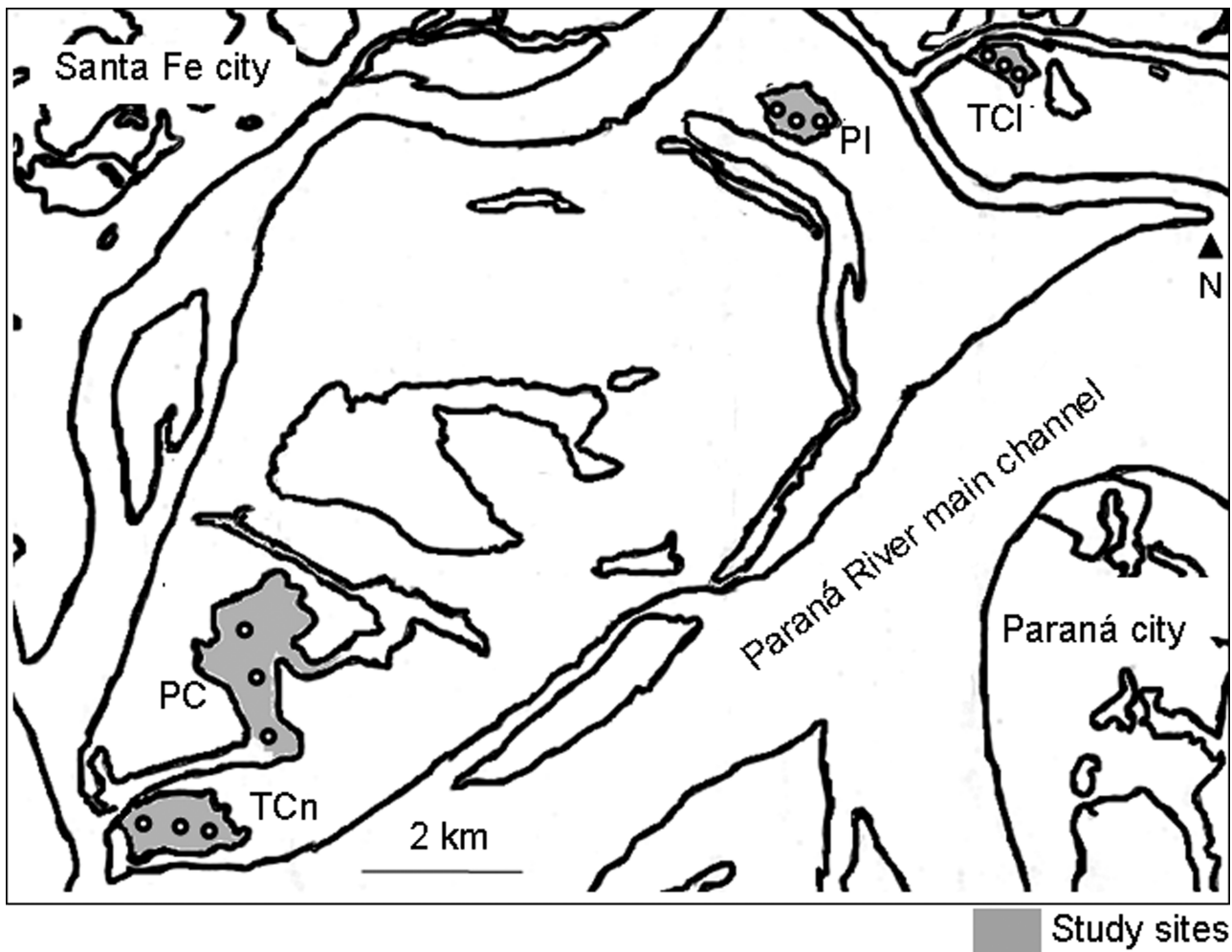


Figure 1. Study area. TCI = temporarily and indirectly connected lake; PI = isolated lake; PC = permanently connected lake; TCn = temporarily and directly connected lake. The sampling stations are indicated (black circles).

105 (1842). The free-floating macrophyte meadows change according to seasonality and lake connectivity, determining the budgets of organic matter.

**Sampling and analysis of habitat characteristics**

110 Samplings were conducted between April 2005 and March 2006. The macrophyte cover of lakes was estimated for each sampling date. Furthermore, two bottom sediment samples were monthly collected in each sampling station (Figure 1) with an Ekman grab (225 cm<sup>2</sup>), to determine the organic matter composition and for granulometric analysis. The proportions of ultrafine particulate organic matter (UFPOM = 63–250 μm), fine particulate organic matter (FPOM = 250–1000 μm) and coarse particulate organic matter (CPOM ≥ 1000 μm) were determined. After wet sieving, each fraction was oven-dried to constant mass, weighed, ashed (muffle furnace), and reweighed. Granulometry of bottom sediments (sand, silt, clay, according to Wentworth 1932) was determined using dry sieving after Bertoldi de Pomar (1976). Physico-chemical characteristics such as depth, transparency (Secchi disk), water pH (colorimetric technique, Hellige pH-meter), conductivity (Beckman conductivity meter) and water temperature (standard thermometer) were measured in the sampling stations in each sampling date ( $n = 3$  in each lake). In addition, water samples were collected monthly in each sampling station to determine the dissolved oxygen concentrations at the lake bottom (Winkler method) and to determine the nutrient concentration (APHA standard methods). To reduce the influence of daytime variations of the measured variables, samplings were always conducted during the morning hours.

**Sampling and analysis of *C. violaceus* traits**

140 For determination of life history traits, annual secondary production ( $P$ ) and turnover ratio ( $P/B$ ), three samples of benthos were collected monthly with an Ekman grab (225 cm<sup>2</sup>) at each sampling station in each lake. Samples were washed through a sieve (200 μm) and fixed with formalin (5%) in the field. On each of the 12 sampling dates, 36 benthic samples ( $n = 9$  per lake) were collected. In the laboratory, *C. violaceus* nymphs were handpicked from samples under a stereoscopic microscope and stored in 70% ethanol. The density of nymphs was determined by direct counting. The standing stock biomass was determined from the dry weight of nymphs (oven dried at 60°C for 48 h). The mean weight of nymphs was obtained for each sampling date according to the following formula:

$$\bar{W} = B/D \quad (1)$$

$\bar{W}$  = mean weight (mg ind<sup>-1</sup>);  $B$  = standing stock biomass (mg m<sup>-2</sup>) and  $D$  = density for the population in each sampling date (ind m<sup>-2</sup>). 155 AQ1

The total body length of nymphs (dorsally, from the anterior edge of the head to the posterior edge of the last abdominal segment) was measured to establish the length–weight relationships of nymphs for the estimations of secondary production. Mayfly nymphs were grouped into nine size classes according to the interocular distance (size class: I = 0.0–0.2 mm; II = 0.2–0.4 mm; III = 0.4–0.6 mm; IV = 0.6–0.8 mm; V = 0.8–1.1 mm; VI = 1.1–1.3 mm; VII = 1.3–1.5 mm; VIII = 1.5–1.7 mm; IX = 1.7–1.9 mm). Diagrams of size–frequency distribution were constructed for the studied period in each lake. For each lake and sampling date, the frequency of each size class was calculated as the number of nymphs per class over the total number of nymphs collected. The measurements were made with a microscope fitted with a micrometric scale, to the nearest 0.01 mm. The annual secondary production and turnover ratio were estimated by the size–frequency method according to the following equation (Hynes and Coleman 1968; Benke 1979): 170 175

$$P = \left\{ i \sum_{j=1}^i (W_j + W_{j+1}) / 2(n_j - n_{j+1}) \right\} \times b \quad (2)$$

$P$  = annual secondary production (mg m<sup>-2</sup> yr<sup>-1</sup>);  $i$  = number of size classes;  $W_j$  = mean dry weight of individuals in each size class (estimated through the regression equation of the relationship between individual length and weight of nymphs);  $n_j$  = mean density of individuals in each size class. The density of the size classes was calculated considering the period when larvae were recorded;  $b$  = period when larvae were recorded in each lake/generation time. 180 185

To show if the frequency distribution of nymphs in the different size classes was significantly different among lakes, a non-parametric test was performed. Additionally, to show whether environmental variables were significantly different among lakes a non-parametric test (Kruskal–Wallis test) was run using Infostat software (Di Rienzo et al. 2010). To assess the differences in density, biomass and mean weight of the species among lakes, similarity analyses were performed considering spatial and temporal factors (ANOSIM routine, log  $x + 1$  transformed data, Bray–Curtis matrices). To analyze the dissimilarity between pairs of lakes for the different attributes statistical analyses were performed (SIMPER routine, log  $x + 1$  transformed data, Bray–Curtis matrices). Additionally, correlation analyses were performed 190 195 200



to test the key environmental variables influencing the patterns of the species (BEST: biotic data were log  $x + 1$  transformed and environmental data were normalized, Bray–Curtis and Euclidean distances data matrices). The analyses were performed using PRIMER-E software (version 6.1).

## Results

### Environmental parameters

The water temperature showed no significant differences among lakes (Table 1). The minimum temperature was registered in July–August and the maximum in January. A pronounced increase (of 5°C on average) in the temperature of lakes was registered between October and November. Furthermore, depth, pH, conductivity, concentration of nutrients and dissolved oxygen near the lake bottom, and composition of bottom detritus were not significantly different among lakes. In PC, TCl, and TCn, the depth varied according to connectivity fluctuations, with an isolation phase during August and September and a peak of connection during November (flooding phase). The pH was close to neutral, and the conductivity had the highest value in TCl. The dissolved oxygen was in general high near the lake bottom, with the highest concentrations in the lakes with the highest degree of connectivity. The highest concentration of nitrates and phosphorous were measured in PI. Nitrites had the highest concentration in PC and ammonium in TCn.

Conversely, water transparency, macrophyte cover, percentage of detritus and granulometry of bottom sediments had significant differences among lakes (Table 1). PI had the highest water transparency, macrophyte cover, percentage of detritus (principally of CPOM) and of clay in bottom sediments. On the other side of the gradient, PC had the minimum cover of macrophytes in all the sampling dates. The bottom sediments had relatively high percentages of clay in PC and of silt in TCn. Moreover, TCn had the lowest content of detritus and TCl had the highest percentage of sand in the bottom sediments.

### Density, standing stock biomass and mean weight of *C. violaceus* nymphs

The density of nymphs had peaks during June (except for TCl) and from January to March, (Figure 2a). The biomass of nymphs was higher from June to October (except in TCl) (Figure 2b). Besides, an increment in biomass occurred between January and March. The mean weight of nymphs was highest from August to October with and increment during January (Figure 3).

TCn and PI had the highest average densities and standing stock biomass of nymphs (Table 2). The mean weight of nymphs was highest in PC and TCn. The lowest density, biomass, and mean weight of nymphs were calculated in TCl. The highest frequency of occurrence in the benthos occurred in PC and TCn.

Table 1. Median and (range) of the environmental variables for four lakes of the Paraná River floodplain, Argentina. TCl = temporarily and indirectly connected lake; PI = isolated lake; PC = permanently connected lake; TCn = temporarily and directly connected lake.

	PC	TCn	TCl	PI
Water temperature (°C)	21 (13–28)	22.5 (13–29)	21.5 (17–29)	19.5 (13–28)
Depth (m)	3.27 (1.79–4.22)	2.29 (0.93–3.13)	2.79 (1.36–3.67)	2.53 (2.14–2.90)
Transparency (m)*	0.505 (0.17–0.67) <sup>A</sup>	0.485 (0.18–0.88) <sup>A</sup>	0.430 (0.19–0.62) <sup>A</sup>	0.985 (0.68–1.26) <sup>B</sup>
pH	7.4 (7.1–7.8)	7.3 (7.1–7.8)	7.25 (7.2–7.6)	7.3 (7.2–7.5)
Conductivity ( $\mu\text{S cm}^{-1}$ )	100 (70–138)	95 (78–107)	104 (72–220)	100 (80–107)
NO <sub>3</sub> <sup>-</sup> (mg l <sup>-1</sup> )	0.270 (0.080–0.500)	0.290 (0.100–0.400)	0.295 (0.040–1.200)	0.300 (0.040–1.700)
NO <sub>2</sub> <sup>-</sup> (mg l <sup>-1</sup> )	0.004 (0.002–0.030)	0.003 (0.001–0.026)	0.004 (0.002–0.008)	0.005 (0.002–0.011)
NH <sub>4</sub> <sup>+</sup> (mg l <sup>-1</sup> )	0.195 (0.030–1.200)	0.205 (0.010–1.290)	0.145 (0.010–0.780)	0.195 (0.010–0.820)
Total phosphorous (mg l <sup>-1</sup> )	0.2275 (0.100–1.400)	0.340 (0.080–1.300)	0.3625 (0.100–1.890)	0.4615 (0.060–2.750)
Bottom dissolved oxygen (mg l <sup>-1</sup> )	9.375 (6.65–10.53)	9.31 (5.91–11.81)	7.35 (5.60–9.50)	8.1 (3.20–11.90)
Macrophyte cover (%)*	2 (1–10) <sup>A</sup>	14 (4–25) <sup>B</sup>	14 (5–40) <sup>B</sup>	23 (21–75) <sup>C</sup>
Organic matter/sediment (%)*	6.46 (5–18) <sup>B</sup>	1.71 (1–3) <sup>A</sup>	5.91 (4–15) <sup>B</sup>	18.25 (14–23) <sup>C</sup>
Ultrafine particulate organic matter (%)	37.46 (26–71)	39.82 (21–56)	32.49 (14–65)	39.53 (15–56)
Fine particulate organic matter (%)	23.11 (20–37)	28.96 (23–56)	24.23 (13–52)	15.11 (9–44)
Coarse particulate organic matter (%)	38.45 (6–43)	26.83 (13–36)	42.26 (13–60)	45.20 (23–68)
Sand (%)*	8.59 (5–14) <sup>B</sup>	3.93 (1–9) <sup>A</sup>	18.66 (12–24) <sup>C</sup>	5.05 (2–7) <sup>A</sup>
Silt (%)*	57.17 (52–62) <sup>A</sup>	70.54 (60–73) <sup>B</sup>	53.89 (48–60) <sup>A</sup>	53.37 (47–59) <sup>A</sup>
Clay (%)*	34.52 (31–39) <sup>B</sup>	26.21 (23–35) <sup>A</sup>	27.82 (23–32) <sup>A</sup>	40.67 (36–51) <sup>C</sup>

\*Indicates the variables with significant differences among lakes (Kruskal–Wallis test,  $p < 0.0001$ ,  $n = 12$ ). <sup>A</sup>, <sup>B</sup> and <sup>C</sup> indicate significant differences between lakes.

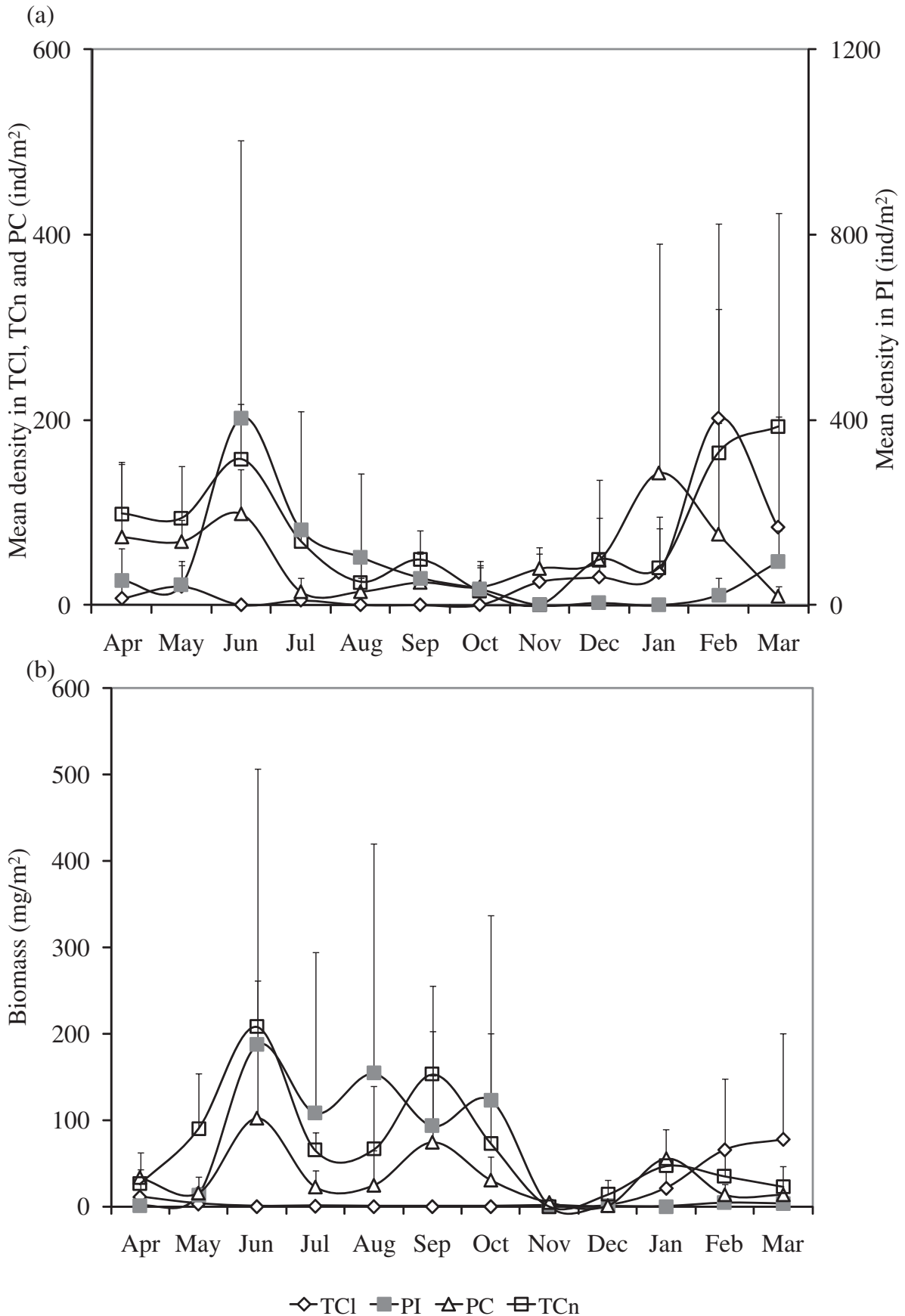


Figure 2. Monthly mean ( $\pm$  SD) (a) density and (b) biomass of *Campsurus violaceus* nymphs in four lakes of the Paraná River floodplain, Argentina. TCI = temporarily and indirectly connected lake; PI = isolated lake; PC = permanently connected lake; TCn = temporarily and directly connected lake.



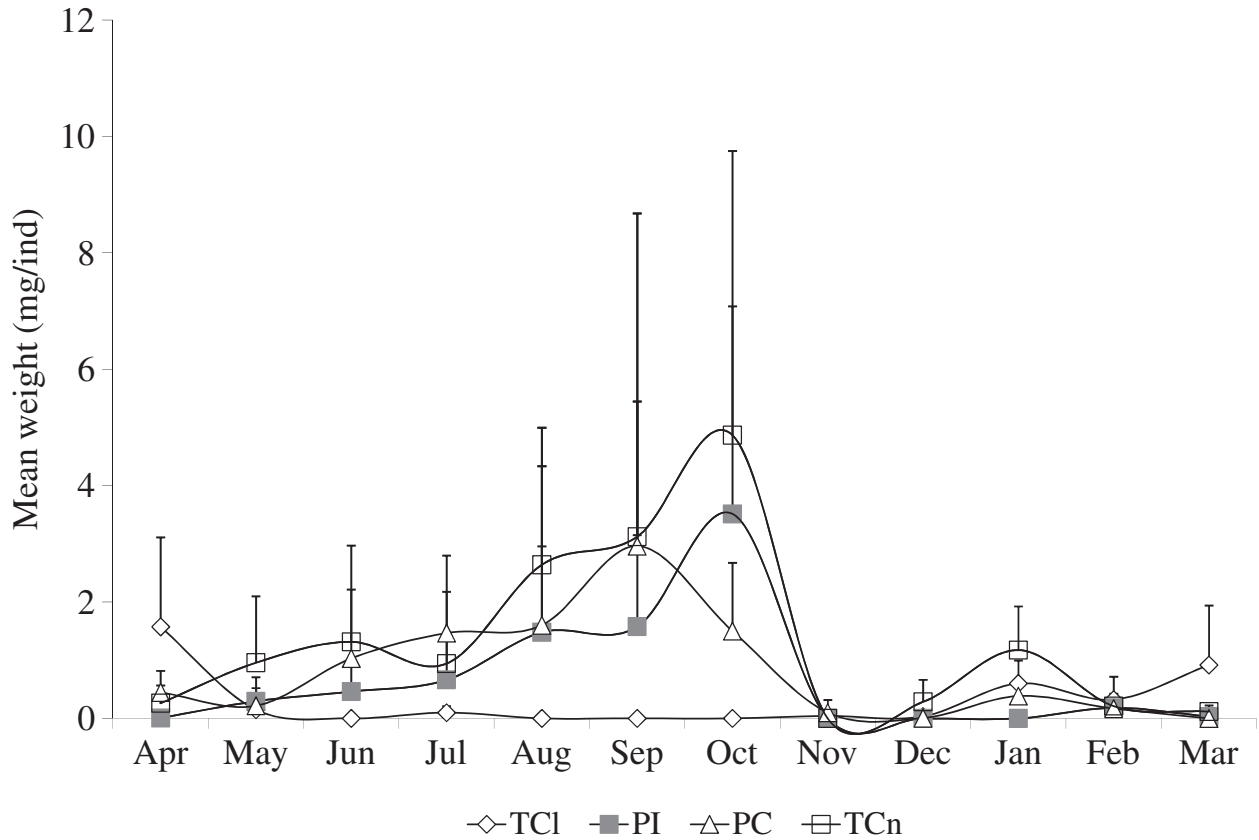


Figure 3. Monthly mean ( $\pm$  SD) weight of *Campsurus violaceus* nymphs estimated in four lakes of the Paraná River floodplain, Argentina. TCl = temporarily and indirectly connected lake; PI = isolated lake; PC = permanently connected lake; TCn = temporarily and directly connected lake.

Table 2. *Campsurus violaceus* life history traits, secondary production, and turnover ratios for four lakes of the Paraná River floodplain, Argentina.

	PC	TCn	TCl	PI
Density (ind $m^{-2}$ ) $\bar{x} \pm SD$	53 $\pm$ 41	80 $\pm$ 70	34 $\pm$ 58	82 $\pm$ 113
Standing stock biomass (mg $m^{-2}$ ) $\bar{x} \pm SD$	31 $\pm$ 31	67 $\pm$ 60	15 $\pm$ 27	57 $\pm$ 71
Mean weight of nymphs $\bar{W}$ (mg/ind) $\bar{x} \pm SD$	0.93 $\pm$ 0.88	1.33 $\pm$ 1.49	0.31 $\pm$ 0.49	0.69 $\pm$ 1.05
Frequency of occurrence (%)	100	92	67	83
Number of generations	2	2	1	2
Generation time (days)	145	145	181	135
Secondary production $P$ (mg $m^{-2}$ $yr^{-1}$ )	1484	1891	216	1757
Turnover $P/\bar{B}$	14	8	4	7

TCl = temporarily and indirectly connected lake; PI = isolated lake; PC = permanently connected lake; TCn = temporarily and directly connected lake.

### Patterns of abundance of *C. violaceus* and environmental variables

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The density, standing stock biomass and mean weight of nymphs had significant differences among lakes and in relation to seasonality during the studied period (two-way crossed ANOSIM,  $p = 0.001$ ). TCl had the highest dissimilarity from the other lakes in relation to density and biomass and from PI in relation to the mean weight of nymphs (two way crossed

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SIMPER) (Table 3). TCn and PC had the highest similarity in relation to all the analyzed attributes of the species. The environmental variables that best explained the patterns of density and biomass of the species in the benthos of lakes were the temperature, water transparency and conductivity, and the percentage of sand of bottom sediments (BEST routine,  $p = 0.002$ ). Furthermore, the pattern of biomass was also explained by the content of detritus of bottom

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Table 3. Dissimilarity (in %) in density, biomass, and mean weight of *Campsurus violaceus* nymphs between pairs of lakes in the Paraná River floodplain, Argentina, during the studied period (SIMPER routine, Bray–Curtis dissimilarity,  $\log x + 1$  transformed data).

	PI	PC	TCn
Density (ind m <sup>-2</sup> )			
TCI	81	81	72
PI		66	65
PC			60
Biomass (mg m <sup>-2</sup> )			
TCI	93	91	85
PI		90	90
PC			77
Mean weight of nymphs $\bar{W}$ (mg ind <sup>-1</sup> )			
TCI	92	89	78
PI		84	88
PC			77

TCI = temporarily and indirectly connected lake; PI = isolated lake; PC = permanently connected lake; TCn = temporarily and directly connected lake.

**Discussion**

**Temperature and life cycle of *C. violaceus*** 305

In the present study, variations in the abundance and mean weight of *C. violaceus* were correlated to changes in the temperature of water. According to Benke (1984), food and temperature are the main factors affecting the life history of aquatic insects. Moreover, several authors showed that the natural variation in temperature is more important in controlling mayfly growth rates than food (Brittain 1982; Clifford 1982; Benke et al. 1992). The steep increment of the mean weight of nymphs between August and October and during January, mainly for TCn, PC and PI, indicates the importance of food quantity and quality for growth of last larval stages. In contrast, reductions of density and biomass of nymphs during winter (mainly between June and July) might be related not only to natural enemies but also to negative effects of temperature on resources. In addition, the absence or lowest density of nymphs obtained during October–November was related to a mass emergence of the species (Zilli pers. obs.). Besides, the reduction in the abundance of nymphs during this period could be strengthened by migration in response to flooding, as was observed in upper reaches of the Paraná River for the species (Melo et al. 1993). 310 315 320 325

The absence of significant differences among lakes for the frequency distribution of nymphs in the different size classes indicates that the species is able to complete its whole cycle in each of our study habitats. However, the significant dissimilarities in density, biomass and mean weight of nymphs show that life history traits of *C. violaceus* are shaped by the degree of connectivity of floodplain lakes. 330 335

**Connectivity degree, abundance patterns and secondary production of *C. violaceus***

According to the results obtained from the similarity analysis, the density, biomass and mean weight of *C. violaceus* were significantly different among lakes. Therefore, secondary production and turnover ratio also differed within the floodplain. The degree of connectivity of lakes was the main reason for the differences found among populations, as it influenced local factors finally determining regional dissimilarities for the species. Besides, the alignment of environmental conditions and habitat requirements of the species determined a heterogeneous distribution of its properties within the floodplain. 340 345 350

*Campsurus violaceus* nymphs require soft silt or clay substrates, as they inhabit the galleries they dig. Therefore, nymphs were more abundant in connected habitats located next to the main channel 355

sediments (BEST routine,  $p = 0.002$ ). The pattern obtained for the mean weight of the species was explained by water temperature, conductivity and percentage of sand and of detritus of bottom sediments (BEST routine,  $p = 0.001$ ). 280

**Size classes and life cycle of *C. violaceus***

The frequency distribution of nymphs in the different size classes did not show significant differences among lakes (Kruskal–Wallis test). The nymphs had peaks of abundance that coincided with the presence of most of the size classes (Figure 4a–d). Thus, nymphs of different classes showed a relatively high coexistence. Nymphs from the largest class were only collected in TCn in different sampling dates (Figure 4c). The frequency of occurrence of the different classes, together with the abundance and the weight of nymphs, indicated the development of two generations, with a duration from 135 to 181 days each, with an average of 152 days for the floodplain lakes. 285 290 295

**Secondary production**

The maximum annual secondary production was estimated for TCn, with a similar value in PI (Table 2). A relatively high secondary production and the highest annual turnover ratio were estimated for PC. In TCI, the annual secondary production was almost eight times lower than in the other lakes. It also had the minimum turnover ratio. 300

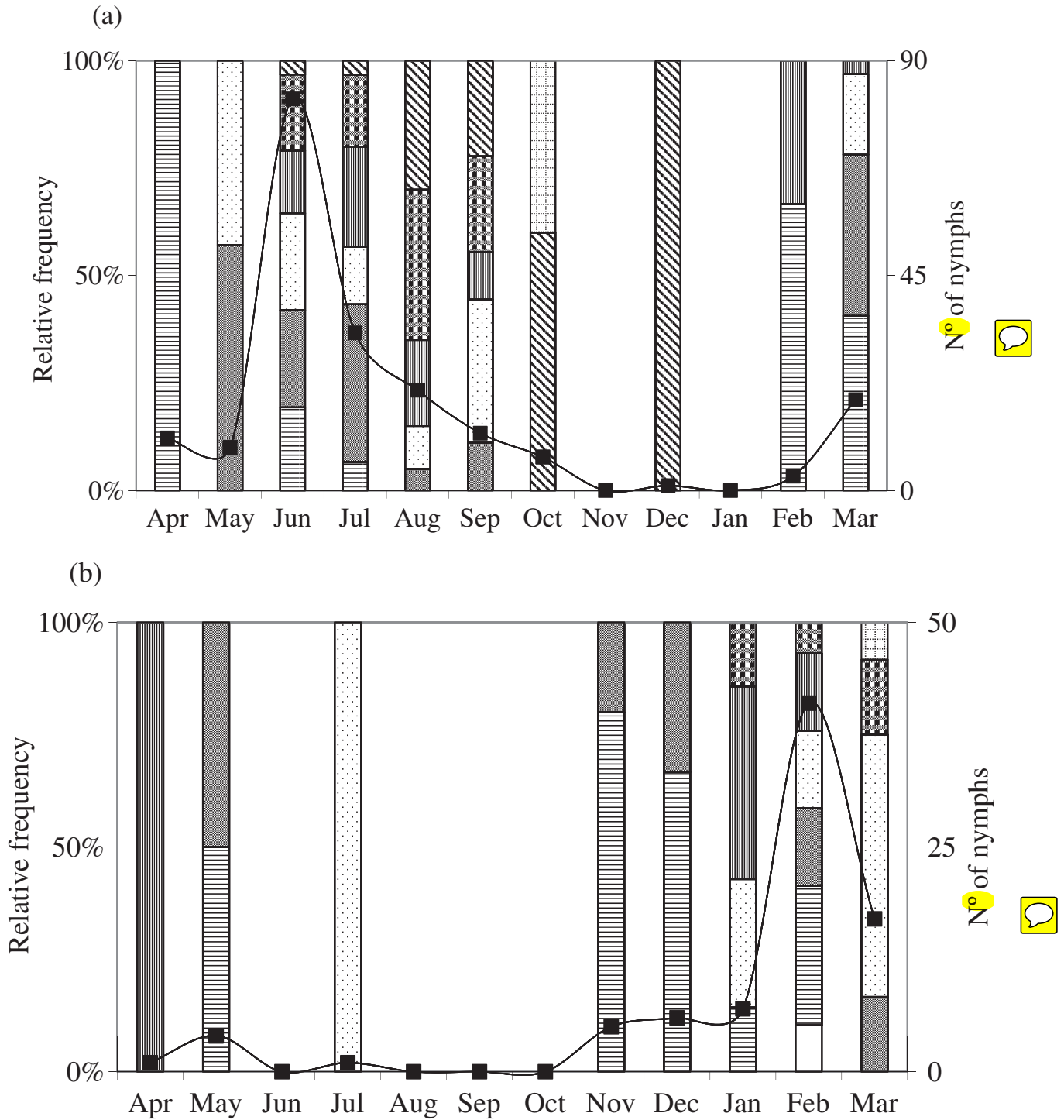


Figure 4. Relative frequency of nymphs of different size classes and abundance of *Campsurus violaceus* in four lakes of the Paraná River floodplain, Argentina. (a) Isolated lake (PI); temporarily connected lakes (b) TCI and (c) TCn; (d) permanently connected lake (PC). Size class (defined by interocular distance in mm): I = 0.0–0.2; II = 0.2–0.4; III = 0.4–0.6; IV = 0.6–0.8; V = 0.8–1.1; VI = 1.1–1.3; VII = 1.3–1.5; VIII = 1.5–1.7; IX = 1.7–1.9.

(TCn and PC), which receive larger quantities of suspended solids coming from the river (Amsler et al. 2007). In addition, for flooding areas and white-water lakes of the Amazon River basin, elevated values of

annual production of *Campsurus* spp. were related to high sedimentation rates of fine particles (Fittkau et al. 1975; Irmiler 1975; Nolte 1987; Fonseca Leal and De Assis Esteves 2000). On the one hand, TCI had the

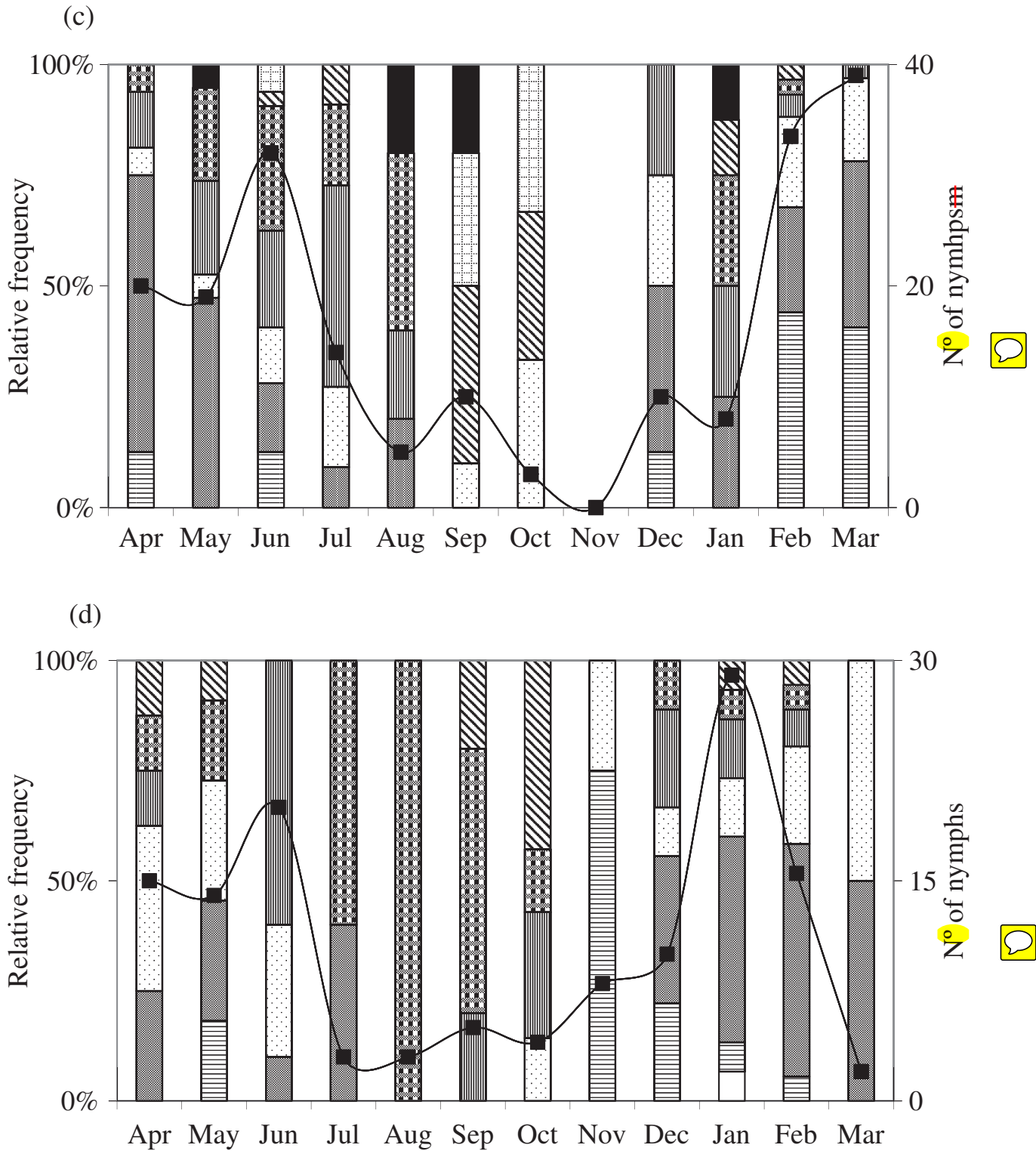


Figure 4. (Continued).

365 lowest abundance and secondary production of *C. violaceus* due to the predominance of sandy habitats. On the other hand, PC and TCn had higher density and biomass of nymphs that were correlated to silt

and clay sediments. Therefore, the different connectivity and location of TCn, PC, and TCl relative to the main channel have determined abundance patterns and secondary production of the species. 370

375 Additionally, the pattern of abundance of *C. violaceus* was determined not only by the type of substrate but also by the content of detritus in bottom  
 AQ2 sediments. Indeed, in all the aquatic environments, detritus represents a diverse food source for macroinvertebrates (Polis and Strong 1996). Nevertheless, the density and biomass of *Campsurus* in isolated lakes located far away from the main channel of the Paraná River was inversely correlated to detritus quantity and to low oxygen concentrations at the bottom (Marchese et al. 2002, Ezcurra de Drago et al. 2007). PI had the highest cover of macrophytes due its isolation and the absence of drift and thus had a constant  
 380 input of autochthonous detritus resulting in the highest CPOM proportions recorded. However, it also had high oxygen concentrations caused by wind and seepage infiltration from the river as PI is located next to the main channel (Zilli 2010). Additionally, high  
 385 abundance, mean weight, and secondary production of *C. violaceus* were found at PI. Oxygen depletion is one of the limiting factors for mayfly development. A steep reduction in the abundance of mayflies should be related to detritus only when it accumulates at the bottom of lakes and produces depletion of oxygen and anoxia, as was found for the benthic community in a lake with prolonged very low connectivity (Ezcurra de Drago et al. 2007). Conversely, the high availability of sites for oviposition (on floating macrophytes), the hydrological stability (reflected by the highest transparency), the availability of abundant food and the predominance of clay sediments (Zilli 2010) positively influenced life history attributes and development of the species in PI.

390 Patterns of abundance and secondary production of *C. violaceus* in lakes of the Middle Paraná River floodplain were related to resources coming from autochthonous as well as from allochthonous sources. Moreover, the location of lakes within the floodplain determined the quantity and quality of allochthonous inputs that they received, with a higher proportion of phosphorous supplied to the habitats located next to the main stem (Poi de Neiff et al. 1994). Therefore, the higher abundance and estimated mean weight of nymphs, mainly in TCn but also in PC, might be related to direct inputs of high quality river-borne detritus (reflected by the high proportion of UFPOM at bottom sediments). Additionally, the annual secondary production estimated for PI, TCn and PC fell within the upper limit of the range expected for mayflies (Waters 1977; Benke and Jacobi 1994).

405 Secondary production, generation time, turnover ratio and other life history traits of *C. violaceus* obtained in the present research were similar to those obtained for other species of the genus in the Neotropics (Irmeler 1975; Pereira and Da Silva 1991;

Melo et al. 1993; Takeda and Gryzbkowska 1997; Fonseca Leal and De Assis Esteves 2000). Despite the fact that similarities were obtained among mayfly traits at different latitudes of the Neotropical region, the dissimilarities found in the present research at a lower spatial scale among lakes exhibit the importance of local variables for resource acquisition and productivity of the species. Moreover, according to the obtained results the species is bivoltine with one generation from June to September–October and another from December to May. However, only one cohort of nymphs was able to complete its life cycle and become adult in TCl. Factors affecting life cycle in TCl, such as unfavorable substrate type, high conductivity and low availability of food sources for nymphs are related to its lower degree of connectivity, but also to a higher predation pressure on the population (Zilli 2010). Hence, significant differences among lakes in density, biomass, frequency of occurrence and number of generations directly affected life cycle, number of generations and secondary production of *C. violaceus*.

Differences among lakes in the development and life history traits of *C. violaceus* were related to their degree of connectivity and position to the main channel. Additionally, biotic interactions not measured here act together with environmental conditions to establish dissimilarities in the characteristics of *C. violaceus* populations at the landscape level. Hence, as mayflies serve as food for aquatic and terrestrial animals, lateral connectivity finally affects river-floodplain system productivity in an integrated perspective. Thus, the present results point out the importance of preserving landscape integrity for the species and for the entire biota.

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