Ecological Responses to Different Degrees of Hydrologic Connectivity: Assessing Patterns in the Bionomy of Benthic Chironomids in a Large River-Floodplain System

Florencia L. Zilli & Analía C. Paggi

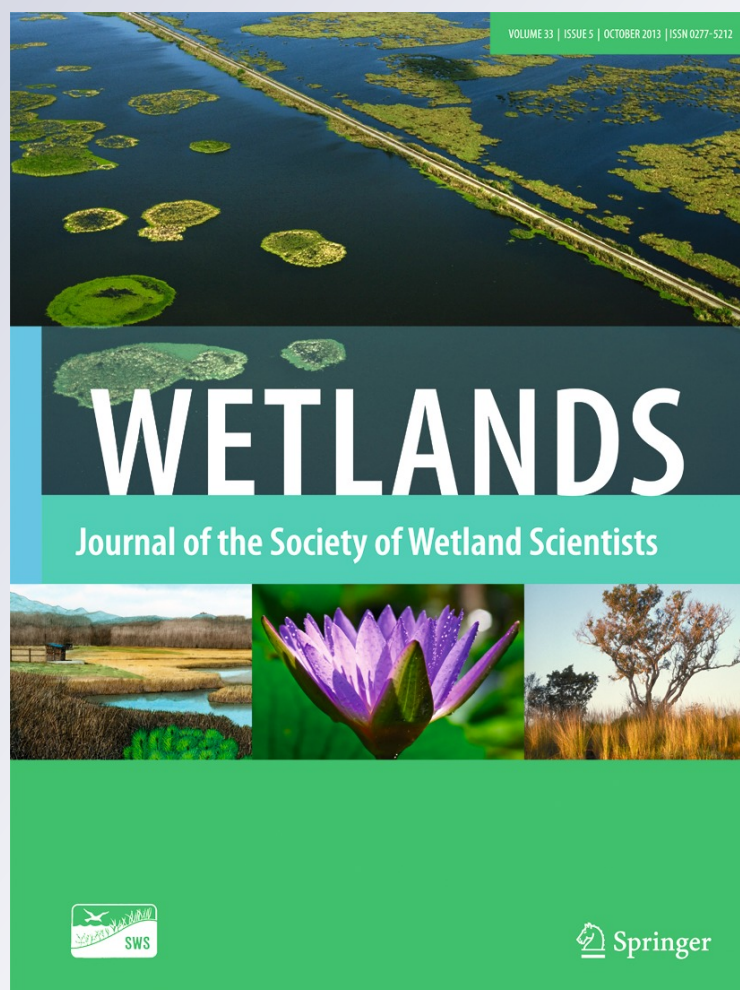## WETLANDS

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Ecological Responses to Different Degrees of Hydrologic Connectivity: Assessing Patterns in the Bionomy of Benthic Chironomids in a Large River-Floodplain System

Florencia L. Zilli · Analía C. Paggi

Abstract Floodplain wetlands of the Middle Paraná River, Argentina, are regulated by their hydrologic connectivity to the main channel as well as by their position within the river network. The Chironomids are the most abundant insects that inhabit the benthos of the Paraná River floodplain habitats. In order to address whether wetlands with different degrees of connectivity (disconnected, temporarily, and permanently connected) exhibit different abundance patterns and secondary production of benthic chironomids, samples were collected during a year comprising high and low water phases. The disconnected wetland exhibited the highest abundance and secondary production of chironomids. Both attributes were positively correlated to the degree of connectivity for most of the predators among the connected wetlands. Differences in assemblages' composition and secondary production were found to be in relation to the degree of connectivity, the cover of macrophytes, the detritus at the bottom, the transparency of water, the proportion of clay in bottom sediments and the location of wetlands within the floodplain. The interaction between local environmental factors mediated by lateral connectivity and regional dynamics of metapopulations established diverse patterns in the metrics of chironomids along the Paraná River floodplain wetlands. Thus, various degrees of hydrologic connectivity of wetlands should be preserved to maintain a high productivity of different chironomids in the floodplain.

Introduction

Lateral water flux in river-floodplain systems represents an important ecosystem linkage and leads to exchanges of biota and nutrients, thus shaping the connectivity between aquatic systems (Neiff 1990; Ward et al. 2002). It has been shown that the existence of seasonal variations of hydrologic connectivity exert positive effects on aquatic biodiversity (Tockner et al. 1999; Amoros and Bornette 2002). Consequently, human alterations of river-floodplain connectivity might have adverse ecologic impacts arising from flow modifications (Hilty et al. 2006; Sims et al. 2012).

An effective way of assessing the results of flow alterations on aquatic insects is using a bioenergetics approach that focuses on secondary production, as well as incorporates aspects of density, biomass, individual growth rate, and survival and generation time (Benke et al. 1984; Benke 1998). Additionally, the incorporation of a trophic perspective in bioassessments has proved to be useful for monitoring hydrologic conditions in floodplain water bodies (Dolédec and Statzner 2010).

Chironomidae (Diptera), or non-biting midges, are the most diverse and abundant dipterans residing the benthos of the Middle Paraná River floodplain habitats (e.g. Ezcurra de Drago et al. 2007; Zilli and Marchese 2011). In contrast to other common benthic groups (such as oligochaetes, mollusks, and hirudineans), chironomid dispersal can occur by aquatic and/or by aerial pathways. Thus midges can transfer matter and energy from basal resources to higher trophic levels in aquatic and aquatic–terrestrial food webs and exhibit patterns of distribution that integrate aerial and aquatic dynamics allowing comparisons in relation to metapopulation dynamics even for hydrologicaly disconnected wetlands.

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An integrated view of ecosystem functioning is obtained only when biotic data are coupled with environmental information (Benke et al. 1984). Therefore, information on the bionomy (i.e. the relationship between organisms and their environment) and responses of benthos abundance and secondary production to river connectivity is essential to understand river-floodplain system dynamics, energetic fluxes, and mechanisms of transfer of resources. Moreover, it is essential to understand the relationships among hydrology, habitat flooding, and ecological processes in order to optimize the restoration efforts (Frazier et al. 2012).

Benthos abundance and richness of other biotic communities have been shown to respond positively to increased lateral hydrologic connectivity (Amoros and Bornette 2002; Ward et al. 2002; Whiles and Goldowitz 2005; Gallardo et al. 2008). In the Paraná River, the distribution of benthos reflects the environmental patchiness that is related to the degree of connectivity of aquatic habitats, and physical and chemical environmental variables (Ezcurra de Drago et al. 2007). Therefore, benthic chironomids as well as other benthic taxa, were found to have increasing density and richness from low connected to highly connected floodplain habitats in relation to bottom environmental conditions (Drago et al. 2003). In spite of the importance of chironomids productivity in the floodplain the relationship between the degree to which the levels of connectivity influence the secondary production of chironomids in the Parana River is still unknown. Thus, the purpose of our study was twofold: (1) to describe the overall metrics of benthic chironomid taxa and trophic guilds, and (2) to explore the patterns of density, biomass, and the production of chironomids in floodplain wetlands in relation to varying lateral degrees of connectivity. Our hypothesis was that metrics of benthic chironomid assemblages are directly related to lateral connectivity, and we predicted that chironomids in low connected wetlands exhibit lower abundance and secondary production; whereas those in highly connected wetlands have higher abundance and secondary production.

Methods

Study Area

Field investigations were conducted monthly between April 2005 and March 2006, comprising low and high water phases in four wetlands located on two different islands in the Middle Paraná River floodplain at the cross-section of Santa Fe city and Paraná city, Argentina (31° 40′ S - 31° 43′ S and 60° 33′ W - 60° 39′ W) (Fig. 1). The sites where the study was carried out, represented the widest range of hydrologic connectivity within the Paraná River floodplain

system from disconnected to permanently connected. To classify wetlands according to their hydrologic connectivity, we considered their duration of connection and distance to the main channel of the river. Sites ranged from lacustrine wetlands disconnected from the surface water (PI, degree of connectivity = 1) to wetlands with an intermediate temporary or a permanent surface water connection to the main channel (TCl, TCn, and PC, with a degree of connectivity from 2 to 4, respectively). Locations and limnological variables of study wetlands are depicted in Fig. 1.

Habitat Characteristics

Physicochemical characteristics including water depth (sounding lead), transparency (Secchi disk), pH (colorimetric technique, Hellige pH-meter), conductivity (Beckman conductivity meter), and water temperature (standard thermometer) were measured on each sampling date. In addition, percentage of macrophyte cover, proportions of total benthic organic matter (TBPOM, ≥ 63 μm) ultrafine particulate organic matter (UFPOM = 63–250 μm), fine particulate organic matter (FPOM = 250–1,000 μm) and coarse particulate organic matter (CPOM $\geq 1,000$ μm), and granulometry of bottom sediments (sand, silt, and clay, according to Wentworth 1932) were determined. In addition, dissolved oxygen concentrations at the bottom water of wetlands (Winkler method) as well as concentrations of nitrites, nitrates, ammonium, and total phosphorous (APHA Standard Methods) were determined. The general characteristics of environmental parameters are presented in Fig. 1, whereas detailed information on habitats can be found in Zilli and Marchese (2011).

Field Collection and Measurements of Larvae

To analyze the chironomid density, biomass, annual secondary production (P), and the turnover ratio (P/B), quantitative samples of benthos were collected monthly with an Ekman grab (225 cm^2) in each wetland. On each of the 12 sampling dates, 36 benthic samples were collected (n =9 in each wetland; total n=432). The samples were passed through a 200 μm sieve and fixed with formalin (5 %) in the field. All benthic larvae were sorted manually under a stereoscopic microscope and stored in 70 % ethanol. Larvae were identified and assigned to trophic guilds (predators or detritivores) according to gut analyses that had been previously performed on genera from the same wetlands (Zilli 2010). The ten most abundant and frequently collected chironomid genera of chironomids belonging to 2 subfamilies were considered in all the analyses to compare among wetland connectivity categories.

Each larva was mounted on slides and measured under a microscope that was fitted with a micrometric scale. The

Fig. 1 Study area.
PI = disconnected wetland;
TCl = temporarily and
indirectly connected wetland;
TCn = temporarily and directly
connected wetland;
PC = permanently connected
wetland
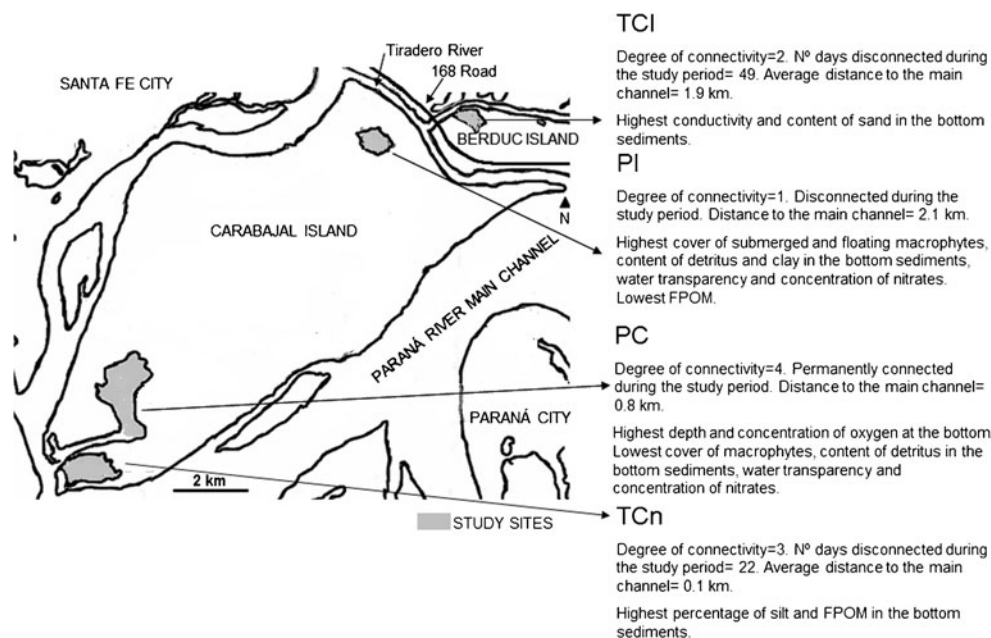
width of the head capsule of each larva was measured across the greatest width perpendicular to the major axis of the body. These measurements were used to calculate the mean head capsule width of each instar and to group individuals into size classes. In addition, the larval body length was measured from the anterior edge of the head to the posterior edge of the last abdominal segment. Body length measurements of Tanypodinae and Chironominae were used to establish length–weight relationships to calculate mean individual dry weight in each size class, biomass, secondary production, and turnover ratio. Mass (dry weight) of different larvae was measured after oven drying at 60 °C for 48 h. to a constant weight.

Annual secondary production ($mg/m^2/yr$) and turnover ratios of genera were estimated for each wetland using the size-frequency method (Hynes and Coleman 1968; Benke 1979).

Data Analyses

To assess overall differences among wetlands, benthic chironomid data (by taxa and grouped into trophic guilds) were subjected to a non-parametric analysis of variance (Kruskal–Wallis test, $\alpha \leq 0.05$) and a post-hoc Wilcoxon comparisons test ($\alpha \leq 0.05$). To further identify chironomid patterns trophic guilds, we used non-metric multidimensional scaling (NMDS) with square-root transformed $\left(\sqrt{x+1}\right)$ data and a Bray-Curtis distance matrix.

The environmental variables responsible for separating wetlands were evaluated by Principal Components Analysis (PCA) with standardized data. Environmental collinear variables (e. g. proportion of silt and UFPOM in bottom sediments) were not considered in the analyses. Additionally, in order to assess differences among sampling dates and water level phases, the environmental variables were subjected to a non-parametric analysis of variance (Kruskal–Wallis test, $\alpha \leq 0.05$) and a post-hoc Wilcoxon comparisons test ($\alpha \leq 0.05$). To identify the primary environmental gradients affecting chironomid patterns among wetlands, we used Pearson-product moment correlations ($\alpha \leq 0.05$) between sample scores of both axes from environment Principal Components Analysis (PCA) and biotic ordination from NMDS. Furthermore, the dissimilarity obtained in the patterns of composition of taxa among wetlands was analyzed using an Analysis of Similarity (ANOSIM) with $\log_{10} x + 1$ transformed data in a Bray Curtis matrix. The analyses were performed using PRIMER-E vs. 6.1.11 (2006) and Infostat vs. 2012 (Di Rienzo et al. 2012) software.

Results

Bionomy and Patterns of Abundance of Benthic Chironomids

During the study period, benthic chironomids biomass averaged 6.26 ± 2.51 (SE) mg/m^2, and density averaged 98.13 ± 31.27 ind/m^2 within the floodplain. The overall density and biomass of detritivores showed significant differences among sampling dates ($H=29.48$, $H=25.59$, d.f.$=11$). Biomass of detritivores also exhibited significant differences between autumn-spring (April and September to November 2005) and winter-summer (June to August 2005 and December 2005 to February 2006) ($H=8.54$, d.f.$=3$, Fig. 2).

The highest density and biomass of chironomids were obtained from detritivores in PI and from predators in PC (hydrologic connectivity = 1 and 4 respectively, Fig. 3).
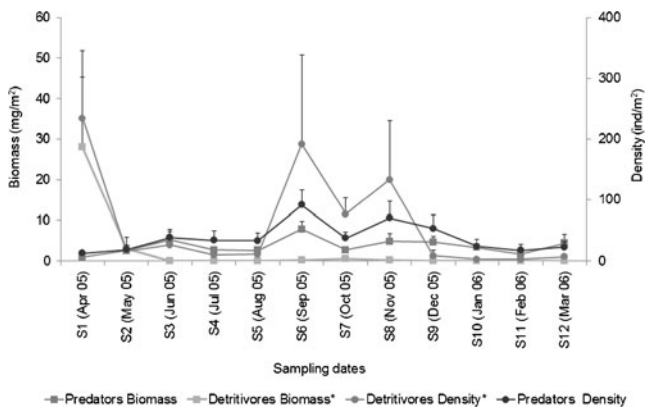
Fig. 2 Monthly mean (+ SE) density (ind/m²) and biomass (mg/m²) of predators and detritivores chironomids in wetlands of the Paraná River floodplain, Argentina. * indicates significant differences among sampling dates and seasons (Kruskal-Wallis test, $p<0.05$)

Significant differences were found among wetlands only for the overall density and biomass of predators ($H=18.64$, $H=9.14$, d.f.=3). This was mainly related to the significantly

higher density and biomass of *Coelotanypus* in PI and PC, rather than in TCl and TCn ($H=13.65$ and $H=9.31$ respectively, d.f.=3, Fig. 3a and b). The density of most predatory taxa increased with the connectivity from TCl to TCn and PC (Fig. 3a and b).

In spite of not having found significant differences in overall density of detritivores ($p>0.05$), significant differences among wetlands were found, however, when analyses were performed for each genus. *Chironomus* density was significantly higher in TCl and PI than in TCn and PC ($H=6.28$, d.f.=3). Larvae of *Saetheria* were only found in the connected wetlands and showed a gradient with increasing density and biomass from TCl to PC with a significantly higher density and biomass in the latter ($H=14.58$, $H=18.30$, d.f.=3, Fig. 3c and d).

The variables that contributed most in separating wetlands in PCA axis 1 were cover of macrophytes, BPOM (TBPOM, FPOM, CPOM), water transparency and the proportion of clay in bottom sediments (44 % of variance explained by axes 1 and 2, Fig. 4a). Only the
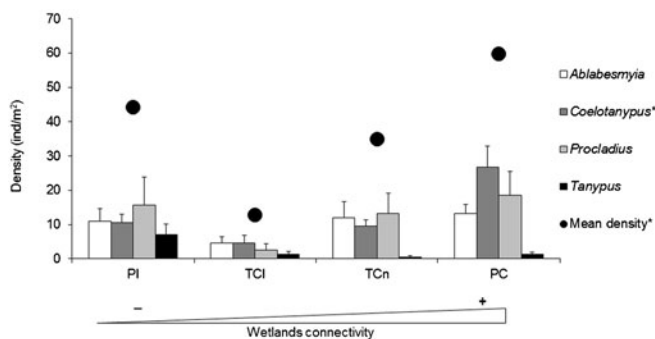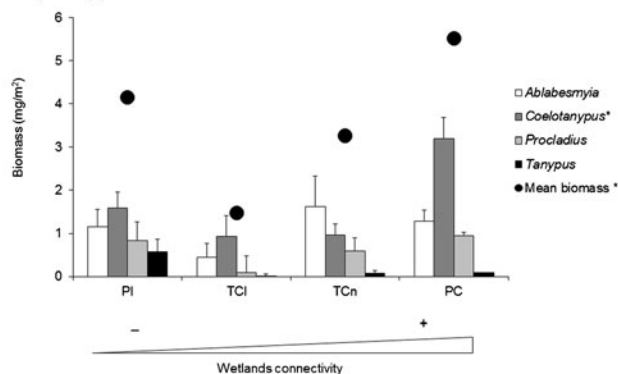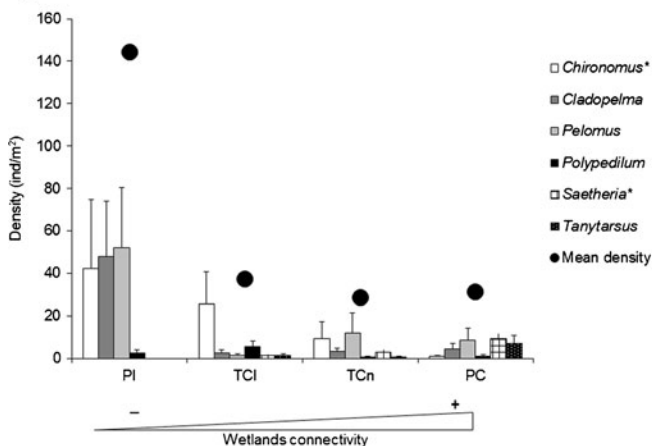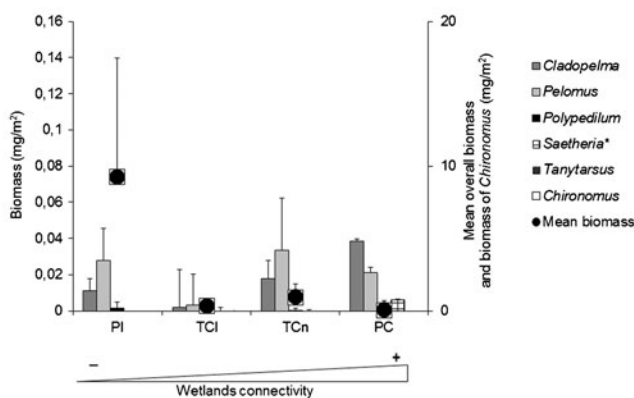
Fig. 3 Mean (+ SE) density (ind/m²) (**a**) and biomass (mg/m²) (**b**) of Tanypodinae predators and mean (+ SE) density (ind/m²) (**c**) and biomass (mg/m²) (**d**) of Chironominae detritivores in wetlands of the Paraná River floodplain, Argentina. PI = disconnected wetland; TCl =

temporarily and indirectly connected wetland; TCn = temporarily and directly connected wetland; PC = permanently connected wetland. * indicates significant differences (Kruskal-Wallis test, $p<0.05$)
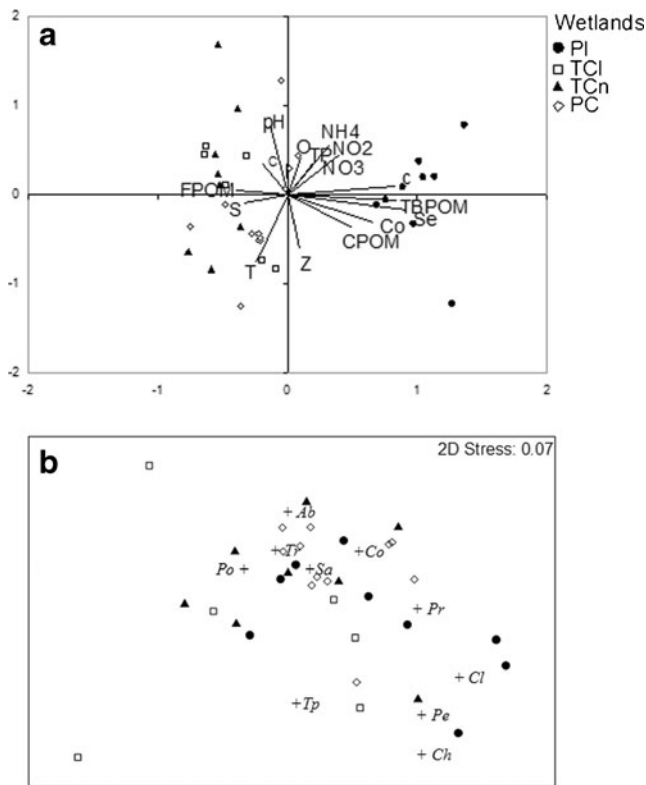
Fig. 4 **a)** Biplot of Principal Component Analysis (PCA) performed with environmental variable data and **b)** Biplot of Non-Metric Multidimensional Scaling (NMDS) performed with density data of macroinvertebrates from the Middle Paraná River floodplain wetlands (Bray Curtis matrix from square-root transformed data). Centroids of taxa are showed. Ab = Ablabesmyia; Co = Coelotanypus; Pr = Procladius; Tp = Tanypus; Ch = Chironomus; Cl = Cladopelma; Pe = Pelomus; Po = Polypedilum; Sa = Saetheria. PI = disconnected wetland; TCl = temporarily and indirectly connected wetland; TCn = temporarily and directly connected wetland; PC = permanently connected wetland

ordination obtained for trophic guilds densities was significantly correlated to the ordination obtained for the environmental characteristics and thus for connectivity degree (PCA axis 1 and NMDS axis 1, $R=-0.5$, $p \leq 0.05$, Fig. 4). *Chironomus*, *Cladopelma*, *Pelomus*, *Coelotanypus* and *Procladius* were the genera that contributed most in the ordination of floodplain wetlands (Fig. 4b). The highest dissimilarities in density of genera were between TCl and the other wetlands, whereas the highest similarity was found between TCn and PC (Fig. 5).

Annual Secondary Production (P) and Turnover Ratio (P/B)

Most of the taxa had several generations per year in the floodplain wetlands (Table 1), with an average of 5 for detritivores and 6 for predators. Overall annual secondary production for both trophic guilds was higher in PI than in the other wetlands, and this was mainly related to the higher productivity of *Coelotanypus* and *Chironomus* (Fig. 6, Table 1). Furthermore, a pattern of increased secondary
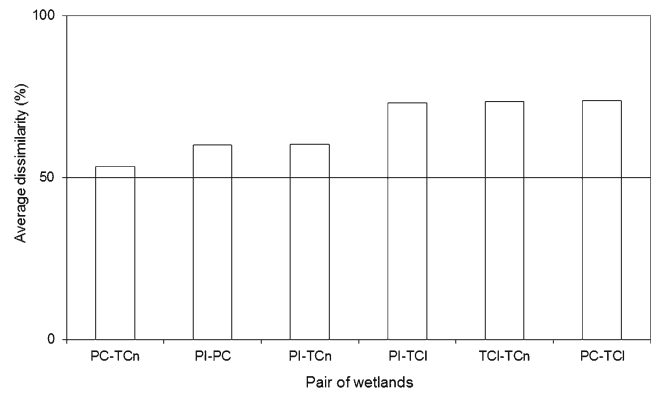

Fig. 5 Average dissimilarity in density (ANOSIM, Bray–Curtis index) between pairs of wetlands of the Paraná River floodplain, Argentina. PI = disconnected wetland; TCl = temporarily and indirectly connected wetland; TCn = temporarily and directly connected wetland; PC = permanently connected wetland

production was observed among the connected wetlands from TCl to PC. This was related primarily to the production of predators, principally of *Coelotanypus*. Among the detritivores, *Chironomus* had a higher production in TCl and TCn and *Cladopelma* in PC.

The highest turnover ratio of predators was calculated in PI (Fig. 6). *Coelotanypus* had the highest turnover ratio in all the wetlands. Only in TCl, *Coelotanypus* had similar P/B ratios to *Tanypus* (Table 1). The highest turnover of detritivores was calculated in PC, principally related to *Saetheria* and *Tanytarsus* (Fig. 6, Table 1). In the other wetlands, the highest turnover ratios were calculated for *Chironomus* and *Pelomus* in PI, *Chironomus* and *Polypedilum* in TCl, and *Pelomus* and *Saetheria* in TCn.

Discussion

In relation to our initial hypothesis, metrics of benthic chironomids were directly related to lateral connectivity, as were previously indicated by other studies in the Paraná and Paraguay rivers (Drago et al. 2003; Ezcurra de Drago et al. 2004, 2007) as well as in other rivers (Whiles and Goldowitz 2005; Gallardo et al. 2008; Pan et al. 2011). Though, contrary to our initial prediction, the highest abundance and secondary production of chironomids occurred in the disconnected wetland (PI). Among connected wetlands, however, abundance and secondary production increased with hydrologic connectivity (from TCl to TCn and PC) for most of the predatory genera, but not for detritivores. Previous studies on the Middle Paraná River found that disconnected or low connected habitats had depauperate benthos due to natural eutrophication, accumulation of large amount of detritus and hypoxia at the bottom resulting from a lower lateral connectivity (Marchese and Ezcurra de Drago 2006). However, such habitats were located far from the main

Table 1 Annual secondary production (P, mg/m²/yr), turnover ratio (P/B), and number of generations (N° Gen.) of chironomids in lakes with different degrees of connectivity in the Paraná River floodplain, Argentina. x indicates that P and P/B were not calculated due to the absence or lack of larvae

| Trophic guild	Taxa	PI			TCl			TCn			PC		
		N° Gen.	P	P/B	N° Gen.	P	P/B	N° Gen.	P	P/B	N° Gen.	P	P/B
Predators	*Ablabesmyia*	4	4.2	3.6	6	1.9	4.3	9	0.8	0.5	6	7.8	6.1
	Coelotanypus	14	52.4	32.9	4	10.1	11.8	6	9.6	10.0	12	34.5	10.8
	Procladius	3	4.8	5.8	x	x	x	x	x	x	4	6.6	7.1
	Tanypus	5	0.1	0.2	1	0.04	11.5	x	x	x	2	0.1	1.1
Detritivores	*Chironomus*	5	94.9	10.3	4	3.9	11.4	2	2.4	2.6	x	x	x
	Cladopelma	4	0.002	0.2	3	0.3	3.4	4	0.002	2.5	9	0.7	18.0
	Pelomus	6	0.3	10.0	x	x	x	5	0.2	4.4	3	0.1	5.6
	Polypedilum	3	0.001	0.6	7	0.037	12.6	x	x	x	x	x	x
	Saetheria	x	x	x	x	x	x	3	0.01	3.7	10	0.01	26.4
	Tanytarsus	x	x	x	x	x	x	x	x	x	6	0.01	26.4

channel, whereas wetlands in the present study are located near the main channel, and are more frequently affected by flood pulses and water seepage from the river (Drago et al. 2003). Thus, despite the fact that PI has been mostly surface disconnected since the late 1990s, its proximity to the main channel probably established frequent seepage connections that positively influenced the environmental conditions (Zilli 2010) resulting in an abundant and rich benthos.

In our study, environmental variables such as percentage of macrophyte cover, BPOM, percentage of clay in bottom sediments, and water transparency differed significantly between connected and disconnected wetlands and were important in determining chironomid density in the floodplain, as demonstrated in the correlation analysis between PCA and NMDS ordinations. These variables were not significantly different among seasons during the study period and consequently the significant seasonal differences in trophic guilds metrics were mainly related to life cycle and phenology of chironomid populations.

The higher density, biomass, and secondary production of detritivores and some predators in PI were directly related to the higher TBPOM and to floating and submerged macrophyte cover. In addition, characteristics of the substrate such as proportion of clay in bottom sediments and habitat hydraulic stability (indirectly evidenced by the higher transparency of water) played a key role in determine the trend of distribution, density and productivity of chironomids which was found for many insect taxa (Danks 2006). Pan et al. (2011) also reported high density, biomass, and production for benthic collector-gatherers, mainly oligochaetes and chironomids (Chironominae), with low lateral connectivity in floodplain-rivers and associated these trends with a reduction of organic-rich sediment as connectivity increases. Additionally, Walthers and Whiles (2011) reported a positive relation between hydrological connectivity with biomass and production of

Fig. 6 Mean secondary production (P) and turnover ratios (P/B) of Tanypodinae predators and Chironominae detritivores in wetlands of the Paraná River floodplain, Argentina. Overall P and P/B are shown. PI = disconnected wetland; TCl = temporarily and indirectly connected wetland; TCn = temporarily and directly connected wetland; PC = permanently connected wetland
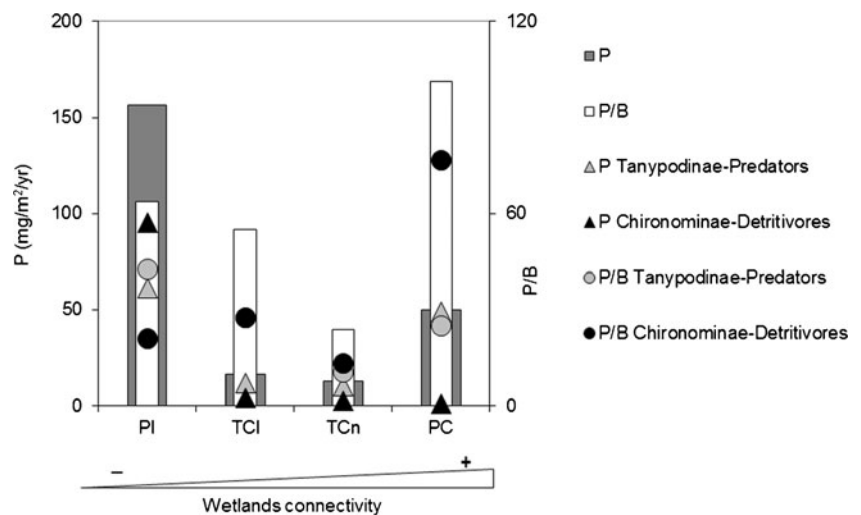
macroinvertebrates and postulated that the availability of benthic organic matter is a major driver of macroinvertebrates production at a large geographic scale. Favorable habitat conditions such as abundant emergent and floating macrophytes enhanced the oviposition and emergence of insects and, ultimately, the secondary production of most chironomids (Mackey 1977; Menzie 1981; Boix et al. 2011). Lerner et al. (2008) concluded that percentage of polarized reflected light in aquatic habitats is the cue by which chironomid females choose their oviposition sites and it was related to the amount of food available for detritivorous larvae. Moreover, predators such as the abundant *Coelotanypus* and *Procladius* feed on detritivorous oligochaetes that are dominant in the benthos of PI (Zilli 2010). Actually, bottom-up controls through the detritus-based food webs in our study wetlands might have directly or indirectly influenced the development and survival of benthic populations within the floodplain.

Food quality can be a limiting factor for chironomids (Benke 1998), and the availability of high-quality food favors higher biomass, growth rates, P/B, and secondary production of populations (Stites and Benke 1989). Hence, despite the similarity in overall detritivore abundance, populations had different number of generations, secondary production and productivity in different wetlands, which were probably related to detrital inputs from different sources due to varying lateral connectivity. Collectors mainly consume fine particulate organic matter. Thus the decrease of the larger body-sized *Chironomus-Pelomus* group probably results from the organic-rich bottom sediment, which diminishes with increasing lateral connectivity for wetlands located next to the main channel. In contrast, populations of smaller larvae of the *Saetheria-Tanytarsus* group probably can reach high biomass and many generations per year by feeding on sediments lower in detritus. Consequently, benthic detritivorous chironomids in the Paraná River floodplain are likely to take advantage of resource subsidies not only from donor habitats such as in PC, TCn, and TCl, but also from autochthonous production in dominant autotrophic wetlands such as PI. Thus the existence of different degrees of lateral connectivity, could favor the coexistence of taxa and the productivity of diverse food resources within the river system.

Other factors which were not measured in the present study, such as trophic interactions, can largely account for significant differences observed in the abundance patterns of macroinvertebrates (Jeppesen et al. 2003) and can be mediated by the hydrologic connectivity. For instance, predator density and biomass increased with an increasing connectivity in the connected wetlands and this could be related to food requirements of each taxa and prey availability. In addition, aerial predation of adult chironomids, wind, riparian vegetation cover, and the morphometry of wetlands also influence the abundance of insects in aquatic habitats (Heino 2000; Jeppesen et al. 2003).

The absence of a correlation between observed biomass patterns of the trophic guilds and environmental variables reflects the availability of high-quality resources and the productivity of all the wetlands, in spite of their degree of connectivity. In addition, results from the present study and from other previously published studies (compiled in Zilli 2010), have shown that chironomids of wetlands located in the Middle Paraná River floodplain are multivoltine with overlapping generations and relatively short life cycles. This fact could suggest both unlimited resources and an elevated and constant flux of energy in the system as was indicated by other authors (e. g. Coffman and Ferrington 1988). Therefore, because the wetlands exhibit different degrees of connectivity and are permanent units of floodplain landscapes, they represent a diverse, constant, and large source of energy, even during periods of low water or river-disconnection.

The distributional pattern of chironomid genera was related to the location of habitats within the floodplain. Therefore, TCl exhibited the highest dissimilarity of composition in density compared with all the other habitats located on a different island, and the dissimilarity increased in relation to the distance within the same island (PC-TCn to PI, see Fig. 1). Chironomids disperse aerially, allowing taxa to (re)colonize environments; whereas dispersal intensity determines the biotic connectivity of metapopulations (Leibold et al. 2004). Therefore, the higher similarity in the composition of neighboring habitats indicated the importance of both, hydrologic connection and aerial connectivity. For instance, the highest dissimilarity found among habitats located on different islands was related to the distance among habitats, probably to obstacles related to aerial dispersion, such as dense riparian forests, presence of strong air currents in the zone of the Tiradero River, and anthropogenic factors, such as the road connecting the study islands (see Fig. 1). The potential for the aquatic and aerial dispersal of some taxa should be coupled with habitat heterogeneity in order to promote coexistence at a regional scale (Mouquet and Loreau 2002); this is also important to sustain the productivity of wetlands regardless of their hydrologic connection. Thus, the interaction between local factors that are driven by the varying degrees of hydrologic connectivity and the regional dynamics of chironomid metapopulations established diverse trends in the metrics along the aquatic habitats located in the Paraná River floodplain.

Additional research is needed to understand better all these ecological processes in floodplain wetlands of the Paraná River as well as in other large rivers. The homogenization of floodplain habitats by human activities could profoundly impoverish such complex and diverse

systems, and the connectivity of functionally variable habitats may be considered a key factor for the design of actions to sustain metapopulations and biological diversity across increasingly fragmented landscapes.

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