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RESEARCH ARTICLE

Distribution of benthic invertebrate biomass and secondary production in relation to floodplain connectivity in a large river system (Paraná River, Argentina)

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An investigation of benthic invertebrates was conducted in the Paraná River (Argentina) floodplain to assess patterns of biomass and production in relation to lateral river connectivity. Environmental and invertebrate samples were collected monthly from April 2005 to March 2006 at sites with different lateral surface-connection. The investigated invertebrate assemblages were characterized by high biomass and high production. The key factor determining the benthic assemblages was river connectivity and indirectly, substrate characteristics, water transparency, and depth. With increasing river connectivity, biomass and production of oligochaetes, native bivalves, and dipterans decreased, whereas both variables increased for non-native bivalves, gastropods and ephemeropterans. Benthic assemblages of most of sites had an average similarity in the composition of about 50% along the study period, but the number of taxa contributing to the overall similarity was lower at sites located at long distance from the main channel than at sites located next to it. Potential production was high compared to literature data, which underscores the importance of preserving floodplain areas and maintaining natural lateral connectivity. High habitat patchiness mediated by lateral-surface connectivity appeared to promote benthic resources diversity, which in turn controls productivity of this floodplain-river system.

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1 Introduction

In large rivers, variation in lateral hydrological connectivity between the river and floodplain environments generates and maintains a high spatial heterogeneity, offers diverse resources to the biota, and affects the productivity of aquatic and terrestrial communities [1, 2]. In large rivers, environmental patchiness will promote increased diversity of resources and thus aquatic communities are often used to assess environmental patterns in different regions [3–6].

In floodplain aquatic communities, benthic invertebrates are important because they convey energy from detritus and primary producers to higher trophic levels. In the Paraná River floodplain environments, the available evidence indicates that physical and chemical variables are the main factors shaping benthic assemblages, which exhibit increasing density, richness, and diversity from the main channel to floodplain sites and the lowest numerical dominance of taxa in highly surface-connected sites [7]. However, the relationship between benthos biomass, as well as productivity, lateral surface-connectivity and

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Abbreviations: BPOM, bottom particulate organic matter; **CCA**, Canonical Correspondence Analysis; **CPOM**, coarse particulate organic matter.

environmental variables has been rarely studied [8], in spite of the importance of these variables for ecosystem functioning of floodplains.

Among environmental variables, substrate conditions were suggested as the main factor affecting invertebrate distribution at the microhabitat scale [9]. In the Paraná River, the density of benthic oligochaetes is mainly associated with the quantity of bottom detritus [7, 10]. On the other hand, the inputs of seston directly affect individual size, development and abundance of filter-feeding bivalves [11]. Thus, as lateral surface-connection and distance of floodplain habitats to the main channel in the Paraná River are related to inputs of suspended and particulate matter [12], bivalve populations should have larger biomass and production in highly connected sites.

In this study, I investigated the relationships between invertebrate biomass and production, and the degree of hydrological connectivity, physical and chemical parameters in floodplain sites of the Middle Paraná River (Argentina). Furthermore, biomass turnover ratios of dominant invertebrates in the floodplain system were calculated. It was hypothesized that the distribution of biomass and potential secondary production of benthic invertebrates are determined by hydrological connectivity. I predicted that higher biomass and potential secondary production of molluscs occur at highly connected sites, whereas higher annelid and insect biomass and potential secondary production should occur at sites with lower connection.

2 Methods

2.1 Study area

Field investigations were conducted monthly from April 2005 to March 2006 in floodplain sites located in the Middle Paraná River in the cross section of Santa Fe city and Paraná city, Argentina (31°40′S–31°43′S and 60° 33′W–60°39′W). Flood was during November 2005, whereas the dry season was during August-September 2005. To assess benthic biomass and potential secondary production within the Paraná River floodplain, 14 sites with different surface-connection located in lacustrine environments and their connection channels to the mainstream were sampled (Fig. 1). In the Middle Paraná River, the distance between the river and aquatic sites in the floodplain is usually related to the frequency of

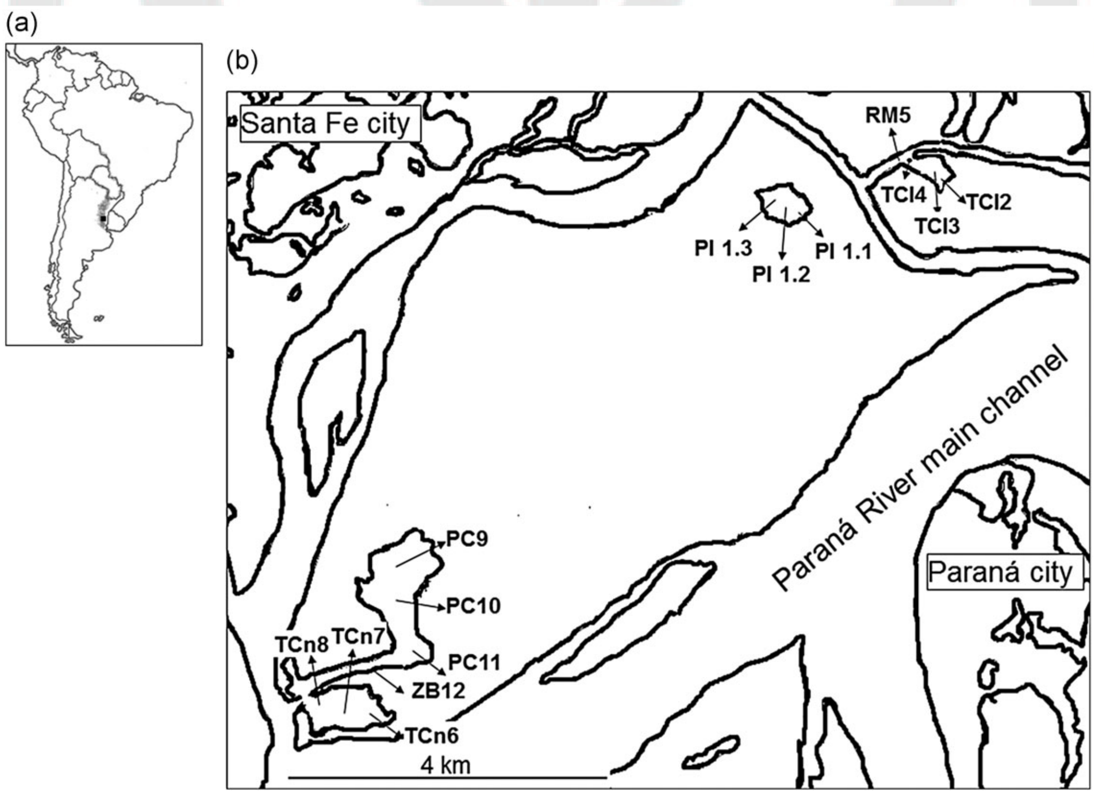

Figure 1. Study site locations in the Middle Paraná River floodplain, Argentina. Lacustrine sites from disconnected (PI1.1, PI1.2, PI1.3), to temporarily connected with relatively lower and higher surface-connection (TCl2, TCl3, TCl4, and TCn6, TCn7, TCn8 respectively) and permanently connected (PC9, PC10, PC11). Permanently connected riverine sites located in the connection channels of lacustrine sites with lower and higher lateral surface-connection (RM5 and ZB12, respectively).

hydrological connectivity [13]. Thus, connectivity categories were assigned to sites taking into account, the period that they remained connected (disconnected, permanently or temporarily connected) and the distance to the main channel and to the connection points (located at longer distance or next to the connection point and within connection channels) (Table 1). Therefore, sites ranged from disconnected (Type 1) to a highly permanently connected site located next to main channel in a connection channel (Type 12).

2.2 Field collection of samples and laboratory processing

Physical and chemical variables such as conductivity (Cond, Conductivity-meter, Model B3338, Beckman Instruments Inc., USA), pH (pH comparator 705, Orbeco-Hellige Inc., USA), depth (Z, sounding line), transparency (Se, Secchi disk), temperature of water (T, standard thermometer) were measured in situ in each site. Three samples of bottom sediments for assessing benthic invertebrates (total number of samples = 504), one sample for bottom particulate organic matter (BPOM), and one sample for granulometry were collected at each sampling site (Ekman grab, 0.225 m^2 of extraction surface). Particle size was analyzed using the dry sieving method and the percentage of sand (S), silt (s), and clay (c) were determined according to the Wentworth [14] scale (methodology described in Bertoldi de Pomar [15]. BPOM, ultrafine, fine, and coarse particulate benthic organic matter (UFPOM = 63–250 μm, FPOM = 250–1000 μm and coarse particulate organic matter (CPOM) = 1000 μm, respectively) were obtained by ignition in a muffle furnace at 550°C for 3 h. The cover of floating macrophytes (Co) was estimated based on photos. Data on environment variables of study sites are given in Zilli and Marchese [16].

Quantitative samples of benthos taken from each site were passed through a 0.2 mm sieve. Samples were preserved in 10% formalin. Specimens were sorted manually from sediment under a stereoscopic microscope and preserved in 70% alcohol. Wet mass of invertebrates was determined with an electronic balance with 10^{-5} g of precision (Model AP250D, OHAUS Corporation, Switzerland) after soaking the specimens for 10 min in water and leaving for a few minutes on filter paper to remove excess water. Dry mass (DM; molluscs without shells) was calculated according to the ratios of dry:wet mass reported by Waters [17].

2.3 Data analyses

Biological and environmental data were $\log_{10}(X+1)$-transformed to stabilize variances and achieve normality of data [18]. To assess the overall differences among sites (with samplings as replicates) and sampling dates (with sites as replicates), taxonomic groups of invertebrates data (Oligochaeta, Hirudinea, Gastropoda, native and non-native Bivalvia, Diptera, and Ephemeroptera) were subjected to non-parametric analysis of variance (Kruskal–Wallis test, $p \leq 0.05$) followed by multiple comparisons [19]. To assess the similarity of the composition of benthic invertebrate biomass along the study period, Similarity Percentage Analysis (SIMPER; Bray Curtis similarity matrix [20]) was used. The uniformity of benthic biomass composition along the study period was assessed by dividing the overall similarity within each site by the number of taxa that contributed to it (mean annual similarity of benthic composition divided by the number of taxa that contributed to more than 4% of annual similarity).

To further identify patterns in the biomass of invertebrates, I used direct ordination methods, such as Detrended Correspondence Analysis (DCA), which is a prerequisite to perform either canonical or redundancy analysis [18]. The length of DCA's gradient was 3.024. Thus, to identify the primary environmental gradients affecting benthic assemblage biomass, I used Canonical

Table 1. Lateral surface hydrological connectivity of the study sites with the Middle Paraná River mainstream

Sites	Connectivity classes
PI1.1, PI1.2, PI1.3	Lacustrine and river-disconnected sites
TCl2, TCl3, TCl4, TCn6, TCn7, TCn8	Lacustrine and river-temporarily connected sites located at different distances from the lake-river connection point. Higher number indicates higher lateral connectivity. TCl and TCn were connected 84 and 94% of the study period respectively.
PC9, PC10, PC11	Lacustrine and river-permanently connected sites located at different distances from the lake-river connection point. Higher number indicates higher lateral connectivity.
RM5, ZB12	Riverine sites located in river-connection channels of lacustrine sites. RM5 located at higher distance from the main channel and with lower lateral surface-connection than ZB12.

Correspondence Analysis (CCA [18]) between environmental variables and the biomass of taxonomic groups of invertebrates (Oligochaeta, Hirudinea, native Bivalvia, non-native Bivalvia, Gastropoda, Diptera, Ephemeroptera). Hydrological connectivity (Con) was considered as an environmental variable along with the rest of the physical and chemical variables. A manual forward-selection procedure was run, which included variables that had a conditional effect significant at the 10% level ($p \leq 0.1$). To assess the significance of the canonical axes, *p*-values were calculated using the Monte Carlo permutation test [18]. Analyses were run using the PRIMER-E® software [21] (version 6.1) and the R program (package Vegan for ordination analysis [22]).

Values of annual potential secondary production of invertebrates (P, in mg DM/m^2/year) were calculated according to the model proposed by Benke [23], with the following equations:

$$\log_{10} P\,\text{Diptera} = 0.409 + 1.009 \log_{10} B + 0.052\,T - 0.182 \log_{10} W_{\text{m}}$$

$$\log_{10} P\,\text{Ephemeroptera} = 0.667 + 1.019 \log_{10} B + 0.032\,T - 0.384 \log_{10} W_{\text{m}}$$

$$\log_{10} P\,\text{Mollusca (used either for bivalves and gastropods)} = 0.783 + 0.945 \log_{10} B - 0.023\,T + 0.143 \log_{10} W_{\text{m}}$$

$$\log_{10} P\,\text{Annelida (used either for hirudineans and oligochaetes)} = -0.859 + 0.978 \log_{10} B + 0.123\,T + 0.106 \log_{10} W_{\text{m}}$$

where B is the biomass (mg DM/m^2), T is mean annual water temperature (°C), and W_{m} is the maximum individual weight (mg DM). A summary of coefficients and a complete description of the model I used in the present research can be found in Benke [23].

To assess the relation between annual biomass and potential secondary production, data were subjected to Pearson correlation analysis ($p \leq 0.05$). Additionally, to assess the effect of lateral connectivity on potential secondary production, sites were grouped considering the duration of river-connection and location within connection channels or lacustrine environments as main factors to define groups (G1 = PI; G2 = TCl; G3 = RM5 + ZB; G4 = TCn; G5 = PC). Potential secondary production was compared among lateral connectivity groups using non-parametric analysis of variance (Kruskal–Wallis test, $p \leq 0.05$) followed by multiple comparisons [19].

3 Results

3.1 Macroinvertebrates biomass distribution

Sites had significant differences in the biomass of taxa and mainly for aquatic annelids and mollusks (Fig. 2, Kruskal–Wallis test with samplings as replicates, $p \leq 0.05$). In general, the biomass of oligochaetes, native bivalves and hirudineans increased as connectivity decreased (Table 2, Fig. 2). Native bivalves reached the minimum biomass in RM5 and ZB12, whereas larger individuals of native bivalves (Hyriidae) were frequent only in PI. Moreover, non-native bivalves were only present in connected sites located next to main channel (from PC9 to ZB12) and gastropods had a higher biomass in surface-connected sites, mainly in PC11 (Fig. 2). Furthermore, only dipterans

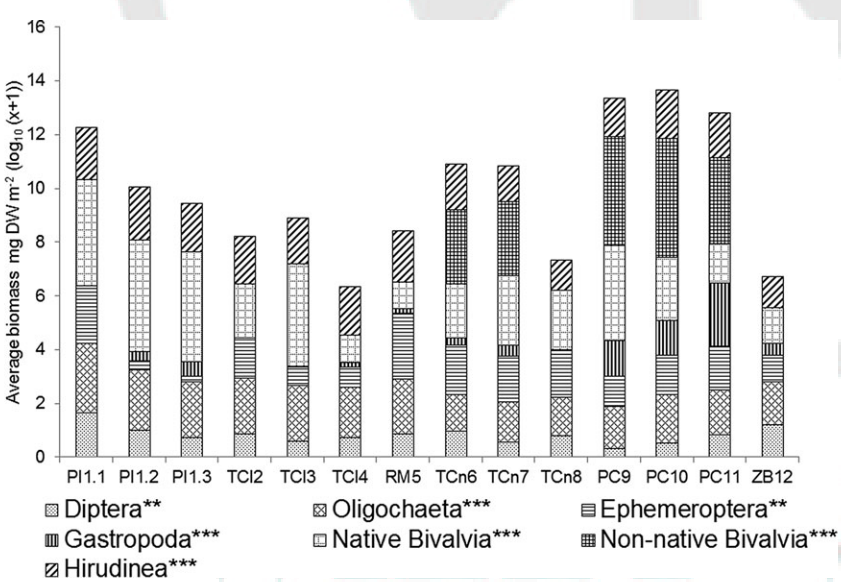

Figure 2. Biomass of invertebrate groups in 14 floodplain sites in the Middle Paraná River, Argentina. Data are mean values of monthly samplings from April 2005 to March 2006. Differences in biomass among sites are significant (with samplings as replicates, Kruskal–Wallis test, $**p < 0.001$, $***p < 0.0001$). Notation of sites as in Fig. 1.

Table 2. Data on correlations between Canonical Correlation Analysis (CCA) axis and environmental variables

	Species CCA Axis 1	Species CCA Axis 2	Environmental CCA axis 1	Environmental CCA axis 2
% Sand (S)	−0.09	−0.16*	−0.09	−0.45*
% Clay (c)	0.25*	0.06	0.27*	0.18
% Fine particulate organic matter (FPOM)	−0.06	0.03	−0.07	0.09
% Fine coarse particulate organic matter (CPOM)	0.01	−0.18*	0.02	−0.49*
% Benthic particulate organic matter (BPOM)	0.35*	0.15*	0.37*	0.43*
Water transparency (Se)	0.52*	0.04	0.57*	0.12
Water conductivity (Cond)	−0.04	0.01	−0.04	0.04
Depth (Z)	−0.05	0.19*	−0.05	0.53*
Connectivity (Con)	−0.91*	0.02	−0.98*	0.04

*Significant linear correlations ($p \leq 0.05$).

and leeches showed significant differences among sampling dates in the floodplain (with sites as replicates, Kruskal–Wallis test, $p < 0.05$). Dipterans exhibited a significant lower biomass during summer and winter, while hirudineans displayed a significantly higher biomass from August 2005 until December 2006 (multiple comparisons, $p < 0.05$).

Benthic assemblages of most of sites had an average similarity in the composition of about 50% along the study period, except for TCn8 and PC11 (Fig. 3). The number of taxa contributing to the overall similarity was lower at sites located at long distance from the main channel than at sites located next to it (Fig. 3), with exception of PI 1.1, PC9, and PC10. Sites at PC were dominated by non-native *Corbicula fluminea*, which accounted for nearly 95% of the total similarity of the community along the study period, whereas PI 1.1 had a higher variation along the study period. Moreover, oligochaetes, hirudineans, and native bivalves characterized benthic assemblages of sites with the lower surface-connection, whereas insects varyingly distributed in disconnected as well as in connected sites. Within each of the surface-connected lacustrine sites, the average annual similarity decreased from the sites located at long distance from the connection points to the ones located next to the connections.

3.2 Primary environmental variables affecting benthic biomass distribution

Of the initial environmental variables included in the CCA, nine were retained as significant contributors, whereas the non-retained were redundant or did not increase the significance of the model (UFPOM, s, Co, T). The first two CCA axes accounted for 89.5% of the total variance explained in invertebrate biomass composition (canonical axes were all significant, Monte Carlo test, $p \leq 0.01$). In the

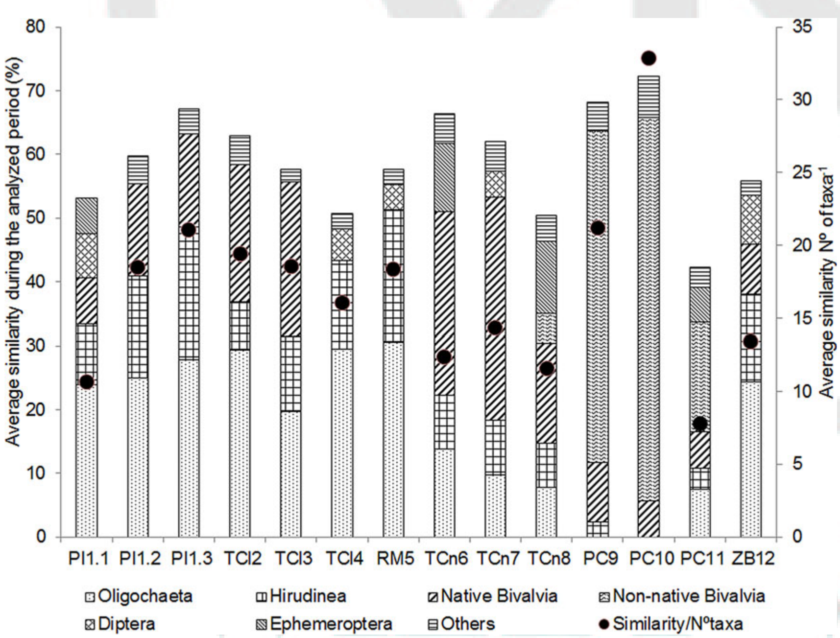

Figure 3. Overall similarity percentage achieved by benthic assemblages within each site along the study period (SIMPER = Similarity Percentage analysis [20]). Contribution of taxa to overall similarity percentage is showed. The overall similarity was divided by the number of taxa that contributed to more than 4% similarity within each site. Notation of sites as in Fig. 1.

two-dimensional ordination, sites distributed in relation to their location within the floodplain, from the ones located next to the main stem (ZB12, PC, TCn) to the ones located at long distance from it (PI, TCl, RM5, Fig. 4a). Additionally, within each group, sites were ordered following their position and distance to each other within lacustrine and connection channel environments.

The first CCA axis explained 79.2% of biotic variance and was mainly defined by hydrological connectivity that was negatively correlated to BPOM, clay, and water transparency (Fig. 4b and c, Table 2). Native and non-native bivalves, gastropods and oligochaetes provided the highest discrimination among highly connected and low connected to disconnected sites. Two groups of sites mainly determined the second axis of the ordination: lacustrine sites located next to connection points (PC11 and TCl4) and sites located in connection channels (Fig. 4a). Thus, RM5 and ZB12 ordinated separately and close to lacustrine TCl4 and PC11, respectively. Substrate characteristics and depth were the main environmental variables contributing to biomass distribution of invertebrates on this axis (Fig. 4b and c). The higher biomass of gastropods characterized deeper permanently surface-connected sites with higher bottom FPOM and located next to the main channel, whereas sites located at a longer distance from the main channel were characterized by a higher biomass of ephemeropterans, a lower percentage of sand and CPOM in the substrate (Fig. 4).

3.3 Floodplain average biomass, potential secondary production and P/B ratios

In the floodplain system, the annual mean biomass was highest for bivalves, followed by oligochaetes, ephemeropterans, hirudineans, gastropods, and dipterans (Table 3). The annual average potential secondary production was highest for bivalves, followed by oligochaetes, hirudineans, ephemeropterans, dipterans, and gastropods, whereas annual P/B values were highest for annelids followed by insect and molluscs.

Potential secondary production of sites was positively related to biomass (Pearson correlation, $p \leq 0.05$), whereas tests based on biomass and production showed the same differences between groups of sites (Table 3, multiple comparisons test $p \leq 0.05$). Higher potential secondary production occurred at PI, TCl3, and PC sites and was mainly due to bivalves, whereas lower production occurred at TCn, TCl2, TCl4, and at sites within connection channels (Fig. 5). Sites located at long distance from the main channel (PI and TCl sites and RM5) had a higher potential secondary production of oligochaetes than sites located next to the mainstream, whereas gastropods had a relatively higher production in PC sites (Table 3). Moreover, potential secondary production of insects and hirudineans was evenly distributed among sites with the highest value for ephemeropterans at RM5. The average benthic production and the production, biomass and

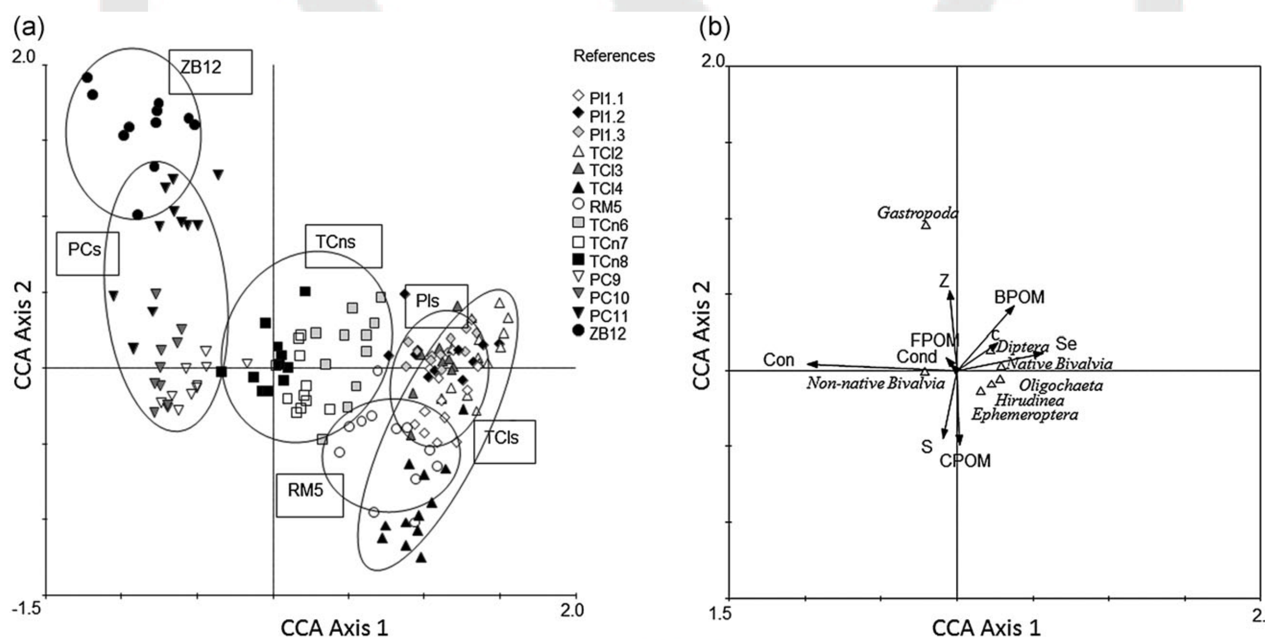

Figure 4. Results of CCA performed with invertebrate and environmental data from the Paraná River floodplain. (a) Scatterplot of sample scores of axis 1 and 2; (b) Biplot showing significant environmental variables and invertebrates of axis 1 and 2; Notation of sites as in Fig. 1. Con: Connectivity; Z: depth; FPOM: percentage of fine particulate organic matter; Cond: water conductivity; S: percentage of sand; CPOM: percentage of coarse particulate organic matter; BPOM: percentage of bottom particulate organic matter; c: percentage of clay; Se: water transparency.

Table 3. Annual mean biomass (mg DW/m^2), potential annual production (mg DW/m^2/year) and annual P/B of benthic invertebrates across all sites and groups of sites studied in the Paraná River floodplain

	All sites combined			Sites combined into groups with different lateral hydrological connectivity: Biomass					Production					P/B				
Taxon	Biomass	Production	P/B	G1	G2	G3	G4	G5	G1	G2	G3	G4	G5	G1	G2	G3	G4	G5
Oligochaeta	101	4369	43	226a	104b	75b	25c	48b	499a	448b	360b	221c	277b	3a	4b	6b	9c	6b
Hirudinea	52	3205	61	79	57	48	28	44	378	400	322	254	304	5	7	11	11	7
Gastropoda	18	69	4	1	0.2	1	1	83	12	5	12	11	98	7	21	14	26	2
Bivalvia	5961	29 555	5	11652a	2084b	15c	596b	14393a	1141a	323b	42c	249b	1003a	0.1a	2a	3b	1a	0.1c
Diptera	9	264	30	19	5	11	6	3	145	94	133	96	70	12	21	13	19	29
Ephemeroptera	53	517	10	48	12	144	58	28	94	74	195	159	111	20	10	5	3	5
Community	6194	37 979	6	12026	2263	293	714	14601	2269a	1345b	1064b	990c	1865b	0.2	4	6	2	0.3

Groups: G1: PI 1.1, 1.2, 1.3; G2: TCl2, 3, 4; G3: RM5 and ZB12; G4: TCn5, 6, 7; G5: PC9, 10, 11.
Means with a different letter indicates significant differences (Kruskal–Wallis, multiple comparisons, $p < 0.05$).

turnover ratios of bivalves and oligochaetes were significantly different among lateral connectivity categories (Table 3, Kruskal–Wallis test, $p < 0.05$). In contrast, no significant differences were obtained for any of these parameters for the other taxa. Potential secondary production of all macroinvertebrates was significantly higher at G1 and significantly lower at G4 than at the other groups of sites. Oligochaetes exhibited significant higher biomass and production in the groups of sites with the lower degree of connectivity (G1 and G2), whereas bivalves had significant higher potential secondary production and biomass in disconnected and lacustrine permanently connected sites (G1 and G5, respectively). Sites with significantly lower and higher production of both, bivalves and oligochaetes, also showed significant higher and lower P/B ratios for these taxa respectively (Table 2, Fig. 5).

4 Discussion

4.1 Patterns of biomass and production

Results obtained in the present study confirmed the initial hypothesis that biomass and potential secondary production, principally of bivalves and annelids, were significantly related to the hydrological connectivity of sites. Sites were ordinated in a gradient related to hydrological connectivity and position within the floodplain in the statistical analysis for biomass data. Nonetheless, sites located in connection

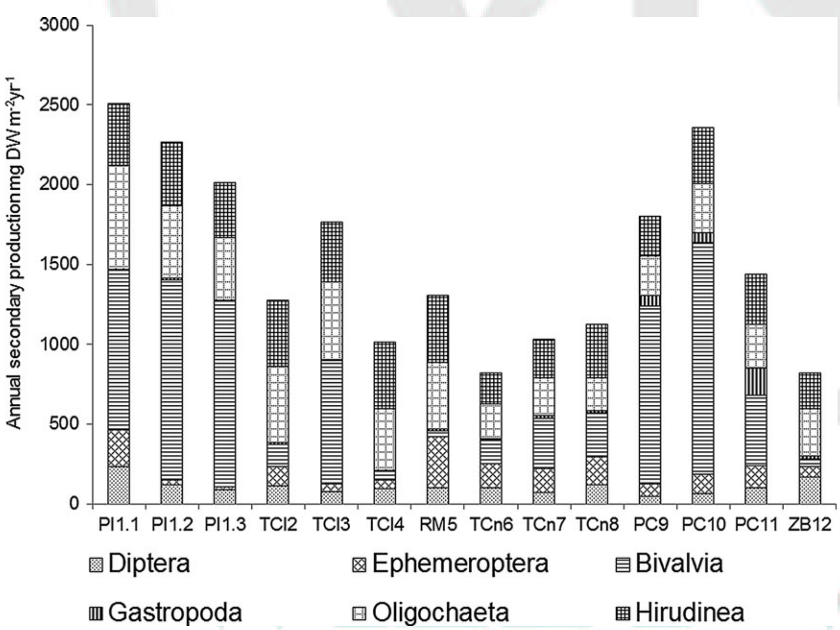

Figure 5. Annual potential secondary production of invertebrates in 14 floodplain sites in the Middle Paraná River, Argentina. Notation of sites as in Fig. 1.

channels were more similar in the biomass composition to proximate sites of lacustrine environments than to each other, demonstrating the existence of complex effects of hydrological connectivity on benthic assemblages. Thus, invertebrate biomass composition displayed a patchy distribution of some taxa like gastropods and mayflies that were more affected by variables acting at a local scale such as depth and substrate composition [24]. Hence, sites with higher depth and bottom FPOM were more suitable for scrapers such as small gastropods, which feed mainly on fine deposited detritus.

Benthic invertebrates, mainly mollusks and annelids, displayed significant differences of biomass and potential secondary production among floodplain environments and though the highest biomass of both were obtained in the disconnected sites, non-native bivalves and gastropods exhibited a larger biomass in the highly connected sites. I initially predicted that higher biomass and potential secondary production of molluscs might occur at highly connected sites, whereas higher annelid and insect biomass and potential secondary production should occur at sites with lower connection. Therefore, the initial prediction was partially confirmed as native bivalves were more productive in disconnected sites. Thus, as a general trend, mainly K-strategists such as oligochaetes Tubificinae and native bivalves [10] exhibited a decreasing biomass and production from disconnected sites and lowest connectivity degree to the highly connected sites. This is in agreement with patterns found in other river-floodplain systems [25, 26].

The present study showed that biomass and production of native bivalves, annelids and dipterans was directly related to BPOM and thus indirectly to lateral hydrological connectivity. Walthers and Whiles [27] also reported a positive relation between these parameters and postulated that availability of benthic organic matter is a major driver of invertebrates production at a large geographic scale. Additionally, substrate characteristics linked to hydrology, such as bottom detritus content, and invertebrate production showed a similar trend along a wide stream continuum [28]. Furthermore, at a high level of river connectivity, the substrate can become unstable and inorganic particles may dominate over organic particles in the water column, so that filterers may not be supported [29]. In agreement with this findings, the results of the present study showed that bivalves had the minimum production in sites located within connection channels. However, invasive bivalves reached a higher biomass and production in the highly connected lacustrine sites next to the mainstream. Therefore, patchy substrates generated by different degree of lateral connectivity may have partly determined taxa biomass and production by regulating benthic resources within the floodplain.

Biotic interactions among other variables not evaluated in the present study, and that can also be shaped by the hydrological surface connectivity in the Paraná River, probably affected the distribution of invertebrates within the floodplain. For example, several investigations showed the selective effects of predation pressure on final size, biomass and potential secondary production of organisms in different environments [30, 31] and indicated that this interaction may be site-dependent [32]. The higher frequency of large bivalves (individuals of Hyriidae) and the highest overall biomass of native bivalves at disconnected sites probably indicated a low effect of predation on mollusks populations. Moreover, insects were abundant in lacustrine sites with the lowest surface-connection. Such sites can only be colonized from the air, and represent environments in which larger predatory insects would benefit from the absence or low density of predatory fish [33].

In spite of the annual variation in the water level of the river that may cause annual changes in floodplain aquatic assemblages of large rivers [1, 2, 29], in the present study, seasonality did not considerably affect invertebrate biomass. Taxa biomass exhibited a high similarity along the study period and only dipterans and hirudineans displayed significant differences among seasons and dates, probably more related to particularities of their life cycle than to water level fluctuations. Certainly, a higher level of taxonomic resolution could have better shown differences associated to seasonality.

Moreover, in a spatial analysis, assemblages were less uniform in the temporarily and permanently connected sites located next to the main channel than in the other floodplain sites. Nonetheless, the dominance of non-native bivalves in the patches that best fulfil their niche requirements [34] homogenized the benthic composition and showed that invasive species interfered with the structure and function of native communities, and can cause the reduction or loss of benthic resources [35]. Nevertheless, as benthic resources availability may be highest at intermediately connected environments [36–38], the existence of different degrees of lateral surface-connectivity might prevent from biota homogenization and favor coexistence and high diversity within the Paraná River floodplain, even when invasive species are present in the system.

4.2 Paraná River floodplain productivity

Since production is highly likely to be a direct function of biomass [23] values of production calculated in the present study were positively related to annual biomass. The potential secondary production obtained in the present study for different taxa can be considered as moderate to high, compared to production estimates for rivers of other climatic regions (compiled in [23, 39]). The overall community production in the Paraná River floodplain was higher than 70% (=35 rivers) of results obtained from 50 rivers within a large geographic scale from USA to Japan [23]. In addition, from the 35 rivers, the 79% had an invertebrate production less than a half of the values that were calculated for benthos in the present study. Additionally the overall potential secondary production of the benthic community within the Paraná River floodplain was more than 10 and 60 times higher than values reported for floodplain lakes and the mainstream of the Yangtzé River respectively (data from several research articles compiled in [26]).

Floodplains are often thought to be the main source of matter and energy in large river systems ([2, 40], among others). Hence, the biomass estimated for floodplain sites in this study were more than 40 times higher than the values of Marchese [41] for sites with 107 to 164 mg DW/m^2 on average. Since floodplain aquatic environments occupy a large proportion of the Paraná River area [13], they should represent the greatest and most diverse supply of macroinvertebrate resources for aquatic and terrestrial food webs within the system.

Analyses of relationships between macroinvertebrate production and its determinants in floodplain systems will become more feasible as the number of studies combining benthic community measures continues to grow. Nevertheless, the high productivity estimated in the present research underscores the importance of preserving natural floodplain systems. Thus, in order to mantain a high productivity and a varying offer of benthic resources that contributes to biodiversity in the Paraná floodplain, the diversity of differently connected sites should be protected.

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