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First spatio-temporal study of macroinvertebrates in the Santa Cruz River: a large glacial river about to be dammed without a comprehensive pre-impoundment study

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First spatio-temporal study of macroinvertebrates in the Santa Cruz River: a large glacialriver about to be dammed without a comprehensive pre-impoundment study

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Abstract

The Santa Cruz River is the last free flowing river in Argentinean Patagonia. Two dams are projected and no comprehensive pre-impoundment study has been undertaken. The present study investigated macroinvertebrate communities along three different hydrological periods and at three river sections located upstream and downstream of future dams. Fifty-three macroinvertebrate taxa were identified, with the most abundant orders being Ephemeroptera, Plecoptera, Coleoptera, and Crustacea (particularly amphipods). Ordination methods (CCA) and generalized linear models (GLM) were applied. According to the CCA, the main environmental variables related to macroinvertebrate density were temperature, suspended solids, depth, and substrate size. For the GLM the main factors associated with macroinvertebrate abundance were location and hydrological period, and variables with the highest influences were temperature, substrate size, current speed and depth. We anticipate that dam construction will modify in-stream habitat conditions, leading to changes in: (i) macroinvertebrate community structure; and, (ii) local fish abundance due to loss of key prey taxa.

Keywords: Dams, Large Rivers, GLM, Southern Hemisphere, Benthos.

Introduction

Large glacial rivers, such as the Santa Cruz River, have unique characteristics, with a strong water flow regulation (Röthlisberger & Lang, 1987; Tagliaferro et al., 2013), low water temperature (Milner & Petts, 1994),and high turbidity (Gurnell & Fenn, 1987; Depetris et al., 2005; Brown et al., 2006) which might obstruct primary production (Johnson et al., 1995). Since glacial rivers show a predictable flood pulse, to which resident aquatic and terrestrial organisms are adapted (Milner et al., 2009; Sparks, 1995); flood, channel stability, and temperature are known to play a major role in the distribution of macroinvertebrates (Milner & Petts, 1994; Castella et al., 2001; Gíslason et al., 2001; Tagliaferro et al., 2013). When environmental conditions at a location are particularly extreme only specialized taxa may be able to establish, and their distribution could be restricted to particular times in the year or 'windows of opportunity' (Milner et al., 2001).

The natural conditions of the Santa Cruz River are expected to change due to the imminent construction of two mega hydroelectric dams that are projected to supply 16% of Argentina's hydropower (Salinas, 2014). The most striking consequences in other large rivers have been extensively studied, and it is widely accepted that river and riverine ecological processes are altered by changes in flow regime, sediment loads, temperature, nutrient cycle, and biota (Gup, 1994; Ligon et al., 1995; Poff et al., 1997; Jakob et al., 2003). Dams alter geomorphological river characteristics, with differential effects depending on river areas (downstream or upstream of dams) with possible river simplification (Ligon et al., 1995); moreover, since the operation of dams depends on energy demand, regulated flow rarely matches the natural hydrological regime. Biological consequences include migration blocking, flooding of spawning areas, reductions in densities of sensitive species, and in biodiversity. In turn, changes in the structure of communities can affect the flow of energy and matter in river ecosystem (De Ruiter et al., 1995; Chapin et al., 2000); consequently, ecologically important components of the annual hydrography are affected (Acreman & Dunbar, 2004).

The Santa Cruz River is the last large un-interrupted river of Patagonia Argentina, with distinctive features. Its water flow is strongly dominated by glacial ice ablation, providing: a) a seasonal cycle with distinct peaks at the end of February (late Southern Hemisphere summer) and low water flow in September delayed up to six months for the other rivers dominated by snowmelt and rainfall contribution; b) extremely stable flow with much less variability than other rivers, both within and between years; c) high inter-annual stability in water temperature (Tagliaferro et al., 2013); and d) high sediment load (Depetris et al., 2005). Freshwater fauna is restricted to a small number of species including perch, galaxiids and exotic salmonids (Pascual et al., 2007; Tagliaferro et al., 2014; Tagliaferro, 2014), and a reduced number of macroinvertebrates (Miserendino, 2001; Tagliaferro et al., 2013): 38 reported macroinvertebrate and 7 fish species (Tagliaferro, 2014).

Dams in the Santa Cruz River will obliterate 51% of currently available lotic habitat, including the most productive sections of the river based upon macroinvertebrate and primary production data (Tagliaferro et al., 2013). Because no comprehensive pre-impact study has been carried out for the dams in the Santa Cruz River, the present study is the first to investigate the temporal variability of benthic macroinvertebrates. We analyzed macroinvertebrate communities in the Santa Cruz River at three specific reaches that are expected to change due to dam construction. This study complements a previous spatial study made by Tagliaferro et al. (2013) with novel information and a temporal perspective. The objective of this research is to evaluate the relationship between macroinvertebrate communities and environmental variables among three hydrological periods (low, intermediate, and high flow) and to evaluate possible scenarios of change based on the understanding of this system.

Methods

Area

The Santa Cruz River (50° S; 70° W) originates in two oligotrophic to ultra-oligotrophic large glacial lakes, Viedma and Argentino, and flows uninterrupted for 382 km across the Patagonian plateau to drain into the Atlantic Ocean (Fig. 1; Brunet et al., 2005). The river has an average discharge of 691 $m^3 s^{-1}$ (min. 278.1 $m^3 s^{-1}$ in September and max. 1,278 $m^3 s^{-1}$ in February-March), which is highly predictable due to the glacial dominated regime (Tagliaferro et al., 2013). It is an un-braided river (100-200 m wide x 382 km length) and temperatures between the upstream and downstream areas differ only by 3-5º C. The two dams projected for the Santa Cruz River (Fig. 1) are located at river km 132 (Kirchner, 50.206° S, 70.785° W) and at river km 197 (Cepernic, 50.185° S, 70.177° W). Together they will dam up 197 km of river, leaving only a lower stretch of 49% of current length of unregulated river. In-river construction began in January 2015.

Sampling

Five sampling sites were selected (Fig. 1) and visited six times between 2009 and 2011 during low water flow (August and September), intermediate water flow (April-May-June), and high flow periods (January). The sites were located at each of the three major divisions of the river upstream, mid-stream, and downstream (SRH, 2013). Upstream, two distinct sub-areas were differentiated: (a) the Santa Cruz River near the mouth of Bote River (26 km from Lake Argentino) and (b) areas with influence from the First Labyrinth (located at 60-75 km of Lake Argentino). Mid-stream sites were located at a distance of approximately 200-215 km from the Lake Argentino; and downstream sites were located 270-285 km of Lake Argentino. For each of these large sampling areas, the number of invertebrate samples taken varied between 3-12 replicates depending on accessibility to the river and safety considerations regarding river depth and fast flow.

Environmental variables

Thirteen variables were recorded at each site (within a 15-50 m radius) including water and river physical characteristics, dissolved matter, and chlorophyll-a concentration on biofilms following Gordon et al. (2004). Bankfull, wet, and gravel bar widths were measured using a laser distance meter (TruPulse 200, LTI Colorado-USA). Average depth was calculated from 3 measurements within the sampling area. Flow velocity was obtained by timing a half-submerged plastic filled cup over a distance of 5 m at each sampling site. Temperature, conductivity and dissolved oxygen were measured using an YSI 85 multi-parameter probe (YSI Environmental, Ohio-USA). Substrate size composition was estimated following the Wolman Pebble count procedure (Wolman, 1954), by walking upstream along a zig-zag line across a working area of 100 m long by 2 to 5 m wide and measuring the width of 100 pieces randomly chosen. A standard area of 11 cm^2 was scratched for biofilm from each of three randomly selected rocks (width range 5 to 30 cm) at each site and stored on a filter, from which chlorophyll-a concentration was estimated (APHA, 1994). Water samples of 500 ml were collected below the surface, filtered using a 47 mm diameter GF/F Munktell filter, and preserved at -10° C to estimate total suspended solids. In the laboratory, samples were dried at 60° C for 24 h, weighed and burned at 500° C for 4 h to assess suspended organic and inorganic matter.

Macroinvertebrates

Macroinvertebrate samples were taken at each of the 5 sites on 6 occasions with a kick-net of 450 µm mesh size, 0.25 m^2 area. Samples were preserved in 70% ethanol and transferred to the laboratory for sorting and identification of organisms to the lowest possible taxonomic level (genera or species depending on available local references) employing a Zeiss stereomicroscope and a Zeiss STD 18 microscope. Taxa were identified following Lopretto & Tell (1995) and Domínguez & Fernández (2009). Relative abundance per taxon (%) and presence along sites (% sites present) were calculated. Functional feeding groups (FFGs) were assigned using available references (Merritt & Cummins, 1996; Ramírez & Gutiérrez-Fonseca, 2014), personal knowledge of feeding modes (mouthpart morphology and behavior), and analysis of gut contents (Merritt & Cummins, 1996; Domínguez & Fernández, 2009). Identifications were made using Optical Service facilities of the Centro Nacional Patagónico (CENPAT).

Data analysis

An analysis of variance (ANOVA) of the total density of invertebrates in relation to the periods of time and river areas under study was conducted, and in relation to river areas (distance to Lake Argentino) by using INFOSTAT software (Infostat-Córdoba Argentina). To evaluate the relationship between the density of macroinvertebrates and the environmental characteristics, an ordination method was applied using Canonical Correspondence Analysis (CCA) downweighing rare species using the CANOCO program (TerBraak & Smilauer, 1999) and R Software (version 3.0.2, R Development Core Team, 2012).Since the length of gradient was 1.943 for the first axis, goodness of fit of environmental variables was evaluated by using a Principal Component Analysis (PCA) and a Correspondence Analysis (CA). Considering the length of gradient and the better adjustment to a CA, the relationship between environmental variables and taxa composition was evaluate using CCA. Macroinvertebrate density data were transformed using log(x+1), which is recommended when the ordination is Euclidean-based and for data with many zero-counts (Legendre & Gallagher, 2001). Total and axes significance were tested using a permutation Monte Carlo test (n = 9999) and the redundant variables were reduced by the value of the inflation factor of variance for each factor or contrast with other factors, and a stepwise model ("stepwise") set under the Akaike information criterion (AIC; Akaike, 1974) was adjusted using the free software R (version 3.0.2) and through a selection test variables by the method of Monte Carlo permutations, retaining those with $p < 0.1$.

Regression models of macroinvertebrate density as a function of environmental variables, time, and site factors were adjusted for most abundant macroinvertebrate orders using Generalized Additive Model (GAM) and Generalized Linear Model (GLM). Outliers, model assumptions, and residuals were evaluated graphically using the “stats” package. Normality was tested using a “qqnorm” plot of residuals and the “qqline” command. Models discrepancy and the relative importance of each variable were also checked. Heteroscedasticity was controlled by updating models with varIdent function. GLM analyses were performed using the "mgcv" package to display the graphical relationship of macroinvertebrate densities with variables, "stats" for linear models and to evaluate relationships between variables, and "MuMIn" to identify relevant variables in the model. Co-linearity and multicollinearity between variables were analyzed using “stats” package. All models were programmed using the software R (version 3.0.2) following the method of Zuur et al. (2009).

Since biological data usually have nonlinear responses to the explanatory variables, multiple linear regression techniques are not efficient; therefore, generalized additive models (GAM) and generalized linear models (GLM) are recommended (Hastie & Tibshirani, 1990). The generalized additive models (GAM) and generalized linear models (GLMs) use a link function that transforms the nonlinear mean of the response variable into a linear predictor. While GLMs use a parametric model to capture the nonlinear mean responses of the data, GAMs use a nonparametric "smoother", making them a flexible tool to explore the shape of the response variable (Wood, 2004). Once the general shape of the response variable was identified for each explanatory variable through GAM models (package "mgcv"), GLMs (with time and distance to Lake Argentino as fixed factors) were applied since it provide a more direct and robust technique to assess the goodness of fit and to interpret results (Guisan & Zimmermann, 2000). Count of individuals was used as the response variable, which is expected to be distributed according to a Poisson distribution. When overdispersion was observed we used a "quasi-Poisson" (overdispersion lower than 15) or a negative binomial error specification (overdispersion higher than 15). Table 2 summarizes the selection of the resulting models. Correlation and multi-collinearity analysis prior to model fitting among environmental variables identified a high correlation between the bankfull and wet width of the river, similar to that obtained by CCA. Models adjusted individually for each of the most abundant orders allowed to identify main variables determining their density. Model selection was performed using the multi-model inference "MuMIn" package based on information criteria (Barton, 2013) and by a stepwise regression procedure.

Results

The environmental characteristics at different sampling periods and areas are summarized in Annex 1. The variables with smaller range of variability were temperature, pH, dissolved oxygen and conductivity, while bankfull, wet, and gravel bar width exhibited intermediate variation coefficients depending on the area and period of sampling. A great variability in the concentration of chlorophyll-a was found, coincident with the pattern found by Tagliaferro et al. (2013). The highest values of chlorophyll-a concentration corresponded to the area of the First Labyrinth (60-70 km Lake Argentino) during September (low flow period). Upstream sites (60-70 km from Lake Argentino) exhibited high concentrations of organic suspended solids, dissolved oxygen and conductivity. On the other hand, mid-stream and downstream areas were characterized by low concentration of fine particulate organic matter (FPOM), with dissolved oxygen decreasing and temperature increasing towards downstream areas (for more detail see Tagliaferro, 2014).

Fifty-three taxa were identified among samples of the five river sites and six periods (Annex 2) with the most abundant orders being Ephemeroptera, Plecoptera, Coleoptera, and Crustacea (particularly amphipods). A total of 7,948 individuals were counted and identified. Mean macroinvertebrate density by sampling site ranged from 12 ind. m^{-2} to 2,188 ind. m^{-2}. The most widely represented groups were insect larvae of Diptera (18), Trichoptera (8) and Plecoptera (6). Within the 53 benthic macroinvertebrate taxa only 8 accounted for 80% of abundance: *Lymnaea* sp. (gastropod), *Hyalella araucana* Grosso & Peralta 1999 (amphipod), *Meridialaris chiloeensis* Demoulin 1955 (Ephemeroptera), *Klapopteryx kuscheli* Illies 1960 (Plecoptera), *Luchoelmis cekalovici* Spangler & Staines 2004(Coleoptera), and *Paratrichocladius* sp. (larvae and pupae, Diptera) and *Cnesia* sp. (Diptera). Both, *H. araucana* and *L. cekalovici* were the most conspicuous taxa, being present in 78% and 71.2%, respectively, of the sampling sites along the different study periods (Annex 2). Following these two species, *M. chiloeensis*, the gastropod *Lymnaea* sp., *Andesiops* sp. (Ephemeroptera), and *K. kuscheli* were present in 62%, 48.5%, 47%, and 46.9% of sites, respectively.

Redundant variables were reduced by analyzing the value of the inflation factor of variance for each factor or contrast with other factors (VIF> 20), leaving the total width of the river out of the analysis. In support of this results, the following variables were retained by a selection test by the method of Monte Carlo permutations ($p < 0.1$), complemented with a stepwise model set under AIC: wet width, gravel bar width, conductivity, pH, flow velocity, and concentration of chlorophyll-a. Density of all 53 benthic macroinvertebrates showed significant differences between study periods (ANOVA: $p = 0.0007$, $F = 4.66$, $df = 5$), but no differences were found between areas in those periods. Macroinvertebrate density in the low water season, September 2010, was significantly higher than that found in other study periods. Also significant differences were found (ANOVA) between densities in April and August 2010 ($p = 0.01$), and between August 2010 and January 2011 ($p = 0.02$).

The ordination result of the 53 macroinvertebrates taxa with the 5 environmental variables (substrate particle size, suspended organic and inorganic matter, temperature, and depth), using CCA, downweighing the rare species (Fig. 2, Table 1) exhibited statistically significant results (for the first axis: $F = 3.158$, $p = 0.0002$). Twenty eight percent of taxa abundance variance was explained by the first three ordination axes. Correlations between taxa and environmental variables were 0.87, 0.86, and 0.84 for the first, second and third axis respectively, and the percentage of variance explained was 81.9%, indicating a strong relationship with the environmental variables analyzed. The three ordination axes were statistically significant according to a non-restrictive Monte Carlo permutation test (significance of all canonical axes: $F = 1.969$, $p = 0.0001$). The first axis explained 11.2%, the second 8%, and 3.9% of third order. The first axis was determined by the substrate particles size and FPOM; the second axis reflected temperature, depth, and substrate particles size, and secondarily the inorganic matter in suspension; while the third axis was strongly associated with depth, temperature and suspended matter (Table 1).

The relationship between macroinvertebrates and environmental variables indicates that (a) annelids and amphipods have a positive relationship with FPOM, (b) Ephemeroptera and most chironomids were associated with low temperature conditions (Table 2), and (c) predators of different orders (Coleoptera, Trichoptera, Diptera and annelids) were distributed randomly showing no association pattern, but instead following the requirements of each species. Only the genus *Chironomus* and the coleopteran *Iguazu* sp., two low occurrence groups found in areas near Lake Argentino, were associated to high levels of suspended inorganic matter. Finally, most of the taxa exhibited a negative correlation with depth.

Gastropoda, Amphipoda, Ephemeroptera, Plecoptera, Trichoptera and Chironomidae densities exhibited statistically significant differences between hydrological periods, with highest values during low flow periods and lowest during high flow (January) (Fig. 3-6). Statistically significant differences were found for all the taxa but Amphipods and Trichoptera between areas of the river: Gastropoda and Plecoptera showed higher densities in downstream areas (Fig. 3), Ephemeroptera and Coleoptera were more abundant in areas with influence of First Labyrinth, 60-70 km from Lake Argentino (Fig. 4 and 5), and Chironomidae showed differences in abundance without a clear pattern. Higher density of chironomids close to Lake Argentino, might be due to the proximity to Bote River, which is an area with exotic riparian willows and some agriculture in nearby farms and, therefore, organic matter enrichment.

The functional response of different taxa to environmental variables varied widely (Table 2, Fig. 3-6). Gastropods density exhibited a quadratic response to substrate and dissolved oxygen, with maximum density values at intermediate values of these variables, and a positive linear relationship with current speed and a negative linear one with local depth (Table 1). Amphipods showed linear relationships with all environmental variables: positive with temperature and negative with chlorophyll-a concentration (Fig. 6). Model fit for Ephemeroptera was more complex and with more significant variables: quadratic relationships with substrate composition, temperature and depth, a positive linear relationship with current speed and conductivity, and a negative linear relationship with wet width (Fig. 4). These conditions were associated to areas with influence from the First Labyrinth. Similarly, the density of Plecoptera was significantly associated with several variables: a positive linear response to conductivity and quadratic responses to depth, chlorophyll-a concentration, current speed and substrate composition (Fig. 3). Densities of Trichoptera decreased with river width and substrate particle size, and were maximal for intermediate current speed and extreme conditions of conductivity and depths. Chironomids showed a positive linear relationship with local depth and substrate particle size, and a negative linear response to chlorophyll-a concentration. Finally, the density of Coleoptera, one of the most abundant taxa along the river, was positively related with substrate particle size, negatively with increasing temperature and maximal at intermediate current speed conditions, and minimal at intermediate depth (Fig. 5).

Discussion

Based on this study, the list of aquatic macroinvertebrate species in the Santa Cruz River was significantly augmented from numbers previously reported by Miserendino (2001) and by Tagliaferro et al. (2013). We identified fifty-three exclusive benthic taxa and analyzed the temporal and spatial distribution patterns of the most abundant orders. In agreement with those previous studies, we found that the density of macroinvertebrates was among the lowest among large rivers of Patagonia, comparable to those recorded in neighboring Baker and Pascua rivers in Chile. The overall low abundance and diversity might be a reflection of the low habitat availability, itself a response to the physical and chemical, geomorphologic, and hydrologic homogeneity characteristic of the Santa Cruz River (Smith et al., 2003; Townsend et al., 1987). In fact, higher densities of certain macroinvertebrate orders within the Santa Cruz were associated with areas of increased habitat complexity (e.g., the “First Labyrinth” and close to the river mouth), supporting the relationship between homogeneity and habitat supply. The higher density of chironomids close to Lake Argentino could be due to a local enrichment effect of the more productive Bote River, separated only 200 meters from the sampling site. Meanwhile, the higher density of macroinvertebrates recorded during the low flow period could be due to a concentration effect or to a functional response to increased gravel-bar habitat availability at higher exposure. The natural stability of the Santa Cruz could be accounting for the conspicuous presence of taxa such as Ephemeroptera and Plecoptera which are known to be sensitive to anthropogenic effects.

The combined use of different statistical approaches improved our understanding of the response of different macroinvertebrate taxa to environmental conditions. Whereas the ordination analysis of macroinvertebrates in relation to environmental variables provided an indication of association between them, the GLM models enabled a more comprehensive evaluation at the order level. The CCA analysis showed a strong association of species or genera with certain environmental conditions, whereas the fit of GLM models provides insight into the specific functional response of sets of species or genera to those variables. In agreement with findings in similar environments elsewhere, the main explanatory variables of macroinvertebrate density were the size of substrate particles, water velocity, depth and water temperature (Malmqvist & Mäki, 1996; Miserendino, 2001; Miserendino & Pizzolón, 2003). Through the CCA ordination, it was possible to identify groups of taxa associated by their feeding habits or habitat requirements: a high affinity of collectors-gatherers with FPOM was found, scrapers were associated to shallow cold waters with low suspended matter, plecopterans (mainly shredders) were more abundant in sites with large substrate size, deep, more oxygenated waters, condition particularly appropriate for *K. kuscheli* and *Antactoperla michaelseni* Klapálek 1904.

One of the main points emerging from the use of GLMs is the shape of relationships found between particular species and environmental variables. GLM models enabled to investigate seasonal changes (related to hydrological periods) that will be particularly important to evaluate management scenarios related to dams. A general and repeated temporal pattern for all macroinvertebrate orders showed that minimum densities occurs during high water flow and maximum tends to occurs during low water flow periods, which might be associated to the scouring effect of high water flow, hydraulic stress and flooding of habitats exposed during low flow.

Dams have profound effects through the fragmentation of an otherwise continuous river corridor, the downstream effects through the intervention and disturbance of natural flow patterns and water characteristics, and the flooding of upstream areas with conversion from lotic to lentic. The effects of fragmentation on macroinvertebrates in the Santa Cruz River are rather unfathomable and largely speculative due to the many unknowns related to life cycles, dispersal mechanisms and community-level processes. Meanwhile, our results can help us conceive some of the likely effects of flow regulation in downstream sections and flooding of upper sections. Of particular importance in flow regulation below dams are the sudden changes in discharge that typically occur in response to energy demands, which introduce a short-term variability in flow uncharacteristic of large rivers. Most important variables influencing macroinvertebrate abundance are related to substrate composition, suspended matter, primary productivity, dissolved oxygen, flow velocity and depth, all of which are likely to experience changes in regulated streams. Jakob et al. (2003) found a negative effect of floods on the number, richness, and density of macroinvertebrates in the Spöl River of the Swiss National Park. A reduction of 53–72% of overall density of macroinvertebrates was estimated to be experienced within 10 days of a flood event (Mc Mullen & Lyttle, 2012).On the other hand, Haxton and Findlay (2008) indicated that macroinvertebrate abundance was lower in areas that were dewatered owing to water fluctuations or low flows, which can be due to the presence of benthic invertebrates inhabiting shallow areas, generally the most productive ones (Gislason, 1985; Tagliaferro et al., 2013). Flow alteration is also able to homogenize the benthic habitat structure (Hart & Finelli, 1999), which can determine the distribution of benthic biota (Sandin, 2009). Specialist species found in flowing water habitats ("fluvial specialists"; Kinsolving & Bain 1993) will be more sensitive to sudden flow changes during dam construction and operation, and may decline and be replaced by more generalist species (Zhong & Power, 1996; Herbert & Gelwick, 2003). For instance, typically sensitive orders in the Santa Cruz River like Plecoptera, Ephemeroptera and Trichoptera, are expected to be reduced in abundance and richness, while some Diptera families are expected to have the same fate. Others, such as some cosmopolitan chironomids genera could strive in the new conditions in a context of reduced competition and predation. Other taxa that are expected to benefit from altered conditions are non-insect taxa, such as gastropods (which had no clear seasonal pattern in the Santa Cruz River) and amphipods (Jakob et al., 2003).

On the other hand, flow regulation in the hyper-stable Santa Cruz River may add a stronger alternation between low and high flow, as well as periodic bed scour and floodplain inundation, adding some new longer term variability in discharge. When naturally occurring, such processes are known to contribute to a checkerboard type of habitat heterogeneity in rivers, to increased biocomplexity, and higher biodiversity (Power et al., 1996). The balance between the expected strong effects of sudden flow changes on given species and the increased variability in flow conditions, mediated by the propagation of species-level effects through the food web, will in the end determine the structure and dynamics of macroinvertebrate assemblages in the free flowing section below dams. Our results help identifying the main actors, their habitat preferences, and their relative susceptibility to specific changes in river conditions, but the construction of future scenarios will require community and food web perspectives.

Dams not only change the flow patterns downstream but also water attributes. For instance, reservoirs may suffer thermal stratification and, through hypolimnetic release, generate substantial changes in the physical and chemical characteristics of the water in the streams below (Haxton & Findlay, 2008; Martínez et al., 2013), and significant changes in the transport of materials (sediments and organic matter)

(Ward & Stanford, 1979, 1982; Poff et al., 1997; Doyle et al., 2003; Léger & Leclerc, 2007). Haxton & Findlay (2008) found that hypolimnetic draw was associated with reduced abundance of downstream aquatic communities and macroinvertebrate abundance due to oxygen depletion. If such changes were to occur in the Santa Cruz River, macroinvertebrate taxa that require high dissolved oxygen concentrations like the Plecoptera *K. kuschelli* and *A. michaelseni*, the Ephemeroptera *M. chiloeensis* and *Andesiops* sp., as well as most Hydrobiosidae species (Trichoptera), could be affected. Another variable of great importance in freshwater systems is water temperature, which is one of the most frequently affected variables by river impoundment (Pozo et al., 1997; Bredenhand & Samways, 2009), and it is a very important factor for the biology and the evolutionary ecology of stream insects (Ward & Stanford, 1982). Epilimnetic or hypolimnetic draws tend to increase or decrease, respectively, downstream temperatures depending on time of year (Haxton & Findlay, 2008).

Our analyses revealed two general patterns of taxon-level macroinvertebrate density along the river: an increase towards the river mouth or a unimodal relationship with distance, with maxima in the central reaches. Likewise, the most productive areas in term of both primary and secondary productivity along the Santa Cruz River were reported to occur in mid-stream areas (60-150 km from Lake Argentino) (Tagliaferro et al., 2013), and above the projected dams, and will shift from lotic to lentic. Furthermore, since the most sensitive macroinvertebrate taxa (located in those areas) are important components of the diet of salmonids and galaxiids present in the Santa Cruz River (Tagliaferro et al., 2015), profound changes in food webs are expected to occur in the new lakes. Thus, we consider that a detailed study on aquatic communities combined with existing extensive research of patterns of macroinvertebrate abundances, relationships between fish and their environment (Tagliaferro et al., 2014; Quiroga et al., 2015) should be evaluated to project the likely effects of dams in the Santa Cruz River.

Finally, regulation, legislation and implementation of law are delayed in relation to the two hydroelectric dams. In-river construction began in January 2015, few official documents are available at the Ministerio de Planificación (2015), and no pre-impoundment study on river biota was done. Official documents indicate that ecological minimum flow (from the study of extremes for annual minimum flows) was set at 180 $m^3 s^{-1}$, and using standard criteria, a period of ten thousand years was considered for extreme design event, that resulted in a flow of 4,100 $m^3 s^{-1}$; with weir gate of 3,927 $m^3 s^{-1}$, and free spillway of 220

m^3 s^{-1}. These “ecological flow” results out of range of min and max flow calculated by Tagliaferro et al. (2013); they exceed the maximum and understate the minimum. Furthermore, since energy requirement are higher during late spring and summer, the functioning of the dams will be adequated to human needs, releasing a large amount of water in a short period of time (Ministerio de Planificación, 2015). Under this scenario, and considering that only fish management is being considered by implementing fish scale, only few of the existing species close to the dams will be able to tolerate these conditions. Poff et al. (2015) emphasized that rapid climate change, population growth and economic trends are generating unprecedented uncertainty about how to achieve sustainability targets for water management and ecosystem conservation, as well as simultaneous opportunities to find common ground. Thus, it is difficult to think of conservation policies such as those raised by the European Union (EC, 2000, 2009) and mentioned by Khamis et al. (2014), in view of the imminent energy crisis that will keep Argentinean people (in populated cities like Buenos Aires) without energy supply for days and water scarcity, in addition to human priorities and those proposed by local stakeholders that consider dams as an economical benefit. In these sense, we agree with Poff et al. (2015) that a global perspective with all stakeholders in the use of water will be needed for better management of resources and to reduced impact on the biological communities.

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Figure Captions

Fig. 1 Map of the Santa Cruz River, Argentina. Vertical arrows show locations of sampling sites and filled arrows show dams position.

Fig. 2 Canonical Correspondence Analysis (CCA) of macroinvertebrate taxa and environmental variables. Inverted filled triangles indicate predators, empty circles indicate collectors-gatherers, filled circles indicate scrapers, squares indicate collectors-filterers, and “x” indicates shredders. Taxa code: *Chilina* sp. (Ch), *Heleobia* sp. (He), *Lymnaea* sp. (Ly), Glossiphoniidae sp1 (G1), sp2 (G2), Haplotaxidae (Hp), Lumbriculidae (Lb), Nadidae sp1 (N1), sp2 (N2), sp3 (N3), Acari (Ac), *Hyalella araucana* (Ha), *H. curvispina* (Hc), *Andesiops* sp. (Ad), *Meridialaris chiloeensis* (Mc), *Baetes* sp. (B), *Aubertoperla illiesi* Frowhlich 1960 (Au), *Antarctoperla michaelseni* (Am), *Araucanioperla* sp. (Ar), *Klapopteryx kuscheli* (Kk), *Limnoperla jaffueli*

Navás 1928 (Lj), *Luchoelmis cekalovici* (Lc), *Mastigoptila* sp. (M), *M. longicornuta* Schmid 1958 (Ml), *Atopsyche* sp. (At), *Rheochorema* sp. (Rh), *Cailloma* sp. (C), *Iguazu* sp. (Ig), *Smicridea dithyra* Flint 1974 (Sd), *Oxyethira* sp. (O), *Eukifferiella* sp. (Eu), *Paratrichoclaudius* sp. (Pcl), *Endotribelos* sp. (En), *Chironomus* sp. (Chr), *Parachironomus* sp. (Pch), *Parametricnemus* sp. (Pmt), *Alotanipus* sp. (Al), Pelecorhinchidae (Pe), Empididae sp. (Em), Muscidae spp. (Mu), *Cnesia* sp. (Cn), *Simulium* sp. (Si), *Pedrowygomia* sp. (Pe), *Hexatoma* sp. (Hx), Rhagionidae (Rha), Tanypodinae (Tan).

Fig. 3 Estimated polynomial adjusted by using GLM for Plecoptera (stoneflies). The dotted lines represent 2 x standard error each point of the curve. Time: April 2010 (Apr), August 2010 (Aug), January 2011 (Jan), May 2009 (May), September 2009 (Sep9), September 2011 (Sep11).

Fig. 4 Estimated polynomial adjusted by using GLM for Ephemeroptera (mayflies). The dotted lines represent 2 x standard error each point of the curve. Time: April 2010 (Apr), August 2010 (Aug), January 2011 (Jan), May 2009 (May), September 2009 (Sep9), September 2011 (Sep11).

Fig. 5 Estimated polynomial adjusted by using GLM for Coleoptera (beetles). The dotted lines represent 2 x Standard error each point of the curve. Time: April 2010 (Apr), August 2010 (Aug), January 2011 (Jan), May 2009 (May), September 2009 (Sep9), September 2011 (Sep11).

Fig. 6 Estimated polynomial adjusted by using GLM for Amphipods. The dotted lines represent 2 x standard error each point of the curve. Time: April 2010 (Apr), August 2010 (Aug), January 2011 (Jan), May 2009 (May), September 2009 (Sep9), September 2011 (Sep11).

Fig. 1. Map of the Santa Cruz River, Argentina. Vertical arrows show locations of sampling sites and filled arrows show dams´ position.

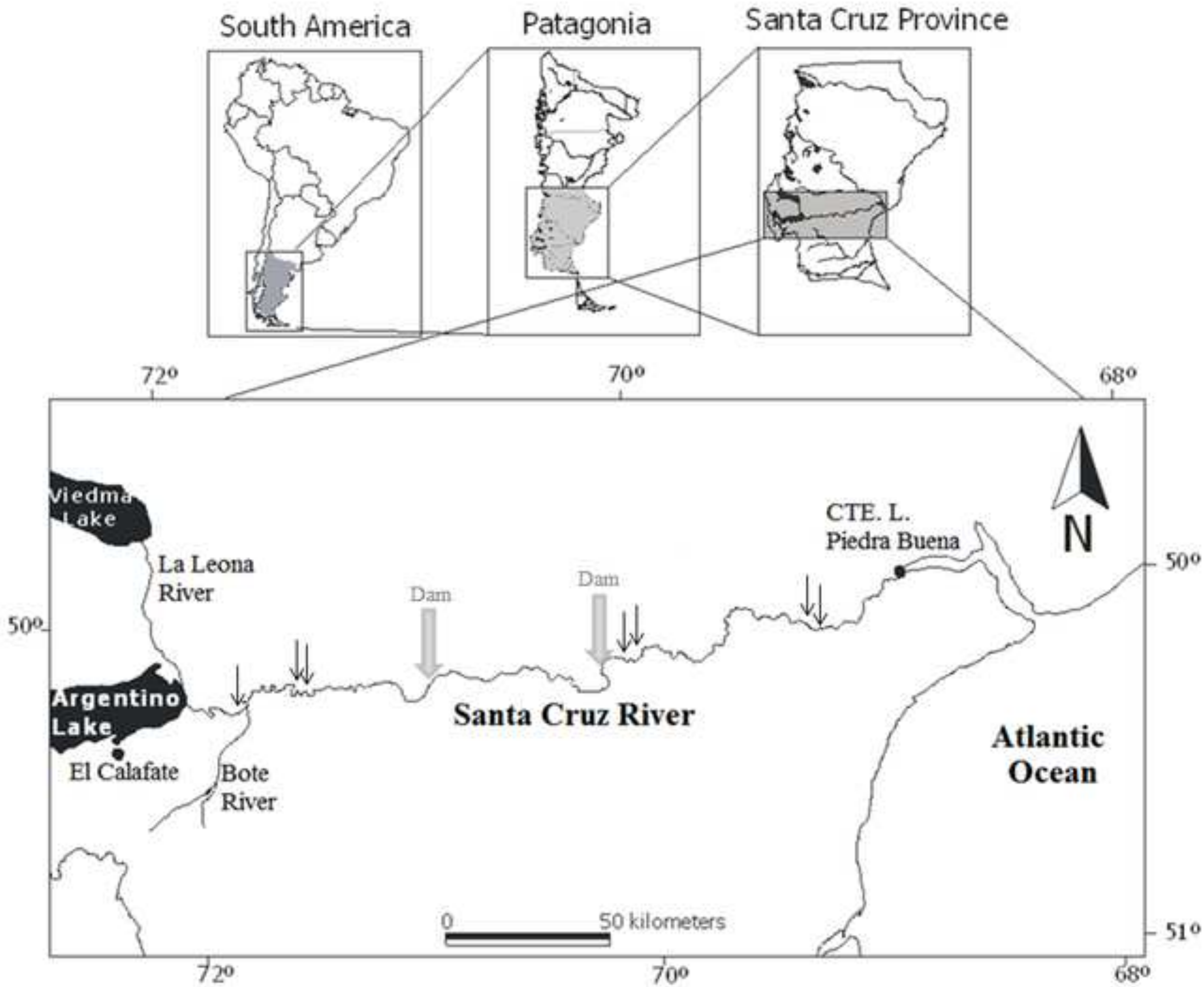

Fig. 2. Canonical Correspondence Analysis (CCA) of macroinvertebrate taxa and environmental variables.

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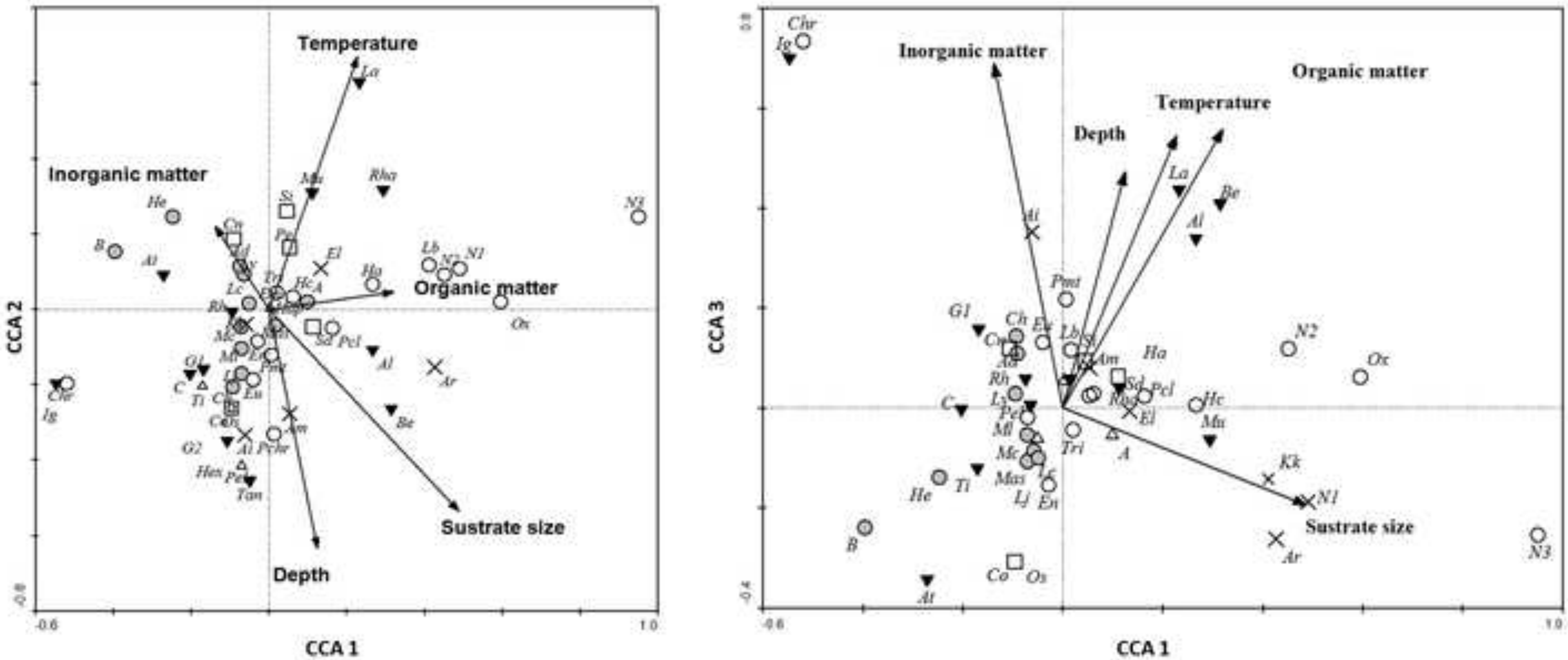

Fig. 3. Estimated polynomial adjusted by using GLM for Plecoptera (stoneflies).

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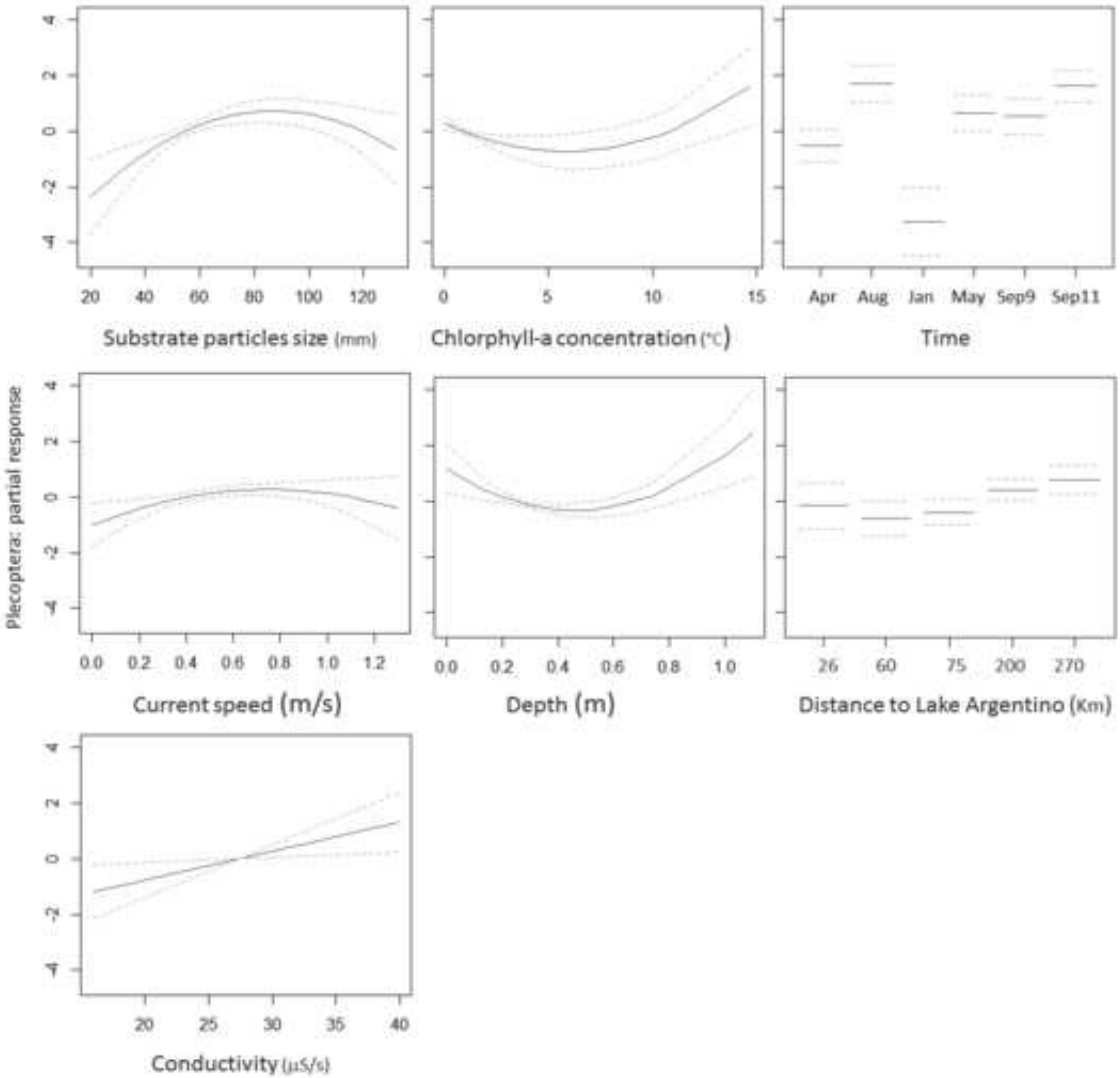

Fig. 4. Estimated polynomial adjusted by using GLM for Ephemeroptera (mayflies).

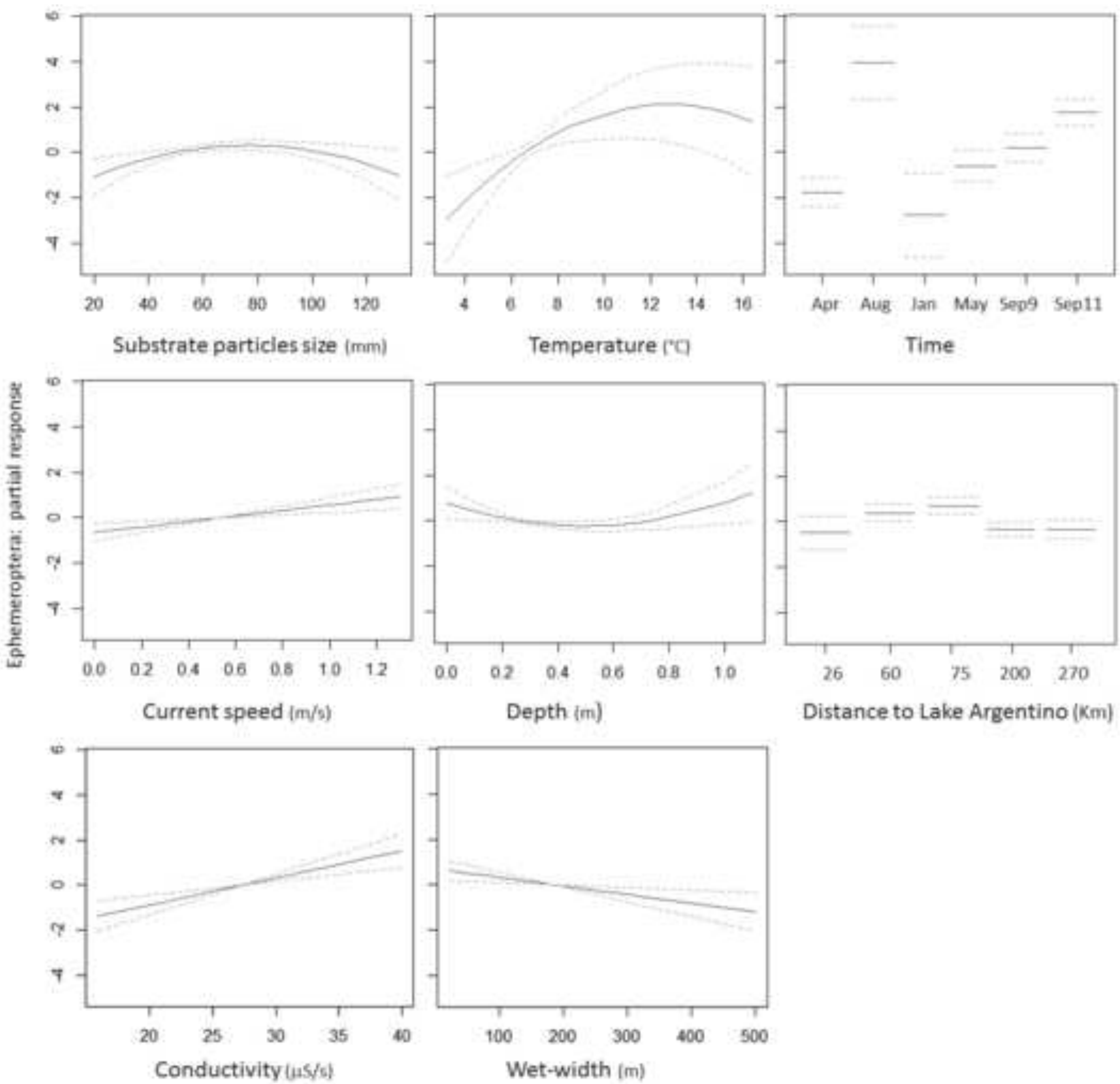

Fig. 5. Estimated polynomial adjusted by using GLM for Coleoptera (beetles).

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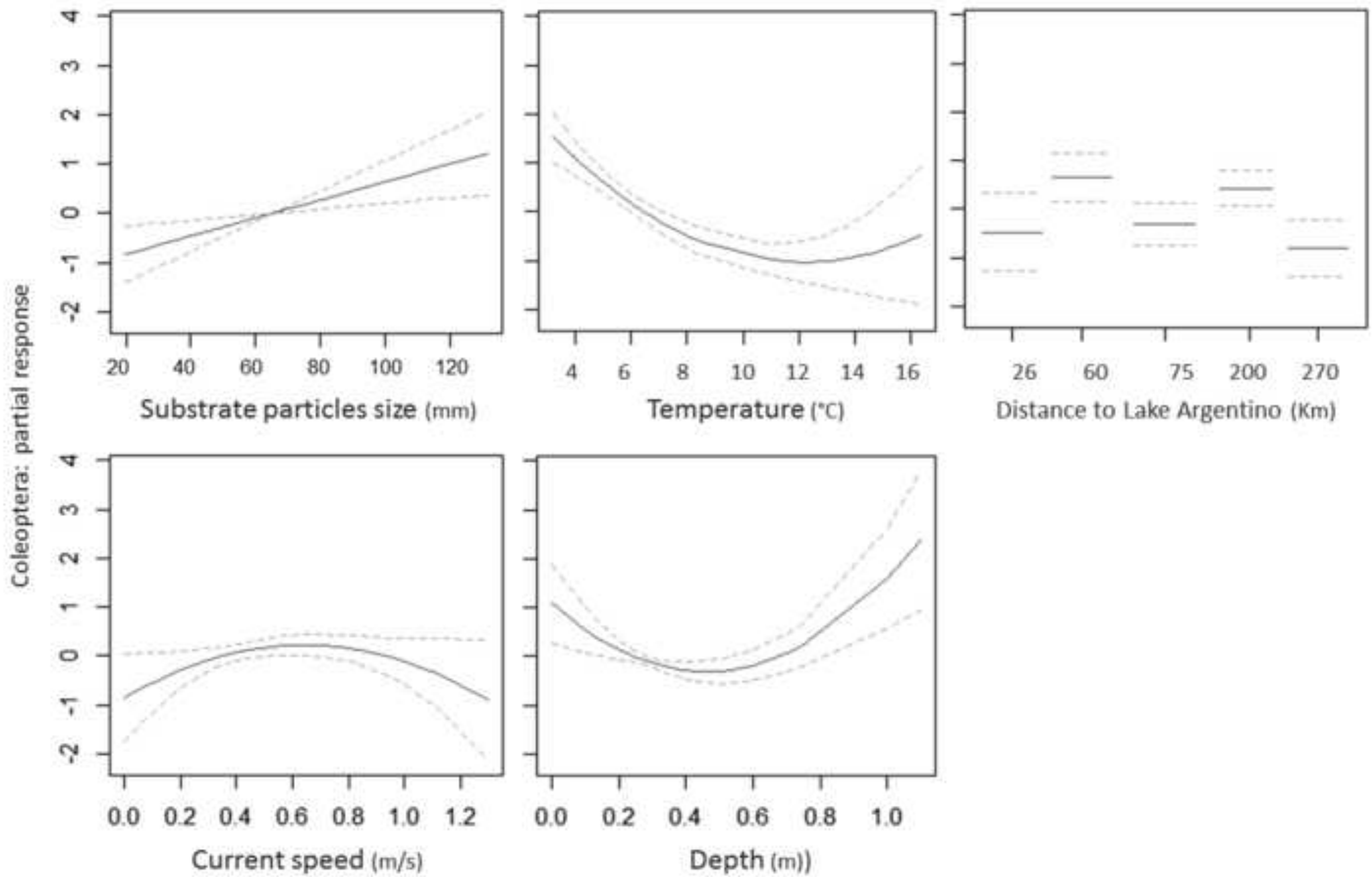

Fig. 6. . Estimated polynomial adjusted by using GLM for Amphipods.

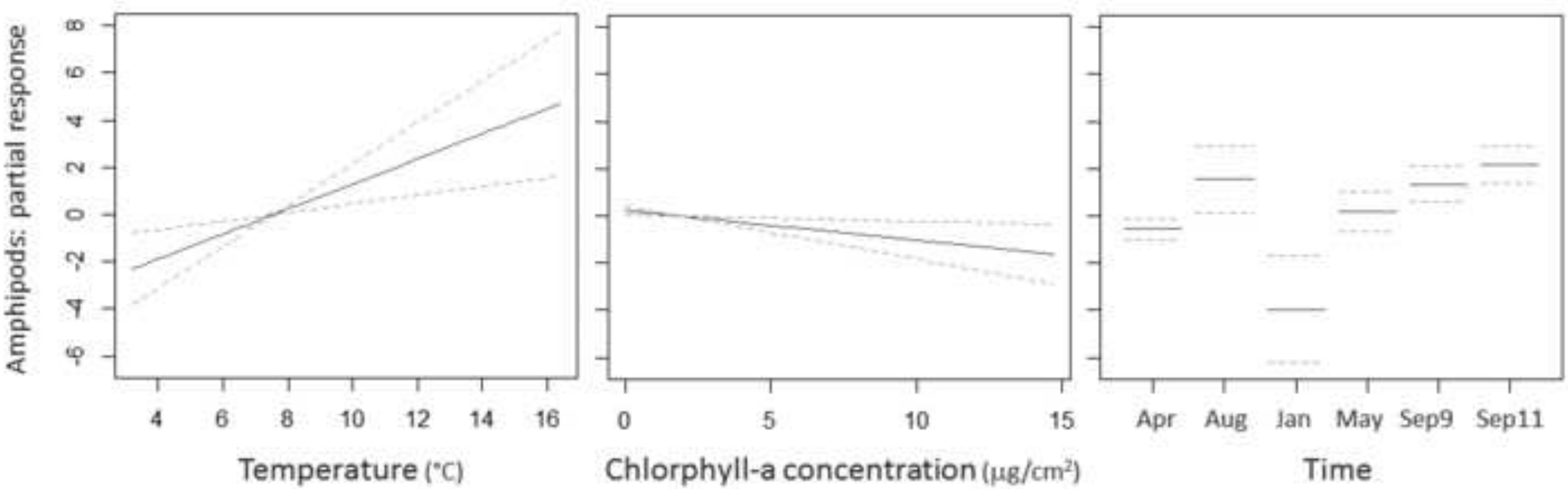

Table 1 Eigenvalues axis values and weight of intraset correlations between the axes of the CCA and environmental variables in relation to the abundance of different taxa of macroinvertebrates. The significance of Monte Carlo test for the axes is displayed below.

	CCA 1	**CCA 2**	**CCA 3**
Eigenvalues	0.12	0.09	0.03
Species-environmentcorrelation	0.87	0.86	0.84
% variance of species explain by data	11.2	8.0	3.9
% cumulated explanation in relation to environment	39.7	68.1	81.9
Correlation with axes			
Depth	0.12	-0.63	0.47
Temperature	0.23	0.67	0.55
Sustratesize	0.48	-0.53	-0.19
Inorganic matter	-0.14	0.22	0.69
Organic matter (FPOM)	0.32	0.05	0.56

Monte Carlo permutation test:
Axis 1: F=3.158. p< 0.0002
All canonical axes: F=1.969. p= 0.0001

Sum of all eigenvalues: 1.211
Sum of all canonical eigenvalues 0.790

Table 2 Model selection. "All" includes all variables: flow velocity (Vc), wet-width of the river (Am), chlorophyll-a (Chl-a), size of substrate particles (Ss), dissolved oxygen (DO), suspended matter (MO, MI), temperature (T), depth (D) and conductivity (cond). When symbol "-"is located between "All" and another variable, it means all variables but that one. Models are composed by a polynomial and a linear relationship with variables. df: indicates degree of freedom. Resid.Dev.: indicates the residual deviation. AIC: indicates the model Akaike value, and % expl., indicates the % of variation explain using the model.

Taxa	Model	Polynomial- 2	Linear	df	Resid.Dev.	AIC	p	% expl.	Distribution
Gastropods	Null	-	-	131	228.25	607.0			bin.neg
	Best	Ss.DO	Vc.D.site.Time	116	118.6	565.9	2.8 E-09	48	bin.neg
	Full	All	Site.Time	102	114.22	577.7	0.6	49.9	bin.neg
Amphipoda	Null	-		131	242.9	789.0			bin.neg
	Best	Cl-a. T	Time	124	145.5	758.0	7.7 E-08	40.1	bin.neg
	Full	All -Ww	Site.Time	104	144.6	767.0	0.2	40.1	bin.neg
Ephemeroptera	Null	-		131	460	846.0			bin.neg
	Best	Ss. T.D	Vc.Ww. Cond.Site.Time	113	155.17	752.0		66.3	bin.neg
	Full	All	Site.Time	102	154.6	759.0		66.6	bin.neg
Plecoptera	Null	-		131	130.58	644.0			bin.neg
	Best	Ss.Chl-a.Vc.D	Cond.Site.Time	113	121.39	546.3		7	bin.neg
	Full	All	Site.Time	102	119.5	556.8		8.5	bin.neg
Coleoptera	Null	-		131	2006				quassi
	Best	T.Vc.D	Ss.Site.Time	120	1155		6.7 E-12	42.4	quassi
	Full	All- Ww	Site.Time	104	806.5		0.06	59	quassi
Trichoptera	Null	-		131	1400				quassi
	Best	D.Vc. Am. Cond	Ss.Site.Time	113	452.7		1.3 E-10	67.6	quassi
	Full	All	Site.Time	102	400		0.6	71.4	quassi
Chironomidae	Null	-		131	235.2	664.7			bin.neg
	Best		Chl-a.D.Site.Time	120	120.4	621.9	1.2 E-09	48.8	bin.neg
	Full	All - Cond	Site.Time	104	122	631.7	0.41	48.1	bin.neg

Annex 1 Physical and chemical variables measured at each sampling point. Mean value and standard deviation: current speed (Vc. m s^{-1}), local depth (D, m), water temperature (T, °C), size of sustrate particles (Ss, mm), dissolved oxygen (DO, mg L^{-1}); pH; conductivity (cond., µS cm^{-1}), suspended inorganic matter (MI, mg L^{-1}), suspended organic matter (MO, mg L^{-1}), river bankfull (Bf, m), wet-width (Ww, m), gravel bar (Gb, m), and chlorophyll-a concentration (Chl-a, µg cm^{-2}). "Km" indicates distance to Lake Argentino.

Period	Km	Vc	D	T	Ss	DO	pH	Cond.	MI	MO	Bf	Ww	Gb	Chl-a
May_09	26	0.3±0	0.5±0	6±0	82±0	15.8±0	6±0	25.3±0	9.4±0	23.8±0	256±0	233±0	23±0	1.1±0
	60	0.6±0.5	0.3±0.1	6.0±0.5	48±13	15.5±1.2	6.3±0.5	26.8±3.4	52.1±24.4	75.0±102.0	84±31	50±25	34±39	0.5±0.2
	75	0.5±0.4	0.5±0.2	6.2±0.2	60±6	14.3±0.6	6±0	28.4±4.5	72.5±1.6	24.0±11.0	256±91	230±109	26±21	0.4±0
	200	0.3±0.3	0.3±0.2	6.3±0.4	61±22	12.6±0.6	6±0	26.0±0.6	28.6±4.9	18.0±28.0	244±49	210±37	32±30	0.6±0.3
	270	0.3±0.2	0.4±0.2	6.2±1.0	73±28	12.4±0.5	6±0	24.5±3.6	11.1±1.8	1.1±0.2	192±23	166±22	25±24	0.6±0.7
Sep_09	26	0.6±0.3	0.5±0.2	6.0±0.6	109±41	14.3±3.5	6.3±0.3	26.3±0.9	16±0	43.3±0.3	178±60	152±47	24±17	0.57±0
	60	0.5±0.2	0.4±0.1	5.4±0.1	30±5	13.9±0.1	6±0	31.7±1.3	18.8±0.2	70.2±2.9	216±37	157±44	59±6	2.2±0
	75	0.2±0.1	0.4±0.1	6.0±0.5	55±12	13.4±1.9	5.9±0.2	32.5±3.8	15.0±0.9	15.9±1.5	268±14	230±10	56±40	0.8±0
	200	0.4±0.3	0.5±0.2	6.4±0.5	68±24	12.6±0.9	6.1±0.2	26.0±4.3	6.5±0.5	1.4±0.7	209±70	169±68	27±16	0.4±1.1
	270	0.3±0.3	0.6±0.3	7.1±0.4	89±12	12.8±0.4	6±0	22.6±2.3	14±0.9	1.2±0.8	178±24	161±20	18±10	0.9±0.5
Abr_10	26	0.5±0	0.3±0	8.2±0	132±0	11.6±0	6±0	29±0	7.0±6.4	9.9±5.4	159±0	143±0	16±0	0.2±0.1
	60	0.5±0.2	0.4±0.2	7.9±0.1	56±7	11.6±0.3	6.3±0.3	28.1±0.3	13.5±6.7	7.0±5.0	215±137	163±134	51±32	0.5±0.1
	75	0.6±0.2	0.3±0.1	8.2±0.2	49±15	12.1±0.4	6.3±0.3	33.7±5.3	39.3±16.4	9.4±6.8	303±170	297±172	10±7	0.4±0.2
	200	0.6±0.1	0.4±0.1	7.5±0.2	53±11	11.9±0.4	6±0	28.0±1.2	6.9±3.6	7.8±7.4	237±30	203±12	29±17	1.8±4.0
	270	0.6±0.1	0.4±0.1	8.3±0.3	57±3	11.6±0.4	6±0	29.7±1.5	9.8±2.2	3.0±1.7	217±18	182±20	34±14	0.2±0.1
Ag_10	26	0.2±0	0.2±0	4±0	116±0	12.7±0	6±0	24.5±0	7.3±0	1.1±0	151±0	117±0	34±0	1.42±0
	60	0.2±0.2	0.2±0.1	3.4±0.2	39±17	12.5±0.1	5.7±0.3	23.2±0.3	3.2±2.5	3.2±0.8	322±52	247±86	74±34	0.4±0.5
	75	0.5±0.3	0.4±0.3	3.9±0.3	79±16	12.7±0.1	6±0	22.8±0.2	6.9±1.8	2.2±0.9	235±33	187±25	44±12	0.8±0.3
	200	0.5±0.3	0.4±0.2	3.9±0.3	66±7	12.5±0.48	6±0	24.1±0.2	6.8±2.1	4.4±3.3	243±35	193±31	50±18	0.4±0.2
	270	0.2±0.2	0.6±0.5	4.1±0.2	67±20	12.3±0.4	6±0	24.0±0.1	3.0±1.6	2±1.8	174±18	125±24	48±25	0.7±0.3
Jan_11	26	0.6±0	0.2±0	11.8±0	62±0	11.5±0	5.5±0	33±0	29.2±0	40.5±0	230±0	214±0	16±0	4.5±0
	60	0.8±0.2	0.4±0.3	13.1±1.1	56±10	11.4±0.1	5.7±0.3	31.3±2.8	27.7±14.0	10.4±16.8	332±29	305±26	26±12	1.8±0.2
	75	0.9±0.3	0.5±0.1	12.4±1.9	39±23	12.4±0.1	6±0	30.1±3.8	8.0±0.6	1.3±0.4	326±76	256±48	70±28	0.9±0.1
	200	0.6±0.1	0.4±0.2	13.8±1.0	66±26	11.2±0.6	6±0	28.2±8.1	10.0±4.5	1.3±0.3	272±36	193±24	42±10	3.5±4.0
	270	0.7±0.2	0.4±0.2	15.9±0.7	55±14	10.5±0	6±0	30.1±3.3	13.8±1.3	2.0±0.6	218±36	182±23	35±20	0.7±0.4
Sep_11	26	1±0	0.3±0	4.8±0	120±0	13.7±0	6±0	25.7±0	8.5±0	3.4±0	156.5±0	116±0	40±0	0.9±0
	60	0.5±0.3	0.3±0.1	5.8±0.4	48±5	10.9±0.4	5.8±0.3	26.4±0.5	9.6±1.1	1.9±0.3	240±10	151±22	88±28	11.0±3.3
	75	0.4±0	0.4±0	6±0	81±0	12.9±0	6±0	25±0	9.4±0	2±0	300±0	260±0	40±0	4.0±0
	200	0.8±0.3	0.4±0.1	6.5±0.6	78±4	11±0.7	6±0	27.4±2.3	10.8±1.6	2.1±0.4	201±57	156±45	45±36	2.6±2.3
	270	0.6±0.2	0.4±0.2	5.8±0	98±15	12.5±0.1	5.8±0.3	29.4±0.8	14.6±1.4	2.0±0.4	179±8	142±19	36±24	2.7±3.1

Annex 2 Macroinvertebrates relative abundance, percentage of presence along all sampling sites, and functional feeding groups (FFG). SH: shredder.SC/GR scraper/grazer; CG collector-gatherer; CF collector-filterer; PR predator.

Taxa	**FFG**	**Relative abundance (%)**	**% sites present**
Mollusca			
Chilina sp. (Ch)	SC/GR	0.2	6.8
Heleobia sp. (He)	SC/GR	0.8	6.1
Lymnaea sp. (Ly)	SC/GR	8.7	48.5
Annelida			
Glossiphoniidae sp1 (Gl)	PR	0.1	5.3
Glossiphoniidae sp2 (Gl2)	PR	<0.1	0.8
Haplotaxidae (Hp)	CG	< 0.1	0.8
Lumbriculidae (Lb)	CG	0.2	11
Naididae sp1 (N1)	CG	0.3	6.1
Naididae sp2 (N2)	CG	<0.1	2.3
Naididae sp3 (N3)	CG	0.1	3
Acari			
Acari spp. (Ac)	SR/GR	1.2	12.1
Crustacea			
Copepoda (Co)	CF	<0.1	0.8
Ostracoda(Os)	CF	<0.1	0.8
Hyalella araucana (Ha)	CG	12.4	78
Hyalella curvispina(Hc)	CG	0.7	18.2
Ephemeroptera			
Baetes sp. (B)	SC/GR	0.1	3.8
Andesiops sp. (Ad)	SC/GR	3.7	47
Meridialaris chiloeensis (Mc)	SC/GR	13.6	62.1
Plecoptera			
Aubertoperla illiesi (Ai)	SH	0.2	2.3
Antarctoperla michaelseni (Am)	SH	1.6	15.1
Araucanioperla sp. (Ar)	SH	< 0.1	1.5
Klapopteryx kuscheli (Kk)	SH	4.9	44.7
Limnoperla jaffueli (Lj)	SC/GR	2.4	23.5
Coleoptera			
Luchoelmis cekalovici (Lc)	SC/GR	13.6	71.2
Luchoelmis cekalovici (El) - adult	SH	0.1	3.8
*Berosus*sp.(Be)	PR	<0.1	0.8
*Lancetes*sp.(La)	PR	<0.1	1.5
Trichoptera			
Mastigoptila sp. (M)	SC/GR	0.3	5.3
Mastigoptila longicornuta (Ml)	SC/GR	2.2	18.9
Atopsyche sp. (At)	PR	0.1	3
Rheochorema sp.(Rh)	PR	1.4	32.6
*Cailloma*sp. (C)	PR	0.4	10.6
Iguazu (Ig)	PR	<0.1	1.5
Smicridea dithyra (Sd)	CF	1.9	14.4
*Oxyethira*sp. (Ox)	CG	0.3	4.5
Diptera			

Eukiefferiella sp. (Eu)	CG	2.4	20.5
Paratrichocladius sp. (Pcl)	CG	17.4	47
Parametriocnemus (Pmt)	CG	0.2	1.5
Chironomus sp. (Chr)	CG	0.1	7
Parachironomus sp. (Pch)	CG	1	7
Tribelos sp. (Tri)	CG	<0.1	1.5
Endotribelos sp. (En)	CG	0.1	2
Tanypodinae (Tan)	PR	<0.1	0.8
Alotanypus sp. (Al)	PR	<0.1	2.3
Pelecorhynchidae (Pe)	PR	< 0.1	1.5
Empididae sp. (Em)	PR	<0.1	1.5
Muscidae sp. (Mu)	PR	0.3	11.4
Rhagionidae (Rha)	PR	<0.1	0.8
Cnesia sp. (Cn)	CF	5.6	40.9
Simulium (Si)	CF	0.2	3
Pedrowygomia (Pe)	CF	<0.1	0.8
Tipulidae (Ti)	PR	0.1	4.5
Hexatoma sp. (Hex)	PR	<0.1	0.8