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Dams in the last large free-flowing rivers of Patagonia, the Santa Cruz River, environmental features, and macroinvertebrate community

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ABSTRACT

Three large rivers have their headwaters in the Patagonian Ice Fields (PIFs) in the Andes Mountains, the largest mid-latitude ice masses on Earth: Santa Cruz, Baker and Pascua. They are the last large free flowing rivers in Patagonia, but plans are advanced for building dams for hydroelectric power generation. The three PIF rivers, with a discharge dominated by ice melt, share a common, unique hydrograph compared to that of the other eight large rivers in the region: a distinct seasonal cycle, and an extremely stable discharge, with much lower variability than other rivers. In this study we present the first extensive survey of habitats and benthic macroinvertebrates in the least studied system, the Santa Cruz River. We assess how much of the natural capital provided and sustained by benthic invertebrates are expected to be lost by flooding and discuss how dams would affect riverine habitat and biota. In the Santa Cruz River, we conducted an intensive field survey during September 2010; a total of 52 sites located at regular 6 km intervals were sampled along the 310 river-km for macroinvertebrates and seventeen habitat variables. Although some habitat structure is apparent at the local scale, the Santa Cruz River could be described as very homogeneous. Macroinvertebrate density and the richness (38 genera) found in the Santa Cruz River resulted to be one of the lowest in comparison with 42 other Patagonian rivers. Albeit weak, the structure of the macroinvertebrates assemblages was successfully described by a reduced set of variables. The reduced flow variation and the lack of bed scouring flows have a direct and negative effect on the heterogeneity of riverbeds and banks. The high turbidity of the Santa Cruz River may also contribute to shorter food webs, by affecting autotrophic production, general trophic structure, and overall macroinvertebrate productivity and diversity. Dams will obliterate 51% of the lotic environment, including the most productive sections of the river according to our macroinvertebrate data. Since Santa Cruz River has a naturally homogeneous flow cycle, dams may provide more variable flows and more diverse habitat. Our data provide critically valuable baseline information to understand the effects of dams on the unique set of glacial driven large rivers of Patagonia.

Introduction

The Patagonian Ice Fields (PIFs) in the Andes Mountains of Chile and Argentina, the largest mid-latitude ice masses on Earth, dominate the discharge of rivers in South America south of 45° S (Barnett et al. 2005; Rivera et al. 2005). Three large rivers have their headwaters in the Ice Fields: Santa Cruz in Argentina, and Baker and Pascua in Chile; mean annual discharge of 691, 875, and 574 $m^3 s^{-1}$, respectively. Because of their remote location and the lack of supporting infrastructure, the three rivers have remained free of dams, something that is bound to change. Chile and Argentina will be building dams in all three rivers in the next ten years. Two dams programmed for the Santa Cruz River are projected to supply 16% of Argentina's hydropower (Quiroga 2008) and a series of five dams to be built in the Pascua and Baker rivers are expected to supply over 20% of Chile's hydropower (Endesa 2006).

Large glacial rivers, such as the Baker, Pascua and Santa Cruz rivers, are expected to have unique characteristics. Glacier regimes provide a strong regulation of discharge, high water volumes will buffer temperature, and turbidity will hamper primary production (Johnson et al. 1995); all these characteristics will project to river ecosystem functions (Puckridge et al. 1998). Glacier rivers also have a predictable flood pulse which allows both aquatic and terrestrial organisms to adapt to the pulse (Milner et al. 2009; Sparks 1995). The poor knowledge of the biological role of natural flow regimes and the reduced integrity of the world's large undisturbed rivers have led many researches to emphasize the importance of studying the few remaining unregulated rivers (Biggs et al. 2005; Glova and Duncan 1985; Puckridge et al. 1998; Sparks 1995; Welcomme 1995) and the modifications produced by dams (Bunn

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and Arthington 2002; Glova and Duncan 1985; Sparks 1995; Poff and Ward 1989).

In the present paper we focused on the natural resources of this remarkable set of remote and poorly known large rivers. The onset of the hydroelectric projects in the Baker and Pascua Rivers prompted the implementation of impact assessments, including the gathering of baseline data on aquatic biota (Salas Contreras 2007). This baseline includes fauna and flora, as well as geological and other physical features. In the Baker River, variations in the abundance and richness of macroinvertebrates taxa were associated to hydrology, whereas hydraulic control (*e.g.* current speed, flow, fluid power) was indicated as the main forcing factor in the Pascua River (Salas Contreras 2007). The Santa Cruz River, on the other hand, has not been studied from an integral viewpoint. Separate studies have examined its physicochemical characteristics (Depetris et al. 2005; Gaiero et al. 2006), its macroinvertebrate assemblages at head waters (Miserendino 2001, 2004), and its exotic fish populations (Pascual et al. 2001; Pascual et al. 2007); information at the community level and on basic environmental variables (*e.g.* substrate size, depth, dissolved oxygen) is virtually non-existent. The first naturalist to set foot in the Santa Cruz almost two hundred years ago, Charles Darwin, underscored the low production and the uniformity of the environment in his description of the river valley (Darwin 1839). A first look at some physical and biological features of the Santa Cruz supports Darwin's observations. The river has a highly predictable discharge (Brunet et al. 2005; Pasquini and Depetris 2011) and a low biodiversity. Previous studies reported the macroinvertebrate density and taxa richness in this river to be one of the lowest as compared to other 28 rivers of Patagonia (Miserendino 2001). Whether this is a result of the particular physical characteristics of the Santa Cruz or not remains unknown so far.

In this study we present the first extensive survey of benthic macroinvertebrate assemblages of the Santa Cruz River in relation to within-river habitats, and within the context of regional rivers. Some general questions motivated our analyses: What are the particular characteristics of the three large rivers associated to the Patagonian Ice Fields, as compared to the set of Patagonian largest rivers? In particular, how typical is the Santa Cruz River among the rivers in the region? Do macroinvertebrate assemblages, a key component of riverine food webs, respond to specific environmental characteristics? How are dams expected to affect the river's structure and how is that expected to influence macroinvertebrate assemblages?

An additional, second tier motivation for our analyses is to generate realistic scenarios for how changes in the macroinvertebrate assemblages could affect the river community. The Santa Cruz River is the only river in the World where a self-sustaining anadromous rainbow trout (*Oncorhynchus mykiss*) population is known to have developed outside of the native range of the species (Pascual et al. 2001). Since freshwater systems in general and lotic systems in particular have strong trophic structures (Carpenter and Kitchell 1993; Power 2001), top predators are expected to be functionally important. Because invertebrates are prime items in the diet of both trout and native fish their study may provide key information to understand important community-level processes mediating the role and impacts of exotic fish.

In this paper we first characterize the Santa Cruz River in terms of its main physical characteristics (area, discharge, and hydrology) within the context of the largest rivers of Patagonia. We then characterize the macroinvertebrate assemblages along the 310 km of the mainstem river as a function of within river variability in habitat variables. Finally, we assess how dams are expected to affect riverine habitat structure and how much of the natural resources provided and sustained by benthic invertebrates are expected to be lost by flooding.

Methods

Study area

Eight of the largest Patagonian rivers were chosen for a general comparison with the Santa Cruz River (Fig. 1): Chubut, Gallegos, Negro and Neuquén within the Atlantic slope rivers, and Baker, Carrenleufú, Futaleufú, and Pascua rivers with a Pacific slope.

The Santa Cruz main stem river (50° S; 70° W) is located in the extra-Andean biozone (Del Valle et al. 1995), a scarcely vegetated plateau with semi-arid grass and low shrubs (Fig. 1). It originates in two oligotrophic to ultra-oligotrophic large glacial lakes (Brunet et al. 2005), Viedma and Argentino, and flows for 382 km across the Patagonian plateau to drain into the Atlantic Ocean (Fig. 1). River discharge is derived primarily from snow and glacial melt, which is in turn governed by the complex interaction between climatic conditions and the dynamics of the South Patagonian Ice Field (Pasquini and Depetris 2011). Average flow is 691 $m^3\ s^{-1}$, with an average minimum of 278.1 $m^3\ s^{-1}$ (September in the Southern Hemisphere) and an average maximum of 1278 $m^3\ s^{-1}$ (March). Annual mean water temperature is 9 °C with maxima registered in January (15 °C) and minima in July (3 °C). As a result of the high runoff (1446 mm $year^{-1}$), total dissolved solids (TDS) and dissolved nutrients are among the lowest among great Patagonian rivers (Depetris et al. 2005). However, suspended particles originated from glaciers are dominated by silt and clay which give the river a characteristic milky color.

The two dams projected for the Santa Cruz River (Fig. 1) are located at river km 132 (Cóndor Cliff, 50.206° S, 70.785° W) and at river km 197 (Barrancosa, 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 regulated river. Construction of supporting infrastructure (roads and accesses) is already under way and in-river construction is expected to begin within the next year.

Hydrological classification of Patagonian rivers

Three indices were calculated to characterize the hydrological regime for all eight rivers as follows. We first estimated an overall discharge function by fitting a single cubic polynomial function to the collection of ten monthly time series randomly selected from a pool of 20–50 years. Discharge range was then calculated as the difference between the maximum and the minimum value in the overall discharge function, divided by the average discharge. Maximum and Minimum flow months were determined from the overall discharge function as well. We then fitted cubic polynomial functions to each of the ten monthly time series. The within-year Coefficient of Variation (CV) was calculated as the square root of the residual variance of these fits, divided by the average discharge. The between-year CV was calculated as the square root of the residual variance of the 10 yearly fits with respect to the overall discharge function, divided by the average discharge (Zar 1984). Discharge data were obtained from Recursos Hídricos (2011) and Dirección General de Aguas from Chile (DGA 2011).

Santa cruz river analyses

In order to characterize within river variation in biological and physical characteristics of the Santa Cruz River we conducted an intensive field survey during September 20–29, 2010 (Min discharge month). Two crews navigated the main stem river downstream, one taking continuous measurements of depths and river widths and the other making stops for stream habitat measurements and biological samples. A total of 52 sites located at regular 6 km intervals were sampled along the 310 river-km. The uppermost site was located at Charles Fuhr (9 km downstream from Lake

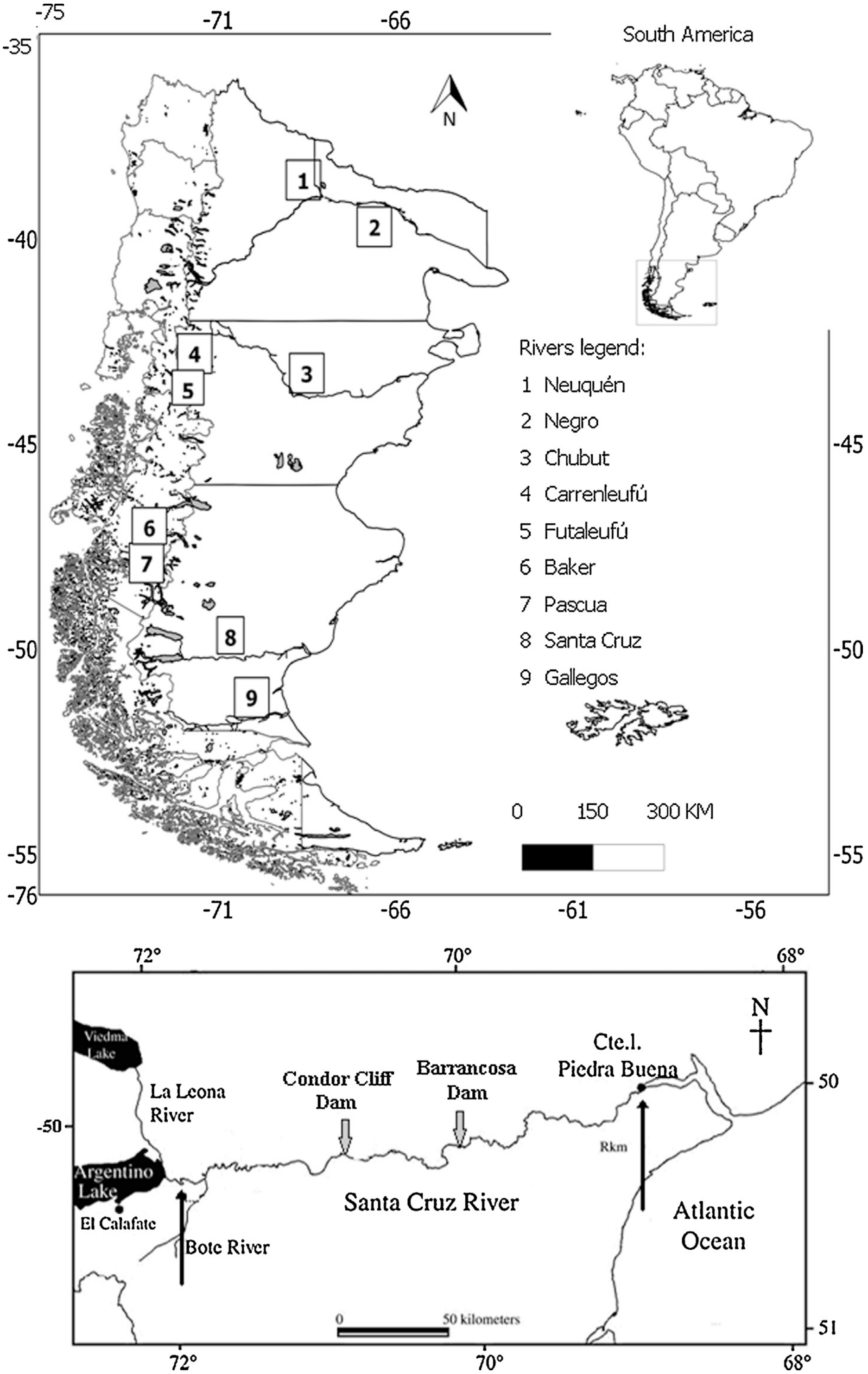

Fig. 1. Large Patagonian rivers: 1. Neuquén, 2. Negro, 3. Chubut, 4. Carrenleufú, 5. Futaleufú, 6. Baker, 7. Pascua, 8. Santa Cruz, and 9. Gallegos. Below: map of the Santa Cruz River, Argentina. Arrows show the starting and ending sampling sites (Charles Fuhr Bridge and Cte. L.Piedra Buena Town).

Argentino) and the lowermost site was located close to the estuary, at the town of Piedra Buena (318 km from the lake).

We designed this one time whole-river sampling scheme to generate a detailed geographic inventory of the river habitats and their biological communities, as a complement of data collected during 8 sampling campaigns of detailed local and seasonal samplings performed between 2008 and 2010 which included river physical characteristics, and invertebrates examinations at 6 sites along the river. That previous work indicated that seasonal and inter-annual variation in community structure was low and we were thus confident that a better baseline could be obtained by a geographically detailed one-time, intensive sampling.

Environmental variables

A total of 17 variables were measured at each of the 52 sites along the river, including water and river physical characteristics, dissolved matter, and chlorophyll concentration on biofilms.

Macro-scale variables of the river (*i.e.* altitude, bankfull and wet width, current speed, and bathymetry) were measured either continuously or every 300 m. Wet and bankfull widths were measured using a laser distance meter (TruPulse 200). Altitude and position were measured using an Oregon 550 Garmin GPS and from a digital elevation map, SRTM, 90 m pixel. The sinuosity was estimated as the ratio between the geographic distance and the river distance between pairs of points separated by 500 m. The bathymetry was recorded with a Lowrance LCX-15MT echosounder. Local variables, within a 15 m radius from the sampling point (*e.g.* dissolved oxygen, depth, current speed, substrate size) were measured at each of the 52 sites following Gordon et al. (2004). Average depth was calculated from 3 measures within the sampling area. Surface current speed 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. 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 and 2–5 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 5–30 cm) at each site and stored in 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 lab 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.

Macroinvertebrate sampling

Macroinvertebrate samples were taken at each of the 52 sites with a kick-net of 450 μm mesh size, 0.25 m^2 area. Samples were preserved in 70% ethanol and then transferred to the laboratory for further separation 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. The different taxa were identified following Lopretto and Tell (1995) and Domínguez and Fernández (2009). We analyzed macroinvertebrate samples in terms of taxa richness, relative abundance (%), density (ind m^{-2}), and wet weight (g m^{-2}) per taxon. To calculate wet weight, individuals were assigned to a given taxon, the excess of water was removed with absorbent paper, and the taxa were weighed on an analytical Shimadzu AUW-220 scale (range: 220 g to 10 mg, error: 1 mg). Functional feeding groups (FFGs) were assigned using available references (Merritt and Cummins 1996), own knowledge of feeding modes (mouthpart morphology and behavior), and analysis of gut contents (Merritt and Cummins 1996; Domínguez and Fernández 2009).

Biological data analysis

We applied ordination methods to analyze associations of macroinvertebrate taxa in relation to environmental variables. Macroinvertebrate abundance data were transformed using $\log(x+1)$, which is recommended when the ordination is Euclidean-based and for data with many zero-counts (Legendre and Gallagher 2001). A redundancy analysis (RDA) based on the original (transformed) species data was used to test the relationship with explanatory variables. All variables, but pH and chlorophyll-a concentration, were transformed using $\log(x+1)$. The RDA-analysis was conducted using both CANOCO (Ter Braak and Smilauer 1999) and the R software. Overall and axis significance were tested using a Monte Carlo permutation test ($n=1000$) for redundancy analysis. Redundant variables were reduced to nine, and the goodness of fit was conducted using the function "vif.cca", which gives the variance inflation factors for each constraint or contrast in factor constraints and extract correlated variables. Finally an automatic stepwise model was fitted under the Akaike Information Criteria (AIC; Akaike 1974) to retain the environmental variables which affected the ordination of species. Kendall's concordance test (Legendre 2005) was performed with the full biological data set to test for the strength of species grouping.

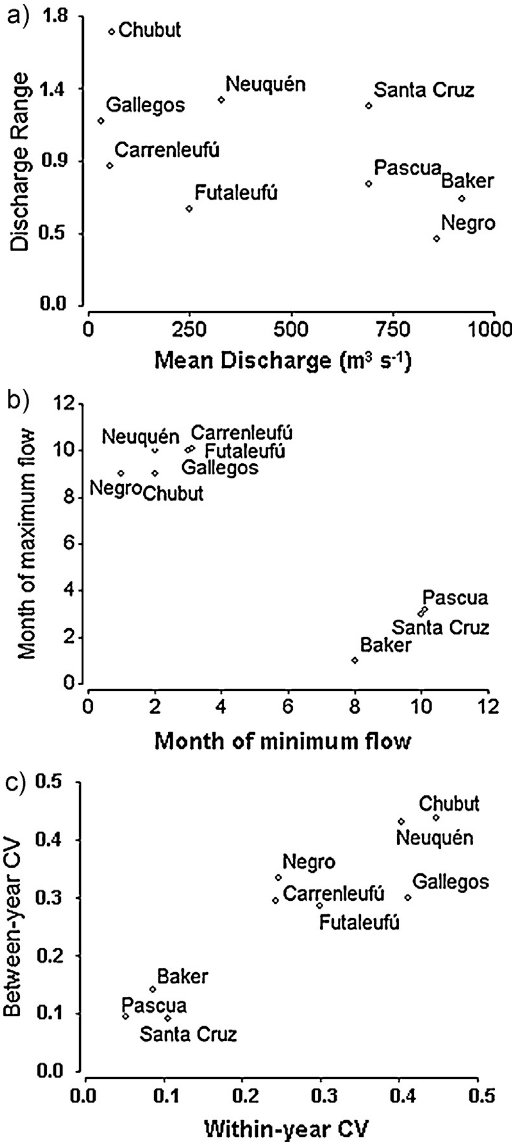

Fig. 2. Hydrological characterization of the largest Patagonian rivers (a) seasonality range and discharge, (b) month of maximum and minimum flow, and (c) flow variation within and between years.

Results

Hydrology of Patagonian large rivers

The Negro, Baker, Pascua and Santa Cruz Rivers are the largest rivers in the whole Patagonia region, all of them with mean discharge of over 600 $m^3\,s^{-1}$ (Fig. 2a). The rest of the rivers analyzed have all discharges of 300 $m^3\,s^{-1}$ or less. In general, and when the two regulated rivers in the set (Negro and Futaleufú) are excluded, rivers with higher discharge have lower seasonality in the discharge (discharge range). The Santa Cruz, however, has a higher

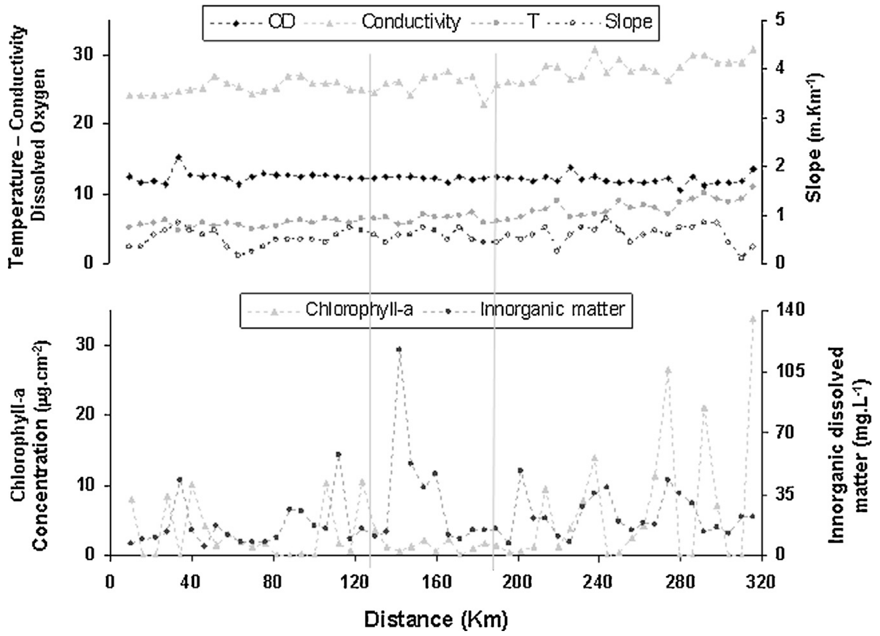

Fig. 3. Environmental variables along the Santa Cruz River. The first figure shows some of the most stable environmental variables (dissolved oxygen "OD", conductivity, temperature slope); while, the figure below shows the trends of variables chlorophyll-a and inorganic dissolved material.

range in discharge than its two Pacific counterparts within the system of the Patagonian Ice Fields (PIFs), the Baker and Pascua. These three rivers, on the other hand, share a common, distinctive streamflow profile as compared to that of other rivers in the region (Fig. 2b); non-PIF rivers, dominated by rainfall and snowmelt, have high flows in spring and low flows in summer. The three PIF rivers, with a streamflow dominated by ice melt, have a reverse pattern, with low flows during spring and delayed high flows in summer (late summer in the case of Santa Cruz and Pascua). The three PIF rivers also cluster together with respect of their very low variability in discharge (Fig. 2c), both within and between-years.

Environmental parameters

Environmental features of the Santa Cruz River are summarized in Table 1. Mean maximum depth ranged from 2.3 to 19.8 m. It showed the lowest values of conductivity, chlorophyll-a concentration, and temperature in comparison with a set of Patagonian rivers analyzed by Miserendino (2001). Primary production, estimated from the chlorophyll-a concentration, was very low, with values of 0.2–33.8 μg cm^{-2}.

Table 1
Physico-chemical variables measured at the sampling sites and specifications of the methods used. Mean, standard deviation and range of variables are consigned.

Variable	Mean	Std. dev.	Range
Altitude (m)			0–179
Bankfull (m)	188.6	40	110–281
Sinuosity	1.3	0.2	1.1–2.0
Slope	0.6	0.2	0.1–0.9
Gravel bar (m)	48	28	6–158
River wet width (m)	139.4	34.1	80–216
Maximum depth (m)	5.7	3	2.3–19.8
Current speed (m s^{-1})	0.3	0.2	0–0.9
Substrate composition (mm)	78.1	25.5	15.5–147.5
Temperature (°C)	6.9	1.4	4.7–11.0
pH	5.8	0.3	5.0–6.5
Dissolved oxygen (mg L^{-1})	12.3	0.7	10.6–15.4
Conductivity (μS cm^{-1})	26.6	1.9	22.8–31
Suspended inorganic matter (mg L^{-1})	22.2	19	5.2–117.0
Suspended organic matter (mg L^{-1})	3.1	2.2	0.6–12.8
Chlorophyll concentration (μg cm^{-2})	5.6	7.4	0.2–33.8

Based on its longitudinal structure, the Santa Cruz could be described as a very homogeneous river, with some structure at a finer scale (Fig. 3). Some environmental variables remain fairly invariant along the river (slope and dissolved oxygen), other show a smooth gradient (temperature and conductivity), whereas other show variability at the locals scale (*e.g.*, clorophyll-a, inorganic matter, substrate size, depth). No patterns were identified that could determine different sections or reaches (covering from 6 to 30 km) based on environmental variables.

Benthic macroinvertebrates

Fourty taxa of macroinvertebrates were identified, two of which were rare, incidentally caught terrestrial/aereal items (Lumbricidae and adult Trichoptera) and were removed from the analysis (Table 2). A total of 4456 individuals were counted and identified, 1378 of which were the amphipod *Hyalella* sp. and 1404 of the elmid *Luchoelmis cekalovici.* Both species were also conspicuous, being present at 92.3% and 90.4% of the sampling sites, respectively. Other widespread taxa were the mayfly *Meridialaris chiloeensis*, the gastropod *Lymnaea* sp., the midge *Paratrichocladius* sp. larvae and pupae, and the stonefly *Limnoperla jaffueli*. Species richness, abundance and wet-mass fluctuated significantly along the river, but without any apparent gradient or clustering by sections or reaches (Fig. 4). Mean total macroinvertebrate density ranged from 4 ind m^{-2} to 2056 ind m^{-2} (Fig. 4). Wet biomass ranged widely, from 1 to 5648 mg m^{-2}.

Albeit weak, we found an association of macroinvertebrate taxa. Three different groups or assemblages could be identified through the RDA analysis (Fig. 5 and Table 3). The association of species within groups was statistically significant and the grouping was supported by Kendall's concordance test. The global concordance test showed a significant result among the taxa ($p = 4.00e^{-3}$ and $p = 2.00e^{-3}$, respectively). To determine which of the individual taxa were concordant with each of the two groups, an *a posteriori* test was conducted. Within the first group, most of the taxa were not concordant with the others, and only the

Table 2
Taxa relative abundance (number of individuals ind m^{-2}, mean, standard deviation and maximum % of sites present). FFG, functional feeding group; SH, shredder; SC/GR, scraper/grazer; CG, collector-gatherer; CF, collector filterer; PR, predator.

Taxa	FFG	Relative abundance (%)	% sites present	% max presence	Site abundance (ind quadrat^{-1})		
					Mean	Std. dev.	Maximum
Mollusca							
Chilina sp. (Ch)	SC/GR	0.4	11.5	14.9	0.3	1.1	7
Heleobia sp. (He)	SC/GR	0.1	5.8	4.8	0.1	0.4	2
Lymnaea sp. (Ly)	SC/GR	6.5	63.5	78.6	5.6	8.1	33
Annelida							
Glossiphoniidae sp1 (Gl)	PR	0.4	28.8	7.1	0.4	0.7	3
Glossiphoniidae sp2 (Gl2)	PR	0.1	1.9	7.3	0.1	0.4	3
Haplotaxidae (Hp)	CG	<0.1	1.9	1.1	0	0.1	1
Lumbriculidae (Lb)	CG	0.1	3.8	2.4	0.1	0.1	2
Naididae sp1 (N1)	CG	0.8	26.9	60	0.7	1.8	10
Naididae sp2 (N2)	CG	0.1	7.7	20	0.1	0.3	1
Naididae sp3 (N3)	CG	<0.1	1.9	1.3	0	0.1	1
Acari							
Acari spp. (Ac)	SR/GR	2.2	28.8	22.9	1.9	4.6	25
Crustacea							
Hyalella araucana (Ha)	CG	30.9	92.3	100	26.5	54.5	298
Hyalella curvispina (Hc)							
Ephemeroptera							
Andesiops sp. (Ad)	SC/GR	0.4	15.4	13	0.4	1.5	10
Meridialaris chiloeensis (Mc)	SC/GR	8.1	78.8	33.3	6.9	8.5	44
Plecoptera							
Aubertoperla illiesi (Ai)	SH	0.3	13.5	12.2	0.3	0.9	5
Antarctoperla michaelseni (Am)	SH	0.5	21.2	14.6	0.4	1.1	6
Araucanioperla sp. (Au)	SH	<0.1	1.9	2.1	0.2	0	1
Klapopteryx kuscheli (Kk)	SH	0.5	25	6.3	0.4	1	6
Limnoperla jaffueli (Lj)	SC/GR	2.4	61.5	21.4	2.1	2.6	11
Coleoptera							
Luchoelmis cekalovici (Lc)	SC/GR	31.5	90.4	64.4	27	34.5	156
Trichoptera							
Mastigoptila sp. (M)	SC/GR	0.1	7.7	20	0.1	0.4	2
Mastigoptila longicornuta (Ml)	SC/GR	1.1	38.5	16.1	0.9	2.1	14
Atopsyche sp. (At)	PR	<0.1	3.8	5.2	0.9	0	2
Rheochorema sp. (Rh)	PR	0.3	17.3	4.3	0.3	1	6
Cailloma sp. (C)	PR	0.2	9.6	7.1	0.1	0.5	3
Smicridea dithyra (Sd)	CF	0.6	23.1	9.5	0.5	1.1	5
Oxyethira sp. (O)	CG	<0.1	1.9	1.1	0	0.1	1
Diptera							
Eukiefferiella sp. (Eu)	CG	0.3	28.8	23	2.7	2	6
Paratrichocladius sp. (Pcl)	CG	8.6	63.5	100	8.1	16.2	76
Endotribelos sp. (En)	CG	0.2	7.7	2	0.3	0.1	3
Parachironomus sp. (Pch)	CG	0.2	13.4	3.1	0.2	0	3
Alotanypus sp. (Al)	PR	0.1	1.9	1.2	0.1	0.1	1
Pelecorhynchidae (Pe)	PR	<0.1	3.8	1.2	0.1	0.1	1
Empididae sp. (Em)	PR	0.1	3.8	1.3	0.1	0.3	2
Muscidae sp. (Mu)	PR	0.3	13.5	2.6	0.3	0.9	6
Cnesia sp. (Cn)	CF	1.9	42.3	16.2	1.6	6.6	47
Hexatoma sp. (Hx)	PR	0.4	11.5	11.3	0.3	1.4	9

Table 3
Axes eigenvalues and weighted intraset correlation between RDA-axes and environmental variables related to macroinvertebrate taxa abundance data from the Santa Cruz River. Significance of the axes by Montecarlo test is given.

	RDA 1	RDA 2	RDA 3
Eigenvalues	0.12	0.09	0.03
Species–environment correlation	0.61	0.69	0.74
% variance of species data explained	12.6	8.1	2.6
Correlation with axes			
Sinuosity	0.68	0.40	0.19
Current speed	0.49	0.01	0.26
Depth	−0.17	0.06	−0.07
Substrate size	0.36	−0.39	−0.59
Temperature	−0.16	−0.86	0.37
Dissolved oxygen	−0.06	0.52	0.37
Inorganic matter	−0.30	−0.01	−0.12
Organic matter	−0.29	0.27	−0.13
Chlorophyll-a	0.17	−0.25	0.58

p-Values for Monte Carlo Permutation test.
Axis1: $F = 4.25$, $p < 0.01$.
All canonical axes: $F = 1.66$, $p = 0.001$.

herbivorous *L. jaffueli*, *Antarctoperla michaelseni* and *Lymnaea* sp. had a significant contribution to the concordance; Diptera larvae of *Paratrichocladius* sp., *Hexatoma* sp., *Rheochorema* sp., *Mastigoptila longicornuta*, and *Acari* spp. contributed to the concordance of the second group; *Klapopteryx kuscheli* and *M. chiloeensis* contributed to the concordance of the third group.

The results of the RDA ordination for 38 taxa and 9 environmental variables (Fig. 5 and Table 3) provided statistically significant results ($F = 1.656$, $df_{\text{residuals}} = 41$, $df_{\text{model}} = 10$, $p = 0.001$). A total of 23.3% of the variance in taxa abundance was accounted for by the first three ordination axes. The species–environmental correlations were 0.61, 0.69, and 0.74 for the first, second, and third axis respectively and the percentage of variance explained by the species–environmental relation was 86.6%, indicating a robust relationship with the environmental variables selected. The first three ordination axes were statistically significant according to an unrestricted permutation test. First axis explained 12.6%, the second accounted for a 8.1% of the ordination, and the third one for a 2.6%. The first ordination axis was determined by water velocity and sinuosity; secondary variables associated were substrate

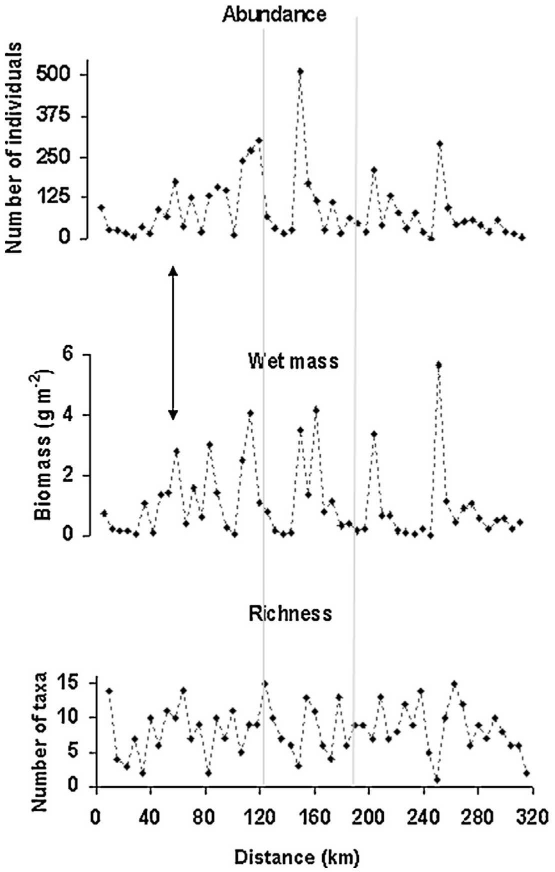

Fig. 4. Macroinvertebrate relative abundance (%), biomass (wet-mass g m^{-2}) and richness on the longitudinal dimension of the Santa Cruz River. Symbols correspond to sampling sites ($n = 52$). Axis-*x* shows the distance (km) from headwaters. Straight lines at 132 km and 190 km approximately indicate where the "Cóndor Cliff" and "Barrancosa" dams will be built. The arrow shows the site where the Primer Laberinto starts.

size, inorganic dissolved matter, and algal biomass (chlorophyll-a concentration). The second axis reflected a temperature, dissolved oxygen, and sinuosity gradient, while the third one strongly accounted for chlorophyll-a concentration, and substrate composition. Both the Akaike Information criterion (AIC) and the step-forward permutation test led to a reduced model including temperature, substrate composition, and sinuosity.

Most taxa were associated to shallow waters, with the exception of *Hyalella araucana*. Some taxa appeared close to the origin of the two first axes reflecting a weak association with environmental variables (*e.g.* Naididae sp3, *Hydrobiosidae* spp.), while others had a strong relationship with environmental variables (*e.g. Paratrichocladius* sp. and *M. chiloeensis*, Fig. 5). The amphipod *Hyalella* sp. and the stonefly *A. michaelseni*, for example, were related to sites with low values of sinuosity, flow speed, and algal biomass (chlorophyll-a concentration), and high values of dissolved matter. On the other extreme, Chironomidae species, particularly *Paratrichocladius* sp., and *Acari* spp. were associated to more sinuous sites with larger substrate sizes, higher current speed, higher chlorophyll-a concentration, and lower depth values. A third group is distinguished in the biplot, composed by the mayfly *M. chiloeensis*, the stonefly *K. kuscheli* which occurred in cooler and shallow waters with higher concentration of oxygen. On the other hand, the gastropod *Lymnaea* sp. and the stonefly *L. jaffueli* were positively related to warmer waters with low sinuosity.

Discussion

The hydrology of Patagonian large rivers

The three large southern rivers associated to the PIFs, Baker, Pascua, and Santa Cruz, have distinctive characteristics, which differentiate them from other rivers of Patagonia as well as from most large rivers in temperate ecoregions of the world (Milner and Petts 1994; Carrasco et al. 2002). A discharge strongly dominated by ice melt provides them with: (a) a distinct seasonal cycle with peaks and low flows delayed by as much as six months with respect to rivers dominated by snow melt and rainfall, (b) an extremely stable discharge with much lower variability than other rivers, both within and among years (Depetris et al. 2005), and (c) a high

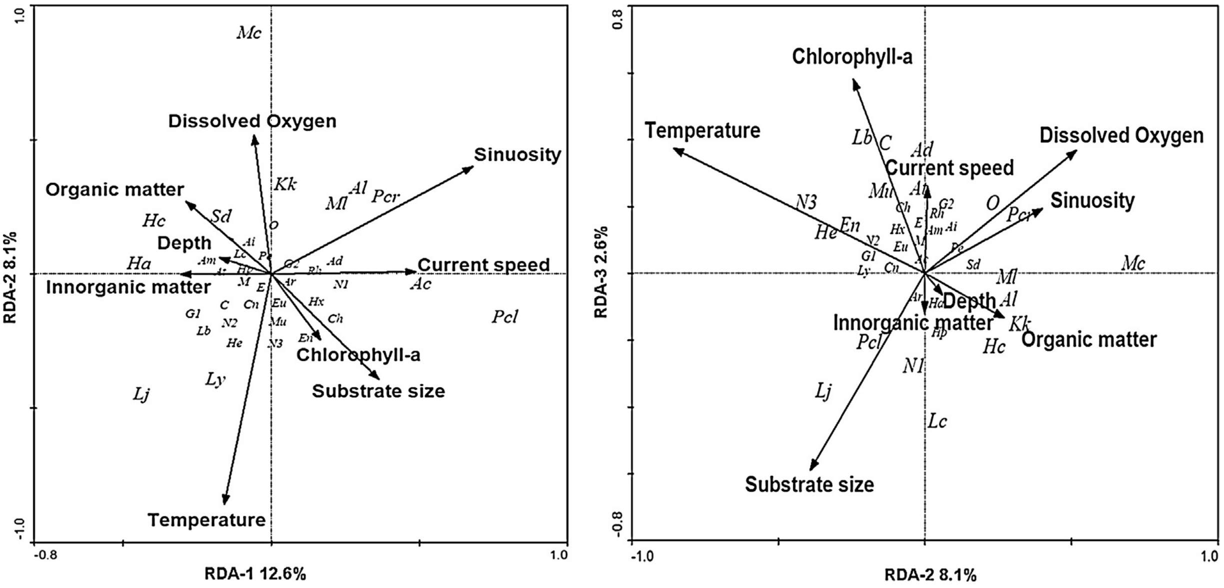

Fig. 5. RDA-biplot with taxa and environmental ordination of log-transformed data of macroinvertebrates community in the Santa Cruz River during the study period. Taxa codes are placed in Table 2. Correlation between RDA axes and environmental variables are placed in Table 3.

sediment load (Brown et al. 2006; Depetris et al. 2005; Milner and Petts 1994).

Environmental parameters – benthic macroinvertebrates – unique fauna

Our more detailed analysis of the Santa Cruz River indicates that this lack of strong variability in discharge is accompanied by an overall uniformity in within river habitat structure. These two characteristics of rivers are expected to be functionally related, as a result of geomorphic responses of the channel and the floodplain to the hydrologic and sediment transport regimes (Jackson et al. 2007; Arscott et al. 2002). The morphological heterogeneity of riverbeds and banks, which is directly associated with the existence of short-term fluctuations in flows and extreme high and low flows, is usually accompanied with a high species richness and complex biological communities (Smith et al. 2003; Townsend et al. 1987). The Santa Cruz River creates the opposite situation where low species richness might be related to highly homogeneous flow cycles, the lack of bed scouring flows, the low valley gradients and environmental factors homogeneity.

From a biological perspective, the lack of river structure and the reduced hydrological variability limits variability in habitat and is expected to impact community structure and species diversity (Townsend and Hildrew 1994; Power et al. 1996). Accordingly, macroinvertebrate density in the Santa Cruz River resulted to be one of the lowest in comparison with other 42 Patagonian rivers (Miserendino 2001, 2009). Although macroinvertebrate abundances and wet weights were generally low, some peaks in density values and wet-weight were seen, largely due to locally high densities of *H. araucana* and *L. cekalovici*, associated to sites with higher dissolved organic matter. Also, the taxa richness found in this study (38) is low compared to those reported for other Patagonian rivers. Data on macroinvertebrate richness at low water season in the Pascua and Baker rivers was documented to be 18 and 73 taxa, respectively (Salas Contreras 2007). In particular, 48 macroinvertebrate taxa were identified from different collects in the Santa Cruz River (Tagliaferro, unpublished), similar to values observed in this study. For comparison, 95 taxa were identified in the Chubut River (Miserendino 2009), and 112 taxa in the Negro River, in seasonal studies (Wais 1987). Species richness is predicted to increase with spatial and temporal heterogeneity in habitats and flows (Townsend and Hildrew 1994; Power et al. 1996), both as a direct reflection of the greater number of niches available (not necessarily a biotic influence) and because of a reduced likelihood of competitive exclusion in patchy environment (a biotic influence). The weak spatial structure of the Santa Cruz River and the lack of extreme flows may reduce the mosaic of habitats available for individual species, limiting disturbance regimes and opportunities for early successional taxa to thrive, ultimately affecting species richness. The high turbidity of the Santa Cruz River may also contribute to shorter food webs (Moore and Townsend 1998; Power 2006; Schmid-Araya et al. 2002), by affecting autotrophic production, general trophic structure, and overall macroinvertebrate productivity and diversity. Good examples of the negative effects of turbidity on macroinvertebrate density and productivity have been documented for large arid and semiarid rivers in Patagonia and in other countries (Shaver et al. 1997; Stevens et al. 1997; Miserendino 2009). Among main causes are the scouring effects on intolerant insect fauna and the decrease in primary production by low water transparency, affecting scrapers, grazers and herbivorous species (Collier 2002; Robinson et al. 2004).

Albeit weak, the structure of the macroinvertebrates assemblages was successfully described by a reduced set of variables. As previously found in similar environments, main explanatory variables were substrate size, water velocity, depth, and water temperature (Malmqvist and Mäki 1996; Miserendino 2001; Miserendino and Pizzolón 2003). The association of macroinvertebrate taxa was congruent with feeding habits. *Chilina* sp. and *Lymnaea* sp., a grazer and an algal scraper respectively, were associated with high chlorophyll-a concentration (Miserendino 2009; Epele et al. 2011). Trichoptera *Smicridea dithyra*, a filterer-collector species (Miserendino and Brand 2007), was positively associated with higher levels of organic matter. Finally, a group composed by *K. kuscheli*, *M. longicornuta*, and *M. chiloeensis* was predictably associated to well-oxygenated habitats. *K. kuscheli* is typically found in fast waters with large substrates, often associated with litter packages, whereas *Mastigoptila* sp. is a scraper and is associated with stable substrata with periphyton. The latter group included different functional feeding groups, though they have similar habitat requirements.

Dams: river conservation and recommendations

The most significant and obvious impact of the two dams to be built in the Santa Cruz will be the obliteration of 51% of the current lotic environment. Above the dams, species with high oxygen requirement like some Plecoptera or Ephemeroptera may reduce their abundance (Jacob and Walther 1981; Jacobsen 2008). Our macroinvertebrate data indicate that the most productive sections of the river will be flooded by the dams. Meanwhile, downstream impacts of dams on river biota through changes in thermal and hydrological regimes, and in nutrient and sediment loads (Ward and Stanford 1979; Petts 1984) are harder to predict. In general, only few species capable to withstand sudden changes in flow are expected to survive below the dams (Poff et al. 1997). In the end, the outcome will depend on specific aspects of the project design and operation, which have not been publicly revealed yet. Typical hydrologic impacts of dams around the world consist of reducing the amount and variation of downstream flow and the frequency of bed scouring flows (Bunn and Arthington 2002; Poff et al. 1997; Sparks 1995). The result of such manipulation of river discharge is a simplification of channel morphology and an impoverishment of the mosaic of river habitats, with negative impacts on community composition and species richness (Power et al. 1996). When trying to apply these general results to the Santa Cruz, a number of critical questions arise: Will flow regulation of the Santa Cruz River further contribute to reducing hydrological variability or it will provide more variable flows? Will sediment retention affect light penetration, increasing primary productivity? In the end, will the river downstream of the dams become a more diverse and more productive river or will dams accentuate the low productivity and species diversity? We have no clear answers to these questions, which at this time may better be regarded as hypothetical alternative scenarios for the future of the Santa Cruz River. On the other hand, our data provide critically valuable baseline information to which future community structure data could be contrasted to understand the effects of dams on the unique group of glacial driven large rivers of Southern Patagonia.

Recommendations to mitigate dam's impact in large rivers typically refer to rivers with large flood-plain, and poor information is available for large rivers such as the Santa Cruz River. Whereas mitigation projects have been elaborated for the Pascua and Baker rivers, proposing to minimize working surfaces, to stabilize slopes and riverbeds, and to preserve physical, chemical and biological in-river features (HidroAysén 2011), only impacts related to flow and turbines operation have been considered for the Santa Cruz River (IMPSA-hydro 2012). The ideas below attempt to suggest alternatives to maintain the biological integrity which is the primary key when performing ecosystem management (Nilsson et al. 2005; Sparks 1995). Since large rivers link distant ecosystem by animal migrations, the transport of water, sediments and nutrients (Poff et al. 2010; Sparks 1995; Ward and Tockner 2001), one of the first issues to address is the connectivity. Above dams, the connectivity will be maximum downstream.

Much of the area covered by the river would be exposed and disconnected from the main channel when dams release the minimum flow (200 $m^3 s^{-1}$, IMPSA-hydro 2012), which is three times lower than the mean annual flow. Moreover, naturally, the riverbed immediately below dams, tend to deepen (Brandt 2000). A possible alternative is to create some disturbance escape areas (TNC 2013), close to the output of high pressure water from the dam, to avoid aquatic communities to be swept. Finally, given that the life cycle of aquatic biota responds to hydrological patterns (Bunn and Arthington 2002; Resh et al. 1988), water regulation should be performed in a way that replicates the natural seasonal flow cycle as closely as possible (Carlisle et al. 2010, 2012; Ward and Stanford 1982). Moreover, since the Santa Cruz River is a glacier river, the macroinvertebrate fauna is expected to be more vulnerable to changes in channel stability (Milner et al. 2009), water temperature and organic matter inputs (Milner et al. 2001). Facing the possibility of these changes, we recommend to keep doing biomonitoring research at species and functional diversity.

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