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ORIGINAL PAPER

Effects of flow regulation, basin characteristics and land-use on macroinvertebrate communities in a large arid Patagonian river

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Abstract Longitudinal distribution and abundance of macroinvertebrate communities were examined in relation to hydrochemical variables along the Chubut River in the Patagonian Precordillera and Plateau, Argentina. The Chubut River (>1000 km) is the largest river in the area and its basin is subject to multiple uses: agriculture, cattle raising, urbanization and the hydrological regime of the lower section is modified by a reservoir. Quantitative benthic samples were collected at 13 sites in the higher, middle and lower sections of the river basin. Sites were visited four times during 2004 and physicochemical parameters, chlorophyll *a* and particulate organic matter (POM) were assessed. Ninety-five taxa were collected in the study, with total species richness per site ranging from 5 to 51, and benthos density averaging 299–5024 ind m^{-2}. Altitude and turbidity were implicated as important factors determining macroinvertebrate assemblages along the river system, and an eutrophication gradient was documented in the regulated/urbanized section of the main river. High turbidity (TSS) and sedimentation limited algal productivity in the middle basin. Below the dam, TSS, total phosphorus (TP) and POM decreased, whereas soluble reactive phosphorus (SRP) and chlorophyll *a* increased. Macroinvertebrate density increased three fold in this area possibly due to habitat improvement and enhanced trophic resources. Mean species richness did not change below the impoundment; however the community was dominated by gastropods, chironomids and flatworms. The Chubut River is complex and its biotic community reflects the landscape attributes. While benthic composition and density was governed by turbidity and flood disturbance in some river segments, a greater environmental heterogeneity resulted in an unexpected high number of species at the main channel upper basin.

Keywords Benthic macroinvertebrates · Chlorophyll · Dam · Floods · Nutrients · Organic matter · Patagonia · River regulation

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Introduction

Identifying the distributional patterns of species is an important first step in determining what processes control the structure of riverine communities. Species respond distinctively along environmental gradients at various spatial scales (Poff and Ward 1990; Bretschko 1995), and according to the River Continuum Concept (RCC, Vannote et al. 1980) lotic invertebrate communities are structured along resource gradients from the headwaters to the mouths of rivers. The RCC applies primarily to natural, free flowing rivers, whereas the serial discontinuity concept (Ward and Stanford 1982) addresses the impact of regulation on rivers and predicts the type and degree of ecological change downstream from an impoundment. By altering turbidity, water temperature, substratum and food resources, flow-regulation is one of the most significant human activities having adverse effects on freshwater communities worldwide (Pardo et al. 1998; Cortes et al. 2002; Collier 2002). The type of dam (epilimnetic or hypolimetic discharge) and its position along the river continuum affect the degree of discontinuity in physical processes (Ward and Stanford 1994, 1995) and biological patterns at all trophic levels (Wanner et al. 2002). Dams can have dramatic effects on river and aquatic biota by altering water quality and habitat, disrupting nutrient cycling and sediment transport, and blocking fish and invertebrate movements (Santucci et al. 2005).

In recent years, several studies on the spatial structure of macroinvertebrate communities and their environmental relationships have been undertaken in Patagonia (Wais 1987; Miserendino and Pizzolón 2000, 2003). The interactive effects of basin features and land use changes on macroinvertebrates have been studied in headwater streams of the cordillera (Miserendino and Pizzolón 2004), and the impact of land desertification on invertebrate assemblages of rivers has been documented (Miserendino 2004, 2006). Although a large number of scientific papers consider the ecology of whole river systems in moderate-rainfall, temperate regions, river ecology in arid/semiarid areas remain largely unexplored (Wais 1990; Stevens et al. 1997).

The Chubut River is the largest and longest watercourse on the Patagonian Plateau (Chubut Province) and provides an excellent opportunity to examine the longitudinal pattern of macroinvertebrates over an extensive altitudinal (1000 m) and longitudinal (>1000 km) gradient across an arid and semiarid region. Furthermore, its basin sustains multiple activities, which include agriculture, cattle-raising and irrigation, and the river itself is regulated in its lower section (Coronato and Del Valle 1988; Sastre et al. 1997; Luque et al. 2000). For more than a century irresponsible land use in the middle and lower Chubut River basin also resulted in severe desertification (del Valle et al. 1995, 1998).

The primary aims of the present study were (1) to analyze benthic macroinvertebrate assemblages in relation to environmental variation from tributaries in the upper basin to the outlet of the Chubut River in the Atlantic Ocean, and (2) to assess the impact of river regulation (Florentino Ameghino Dam) on physical and chemical features and macroinvertebrate communities of the river. I also took the opportunity to examine the effects of a 50 year flood on the density and richness of macroinvertebrates along the river.

Study area

The Chubut River flows from west to east through the Patagonian ecoregion and drains into the Atlantic Ocean (Fig. 1). Its basin (25,225 km^2) is located in two main biozones: the Extra-Andean Oriental and Extra-Andean Occidental (Del Valle et al. 1995; Paruelo et al.

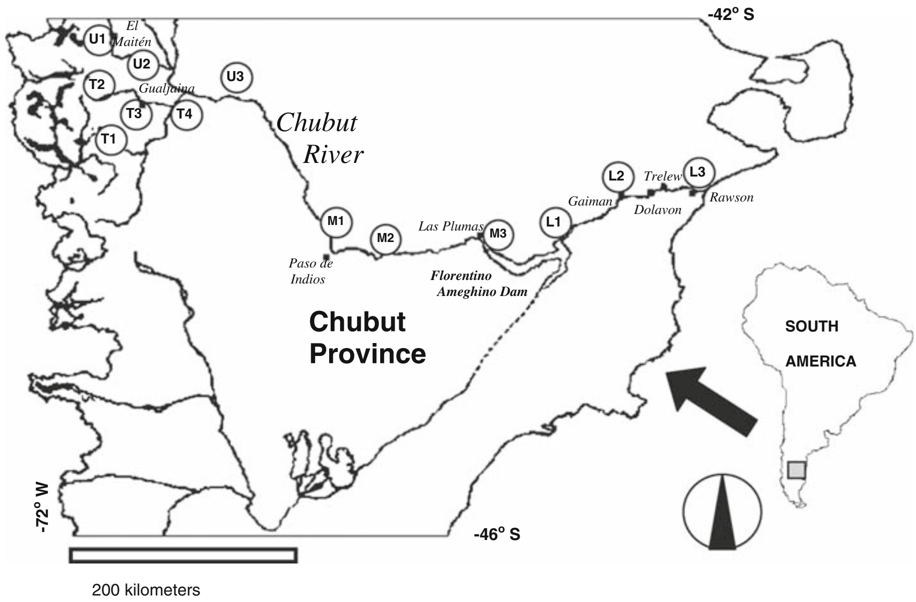


Fig. 1 Map showing the locations of the 13 sampling sites in the Chubut River, Patagonia Argentina. Names of the sites are in Table 1

1999). Geomorphologic features and local climatic characteristics divide the basin into three parts. The upper basin (7000 km^2) is characterized by a strong west-east rainfall gradient (500–100 mm year^{-1}) and being near the cordillera has the lowest temperature (mean annual air temperature 8.5°C). The middle basin (12,000 km^2) has an average rainfall of 150 mm year^{-1} and mean annual temperature of 13.2°C. The lower basin, the regulated section of the river, has the smallest area (6000 km^2) and rainfall of 150 mm year^{-1} (Coronato and del Valle 1988). Dominant soils in the basin are aridisols, entisols and vertisols (del Valle et al. 1998), all of which are characteristic of arid and semiarid Patagonia. Most of the Chubut River is on the Patagonian Steppe, where the low precipitation has resulted in xerophytic, herbaceous-shrub-like steppe vegetation that includes *Mulinum spinosum*, *Stipa* spp., *Senecio filaginoides*, *Colletia spinosissima*, *Adesmia campestris*, *Fabiana imbricata* and *Chuquiraga avellanedae* (Tell et al. 1997). In several parts of the upper and middle basins, the riparian corridor consists solely of the exotic willow, *Salix fragilis*, but in some lower sections the native willow *S. humboldtiana* is also present.

Land use adjacent to the river is mainly agricultural, with extensive livestock grazing in the upper and middle sections, and mainly smaller farms and industries in the lower section. In the middle basin, anthropogenic activities in the last century (overgrazing, wood collection) have accelerated land cover degradation, including desertification that ranges from moderate to very severe (del Valle et al. 1998). Recently, landowners have started to cultivate potatoes, corn, and alfalfa (for forage production) on this low-productivity land, and water is taken from various segments of the river for irrigation. The soil improvement system is mostly by green manuring, no herbicides are used on crops and water returns to the river by natural gravity (Luque et al. 2000). Cities along the river in the lower basin take potable and irrigation water from the Florentino Ameghino Dam (74 km^2) via a network of channels in the lower valley. In this area there are approximately 25,000 ha under irrigation. The three largest cities, Gaiman, Trelew and Rawson together have more than 250,000 inhabitants.

Materials and methods

Sampling sites

Thirteen sampling sites were established within the river system (Fig. 1). T1 (Madera Stream) and T2 (Lepá River) were located on upper tributaries, U1 was on the Chubut River alongside El Maitén (3500 inhabitants) and U2 was on the Chubut River further downstream. T3 (Lepá River) was located alongside Gualjaina City (1000 inhabitants) and T4 was further downstream where the Gualjaina River joins the Lepá River. To assess possible changes in the river fauna in response to land use in the upper and middle basin, four sites (U3, M1, M2 and M3) were selected in the Chubut main channel. Finally, M3 was established next to the rural town of Las Plumas (500 inhabitants), L1 was sited 1 km below Florentino Ameghino Dam and L2 and L3 were located in the more developed and urbanized lower Chubut River basin.

Macroinvertebrate collection

All 13 sites were sampled in February, May, September and December 2004. Three macroinvertebrate samples were taken from run/riffles at each site with a modified kick-net sampler (frame area 0.25 m^2, 250 μm pore size) (Hauer and Resh 1996). Samples were fixed in a 4% formaldehyde solution and were sorted under 5× magnification before being stored in 70% ethyl alcohol. Species were identified using available keys (Lopretto and Tell 1995; Fernández and Domínguez 2001).

Environmental variables

Substrate composition was estimated as percentage of each fraction: boulder, cobble, gravel, pebble and sand. The relative proportion of substrate was assessed using a grid (1 m^2) at each sampled reach (Gordon et al. 1994). Substrate was also classified giving a weighed index increasing with particle size (Armitage et al. 1987). Stream order was obtained from Coronato and Del Valle (1988). Average depth was calculated from five measurements taken on a transect across the channel. Surface current speed was obtained by timing a bobber (average of three releases) over a distance of 10 m (Gordon et al. 1994). Air and water temperature were measured with a mercury thermometer (−10/+60°C) on each occasion, and daily discharge data for the Chubut River (U1, U3, M2, M3, L2, L1) and its tributaries (T3, T4) were kindly provided by the Secretaría de Recursos Hídricos de la Nación.

Water samples were collected below the surface and kept at 4°C prior to analysis. Specific conductance, pH, total alkalinity, total suspended solids (TSS), and selected nutrients were analyzed in the laboratory. Specific conductance was measured with a Horiba U2-probe, and pH with an ORION 720 SA meter, both at 20°C. Total alkalinity was determined by acid titration with a colorimetric end-point. Total nitrogen (TN) and total phosphorus (TP) were determined on unfiltered samples digested with persulphate, whereas nitrate plus nitrite nitrogen ($NO_3{}^+NO_2$), ammonia (NH_4), and soluble reactive phosphate (SRP) were analyzed on filtered samples using standard methods (APHA 1994).

Particulate organic matter (POM) in each benthic sample was separated by sieving (pore size 250 μm), dried at 60°C for 24 h and weighed. Algal biomass (as chlorophyll *a*) was determined by scraping algae from five randomly selected rocks (length range: 5–16 cm) collected within a 20 m run/riffle reach at each site. Scrapings were kept dark and on ice in 120 ml water for up to 3 days before they were brought back to the laboratory and drawn on to GF/FF filters. Chlorophyll *a* was extracted from pulverized filters in 90% acetone and the extract was measured, spectrophotometrically as described by Wetzel and Likens (1991).

Data analysis

Two-way ANOVA was used to test for flooding effects on benthic attributes (sites and times as effects) and to examine the effects of regulation on macroinvertebrate communities at sites M3 (unregulated) and L1 (regulated). Homogeneity of variances was examined with Levene's test and data were transformed (log x + 1) to improve normality prior to running ANOVAs. Significant differences between means were assessed with Tukey's test, in post hoc comparisons (Sokal and Rohlf 1995).

Canonical Correspondence Analysis (CCA) with down-weighting of rare species was run using CANOCO (ter Braak and Smilauer 1999) to assess relationships between macroinvertebrate assemblages and environmental variables. Average seasonal values (means of three samples per site) were used in the analysis, however, data for site L3, which included extreme outliers were excluded. All environmental variables included in Table 1, Fig. 2 (except land use) and Fig. 4 were used, initially to evaluate the response of species and sites to environmental gradients. Variables (except pH and chlorophyll *a*) and species density were transformed (log x + 1), prior to analysis. Variables that were strongly intercorrelated with others (those with an inflation factor >20) in the initial analysis, were removed (conductivity, dry channel width, stream order, TP, distance from the source, substrate size) and a further analysis was carried out with the 15 remaining environmental variables. The forward selection option provided by CANOCO was applied and those variables with $P < 0.1$ (Monte Carlo permutation test) were kept for the analysis (pH, wet channel width and NO_3 were omitted). The CCA was then run using the significant environmental variables (ter Braak and Smilauer 1998).

Results

Environmental features of the Chubut River

River order ranged from 3 to 6 and elevation of the sites was between 4 and 936 m a.s.l. Substratum size was similar at most sites, and consisted mainly of boulders, cobbles, and pebbles (Table 1). Sites M1, M2, and L3 had a higher percentage of sand than the other sites. Monthly water temperature patterns (Fig. 2) show a clear discontinuity in the thermal gradient at L1, immediately below the dam, where temperature was 5°C lower than at M3 in February and December.

Maximum current velocity (2.1 m s^{-1}) was recorded at U2 in February and the minimum (0.2 m s^{-1}) was recorded at T2 in summer when water was being abstracted for irrigation (Table 1). Discharge showed an exceptionally high peak in the main channel of the upper and middle sections of the Chubut as a consequence of strong rains in July. Flow decreased in the lower basin below Florentino Ameghino Dam (L1 and L2) (Fig. 3).

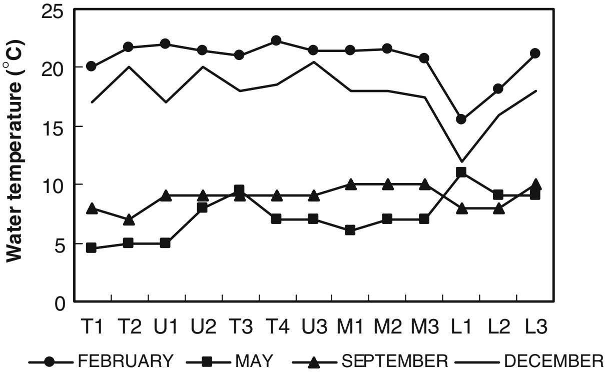
Table 1 Environmental features, detritus and autochthonous production measured at 13 sampling sites on the Chubut River basin, Patagonia, Argentina

Sites codes	River location	Main land use	Altitude (m.a.s.m.)	Stream order	Distance from the source (km)	Dry channel width (m)	Mean wet channel width (m)	Depth (min–max) (cm)	Velocity (min–max) ($m\ s^{-1}$)	Substrate index	Chlorophyll *a* ($mg\ m^{-2}$)	Benthic organic matter ($DM\ g\ m^{-2}$)
T1	Madera Stream	Cr	936	3	24.5	12	8.5 ± 8	8–19.2	0.3–1.7	7	2.75 ± 1	9.0 ± 4.5
T2	Lepa River	Cr	829	4	27	20	2.7 ± 3	17–40	0.2–1.2	9	2.96 ± 2.5	4.7 ± 3.3
U1	Ch, El Maitén	Ur	702	4	67	100	51.7 ± 39	38–45	1.2–1.7	6.5	3.49 ± 2.9	7.7 ± 3.4
U2	Ch, Fofo Cahuel	Cr	500	4	158	80	52.5 ± 24	36.6–45	1.1–2.1	6	2.35 ± 2.6	12.0 ± 10
T3	Lepa River, Gualjaina	Ur	518	5	76.1	100	32.4 ± 20	27.2–45	0.3–1.6	6	2.81 ± 1.8	2.0 ± 1.9
T4	Gualjaina River, After Gualjaina	Cr	476	6	90	50	30.5 ± 16	32.8–45	1–1.4	6.5	1.47 ± 0.3	5.1 ± 3.2
U3	Ch, Piedra Parada	Cr	440	5	208	200	105 ± 65	45–53.7	0.9–1.2	7	2.50 ± 4	7.2 ± 7.4
M1	Ch, Paso Berwyn	Cr/A	308	5	394	160	125 ± 56	23–45	0.5–1.6	4	2.44 ± 2.1	6.2 ± 7.8
M2	Ch, Los Altares	Cr/A	243	6	480	200	117 ± 58	30–45	0.8–1.2	4	1.92 ± 1.8	3.3 ± 1.8
M3	Ch, Las Plumas	Ur	158	6	583	300	215 ± 23	19.6–45	1.7–1.9	6	1.93 ± 1.3	9.7 ± 4.7
L1	Ch, D. F. Ameghino	R	74	6	686	70	64 ± 5	45–60	0.7–0.9	3.5	6.12 ± 3.9	0.8 ± 0.4
L2	Ch, 28 de Julio	R-Ur	32	6	737	40	35 ± 4	46.7–60	0.9–1.4	3	1.65 ± 1.3	3.6 ± 3.8
L3	Ch, Estuario	Ur	4	6	838	160	151 ± 2	33–60	0.8–1.1	2	11.87 ± 6.8	0.3 ± 0.3

Mean values ± SD ($n = 4$)

T tributary, *Ch* Chubut main channel, *U* Upper basin, *M* middle basin, *L* lower basin. Land use codes: *Cr* cattle raising, *Ur* urban, *A* agriculture, *R* flow regulation

Fig. 2 Water temperature records at all sites during the study period



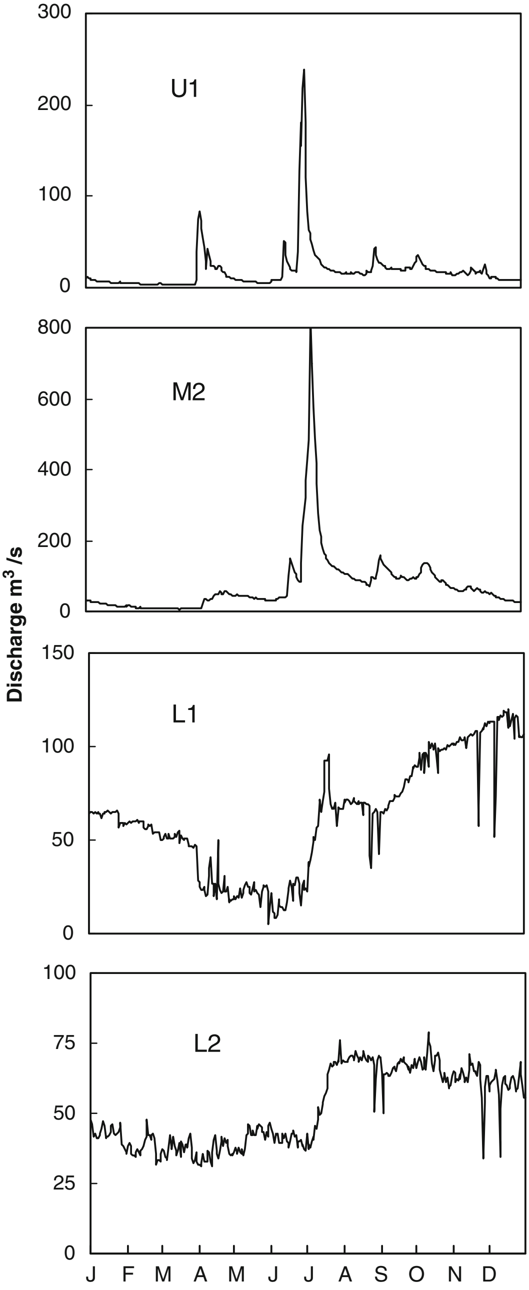
Chemical and physical data provided a clear distinction between the upper catchment sites and those in the middle and lower catchments (Fig. 4). Conductivity in the middle basin was 141–275 µS cm^{-1}, whereas in the lower basin it reached 2960 µS cm^{-1}. TSS values were higher in the middle basin (40.1–88.6 mg l^{-1}) and at the lowermost site L3 than elsewhere. However, an increase in TSS values was observed at the Chubut main channel sites, starting at U2 (Fig. 4), near the point where the Fita-Michi River flows into the Chubut from the north. Parent rocks in this section (Collon Cura formation; Ardolino et al. 1999) are dominated by friable tuffs, which provide a source of clay sediments when in contact with water. Mean values (per site) of TN ranged from 201 to 258 µg l^{-1} at middle basin sites, although values were highly variable (Fig. 4). Mean values of NH_4 (24.5–35.7 µg l^{-1}) and TP (54.3–84.3 µg l^{-1}) at middle basin sites were 2–3 fold higher than at upper basin sites, and may have been related to the presence of livestock in that section of the river. The highest values of NH_4 and NO_3 were obtained at L3, and probably reflected the presence of important industrial and urban development in the area (Fig. 4).

Longitudinal assemblage structure

Ninety-five macroinvertebrate taxa, mainly insects, were identified in the entire basin, with Diptera (30), Trichoptera (15), Ephemeroptera (13), Plecoptera (9) and Coleoptera (8) the best represented orders (Table 2). Numbers of taxa recorded per site ranged from five (L3) to 51 (U2), whereas mean taxon richness per site ranged from 1.8 (L3) to 22.4 (U1). Between U3 in the upper basin and M1 in the lower basin, species richness decreased, strongly. Mean total macroinvertebrate density ranged from 299 ind m^{-2} (L2) to 5024 ind m^{-2} (T3) (Table 2).

Plecoptera richness decreased from the upper basin to the lower basin sites and with the exception of *Antarctoperla michaelseni* and *Potamoperla myrmidon* stoneflies were practically absent below the impoundment (L1). Of the Ephemeroptera, the baetids *Andesiops torrens* and *Americabaetis* sp. were ubiquitous along the river system. However, the leptophlebiids *Traverella* sp. and *Meridialaris laminata* contributed strongly to overall relative abundance at some sites (37% at L2 and 26% at T4, respectively), and *Americabaeti*s sp. peaked in abundance at regulated sites L1 and L2. Trichoptera richness increased from upper tributaries to main channel sites in the upper basin, and decreased from U1 to M3. In the middle basin, Hydropsychidae was the best represented family at all sites except U1, U2, M1 and L1 (Table 2). The sericostomatid *Parasericostoma ovale* was abundant at U1 and U2, whereas two species of Hydroptilidae were the only caddisflies at L1.

Fig. 3 Daily discharge values ($m^3\ s^{-1}$) at main channel sites on the Chubut River during the study period. Non regulated sites: U1 and M2; regulated sites: L1 and L2



Diptera comprised more than 30% of individuals from T1 to T3 and from U3 to L1. Chironomidae (especially Orthocladiinae) was the best-represented dipteran family. Of the non-insect taxa, the oligochaete *Nais communis* (Naididae) peaked in abundance at T3, was also common at T4, and below the dam at L1. Two species of Gastropoda comprised more

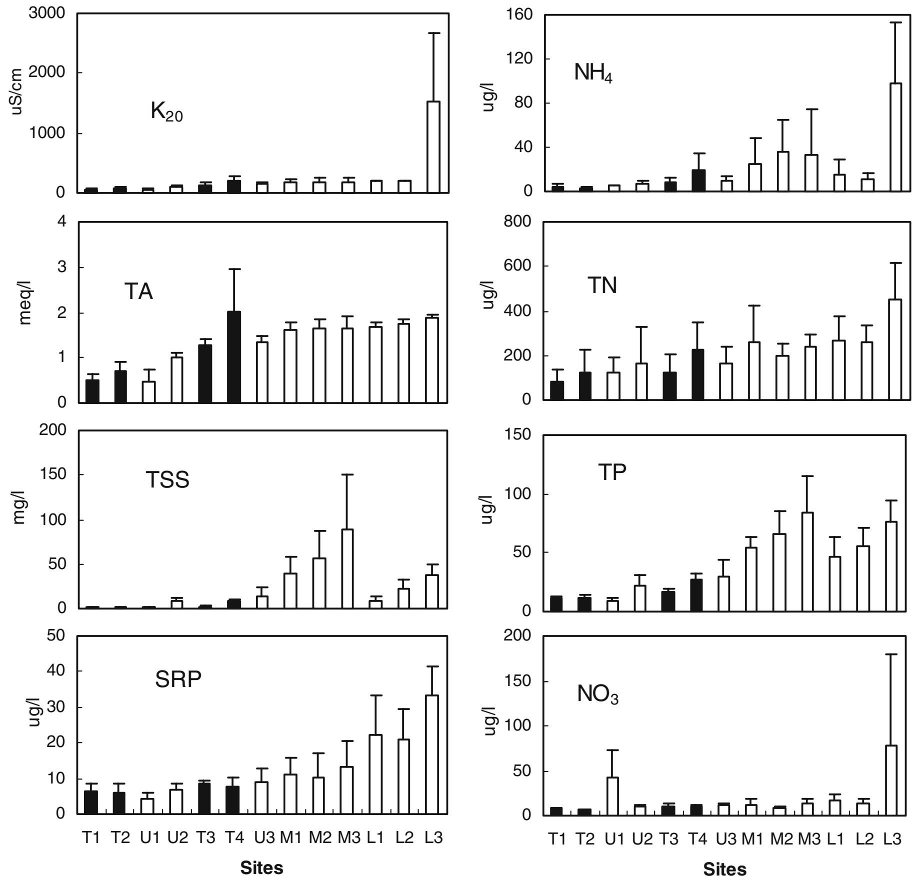


Fig. 4 Mean values (±SD) of the chemical variables in 13 sampling sites of the Chubut River basin, Patagonia, Argentina, during 2004. Dark bars: tributaries, open bars: main channel sites. K_{20}: conductivity, *TA* total alkalinity, *TSS* total suspended solids, *SRP* soluble reactive phosphorus, NH_4 ammonia, *TN* total nitrogen, *TP* total phosphorus, NO_3 nitrate plus nitrite nitrogen

than 35% of the fauna at L1. *Limnodrilus* sp. (Tubificidae) made up 97.5% of the invertebrate fauna at L3 where fine substrata, predominated.

Effects of flooding on macroinvertebrates

Significant differences in species richness were found before and after the July flood ($F_{(1,52)} = 32.5$, $P < 0.0001$). Richness decreased, dramatically at the main channel sites U2, M2, L1 and L3, and sites in the upper basin tributaries (T3 and T4) were also affected (Fig. 5). Changes in density were also significantly lower after flooding at U2 and L1, and at T1, T3 and T4 on the tributaries ($F_{(1,52)} = 25.3$, $P < 0.0001$) (Fig. 5). Although mean density declined by 50% at the main channel site U3, the decrease was not significant. Several species of Ephemeroptera, Plecoptera, Trichoptera and Coleoptera that had been present in samples before the flood were not found in September, but the relative abundance of Diptera increased in the upper tributaries and at main channel sites. Mollusca and Crustacea were reduced in abundance at regulated site L1 (lower basin) after the flood

Table 2 Mean relative abundance (percentages) of macroinvertebrate species in 13 sampling sites of the Chubut River Basin, Patagonia, Argentina in the study period

Taxa	T1	T2	U1	U2	T3	T4	U3	M1	M2	M3	L1	L2	L3
Plecoptera													
Klapopteryx kuscheli Illies (Kk)	0.03												
Kempnyela genualis Navás (Kg)			0.01										
Notoperla magnaspina Mc Lellan (Nm)	0.02	0.2											
Notoperlopsis femina Illies (Nf)	3.0	2.1	1.0	0.4	2.5	4.9	1.0						
Antarctoperla michaelseni Klapálek (Am)	2.5	0.7	0.1	0.5	1.5	1.2				0.2		5.6	
Limnoperla jaffueli Navás (Lj)	0.3	0.3	3.2	0.8	0.1	0.05			1.5				
Chilenoperla semictinta Illies (Chs)			0.01										
Aubertoperla illiesi Illies (Ai)	0.4	0.3	0.5										
Potamoperla myrmidon Illies (Pm)	0.6	0.2	0.04	10.5	0.9	2.6	12.7	30.4	14.4	22.4	0.02	15.0	
Ephemeroptera													
Chiloporter eatoni Lestage (Che)			0.1										
Andesiops torrents (At)	5.4	4.5	1.7	0.7	0.05	0.4	0.04	0.4	1.1	0.1	0.2	1.1	
Americabaetis sp. (A)	0.1		0.8	0.2	0.5	1.3	0.04	0.6	4.2	1.2	9.0	4.6	
C. penai Travers & Edmunds (Cp)				1.0			0.5			0.03			
Caenis sp. (Cae)		0.03		1.2	0.9	0.6	4.8		0.7				
Traverella sp. (Tr)				0.01			0.3	10.9	21.7	29.8		37.3	
Meridialaris laminata Ulmer (Ml)	7.7	6.9	17.4	10.1	16.6	26.3	0.7		0.1		0.9	1.3	
Meridialaris chiloeensis Demoulin (Mc)	10.3	9.6	1.2			2.9							
Penaphlebia chilensis Eaton (Pc)			0.01	0.03		0.1	0.02						
Nousia delicata Navás (Nd)	0.02					6.7	0.1						
Nousia crena Pescador & Peters (Ncr)					14.4								
Nousia bella Pescador & Peters (Nb)		0.03											
Nousia maculata Demoulin (Nma)	1.4	2.9											

Table 2 continued

Taxa	T1	T2	U1	U2	T3	T4	U3	M1	M2	M3	L1	L2	L3
Trichoptera													
Brachysetodes major Schmid (Bm)			1.7	0.2	0.01	0.1	0.3	0.8		0.03			
Parasericostoma ovale Schmid (Po)		0.2	13.6	5.1		0.04	0.3		0.04				
Cailloma sp. (C)	0.4	0.1	0.1	0.1	0.01								
Neoatopsyche chilensis Schmid (Nc)	0.02	0.3	0.2	0.04	0.4	0.4							
Amphichorema sp. (Amp)			0.03										
Neopsylochorema tricarinatum Schmid (Nt)	0.1	0.8	1.7		0.5	0.01							
Smicridea annulicornis Blanchard (Sa)	27.8	22.3		0.9	3.5	16.1	1.7						
S. frequens Navás (S)			1.6				1.7					12.7	
S. dithyra Flint (Sd)								0.6	1.1	4.2		10.5	
Smicridea sp (Smi)	3.1	1.9											
Mastigoptila longicornuta Schmid (Mlon)			0.5	0.2		0.05				0.1			
Monocosmoecus sp. (M)			0.04										
Oxyethira bidentata Mosely (Ob)								0.3			1.4		
Metrichia neotropicalis Schmid (Mn)		0.1		0.1	0.1	0.2	0.1		0.04	0.1	2.7	0.1	
Neotrichia sp. (N)			19.9		0.05	0.02		0.1					
Diptera													
Paratrichocladius sp1 (Par 1)	3.3	5.3	10.8	3.0	18.1	5.2	9.4	5.7	31.6	3.9	1.8	1.4	
Paratrichocladius sp2 (Par 2)	4.8	19.2	2.9	40.6	4.8	6.5	28.8	29.7	0.5	10.4	6.6	2.6	
Cricotopus sp. (Cri)	0.03	0.2	1.6	0.4	1.6								
Thiennemanella sp. (Thi)	0.2	0.1	1.1	0.3		1.0	0.2	0.2					
Lopescladius sp. (Lo)										0.03			0.03
Pseudosmittia sp. (Ps)	3.5	2.4	0.3	0.4	0.1	0.9	0.5	0.2			3.3	2.0	
Parametriocnemus sp. (Paps)	0.3	0.03		1.8	2.0	6.6	1.8	0.2	0.04	0.1		0.4	
Orthocladinae sp (Ort)			0.1		0.1			1.4			17.1		

Table 2 continued

Taxa	T1	T2	U1	U2	T3	T4	U3	M1	M2	M3	L1	L2	L3
Orthocladiinae sp1 (Ort1)	0.5	3.0	1.0		0.2								
Orthocladiinae sp2 (Ort2)	0.02	0.4	0.6	0.6	0.2	0.2	0.04						
Orthocladiinae sp3 (Ort3)								0.2					
Orthocladiinae sp4 (Ort4)		2.8		6.4			10.9		0.5				
Podonominae sp (Pod)	0.2	0.3											
Tribelos sp. (Tri)					0.1			0.5					
Dicrotendipes sp (Dicr)						0.05	0.2						
Crypotochironomus sp. (Crip)				0.03									
Rheotanytarsus sp. (Rhe)	0.2	0.3	0.04	3.6	1.8	0.5	4.0			0.1		0.7	
Parachironomus sp. (Parch)			1.0	0.1									
Polypedilum sp. (Pol)									0.1	0.5	0.1		
Tanypodinae sp (Tan)	1.3	2.7	0.7	0.9	3.8	1.1	1.1	0.7	0.9	0.9	0.3	0.6	
Simulium sp. (Sim)	12.3	2.5	9.8	0.5	0.4	0.5	0.9	14.2	7.8	21.7	0.1	1.1	
Hexatoma sp. (Hex)	2.6	3.3	0.3	0.4	0.8	0.3	0.3		0.1				
Limnophila sp.(Lim)				0.03									
Molophilus sp. (Mol)											0.01		
Dasyoma sp. (Das)	0.5	0.4	0.04	0.01	0.1	0.1	1.6						
Empididae sp (Emp)	0.3	0.2	0.2	0.2	0.01	0.1	1.0	0.7	0.2		0.1		
Lispoides sp. (Mus)	0.02	0.2			0.3	0.1			0.4	0.03			
Ceratopogonidae (Cer)	0.02	0.2	0.1	0.4									
Tabanidae sp (Tab)	0.03			0.4		0.04	0.3	0.2	0.1				
Psychodidae sp (Psy)				0.01		0.01					0.02		
Coleoptera													
Hemiosus dejeani Solier (Hd)			0.01	0.8	0.4	1.2	0.9						
Andogyrus seriatopunctatus Régimbart (As)			0.01										

Table 2 continued

Taxa	T1	T2	U1	U2	T3	T4	U3	M1	M2	M3	L1	L2	L3
Hydora annectens Spangler & Brown (Ha)						0.02	0.02		0.1				
Austrelmis sp. (Aus)	0.2	0.2	0.1	0.4	0.1	0.7	1.2	0.2	0.3	0.03			
Austrolimnius spp. (Alim)	1.0	1.3	1.1	2.2	0.1	2.2	2.2	0.2					
Luchoelmis sp. (L)			0.01	0.6			0.1						
L. cekalovici Spangler & Staines (Lc)	2.5	0.2	0.5	2.2			0.3						
Stethelmis kaszabi Hinton (Sk)			0.1	0.01									
Crustacea													
Hyalella curvispina Shoemaker (Hc)				0.01	0.01	0.01					0.05	0.3	
Decapoda													2.4
Aegla sp.			0.01	0.1		0.1	0.02		0.1	0.1		0.8	
Acari sp1 (Ac1)						0.01							
Acari sp2 (Ac2)							0.02						
Annelida													
Lumbriculus variegatus Müller (Lv)	3.0	1.4	2.1	1.6	0.2	0.9	7.0	0.8	2.5	3.1		0.8	
Limnodrilus sp. (Limn)				0.2		0.1		0.5	9.6		1.3	0.3	97.5
Nais communis Piguet (Ncom)					22.7	7.2					7.3		
Phreodrilus sp. (Phr)											0.7		
Glossiphonidae sp1 (Glo)			0.1	0.01							0.6		
Glossiphonidae sp2 (Glo2)							0.1						
Nereis sp. (Ner)													0.1
Turbellaria													
Girardia sp. (Gir)				0.1	0.02	0.1	0.2	0.2		0.03	11.3	0.4	
Temnocephalidae sp. (Tem)						0.05							

Table 2 continued

Taxa	T1	T2	U1	U2	T3	T4	U3	M1	M2	M3	L1	L2	L3
Mollusca													
Chilina sp. (Chil1)							1.9						
Chilina patagonica Sowerby (Chp)			0.2	0.1	0.1	0.2	0.3	0.2	0.5	0.8	25.0		
Gasteropoda sp. (G)													0.03
Lymnaea diaphana King (Ld)					0.01		0.2				9.6	0.3	
Glundachia concentrica d'Orbigny (Gc)											0.5		
Mean species richness (± SD)	18.8 (2.1)	17.8 (2.9)	22.4 (2.1)	19.9 (5.7)	17.4 (4.3)	21.3 (7.5)	17.3 (2.8)	7.8 (2.0)	8.8 (3.2)	8.8 (2.3)	10.9 (4.1)	7.3 (3.6)	1.8 (0.9)
Total richness	40	41	50	51	41	48	44	26	26	24	25	22	5
Mean abundance (ind m^{-2}) (± SD)	1955 (561)	1028 (455)	3412 (862)	2435 (333)	5024 (1492)	2732 (1214)	1755 (548)	433 (302)	850 (320)	1027 (189)	2946 (1293)	299 (109)	1314 (591)

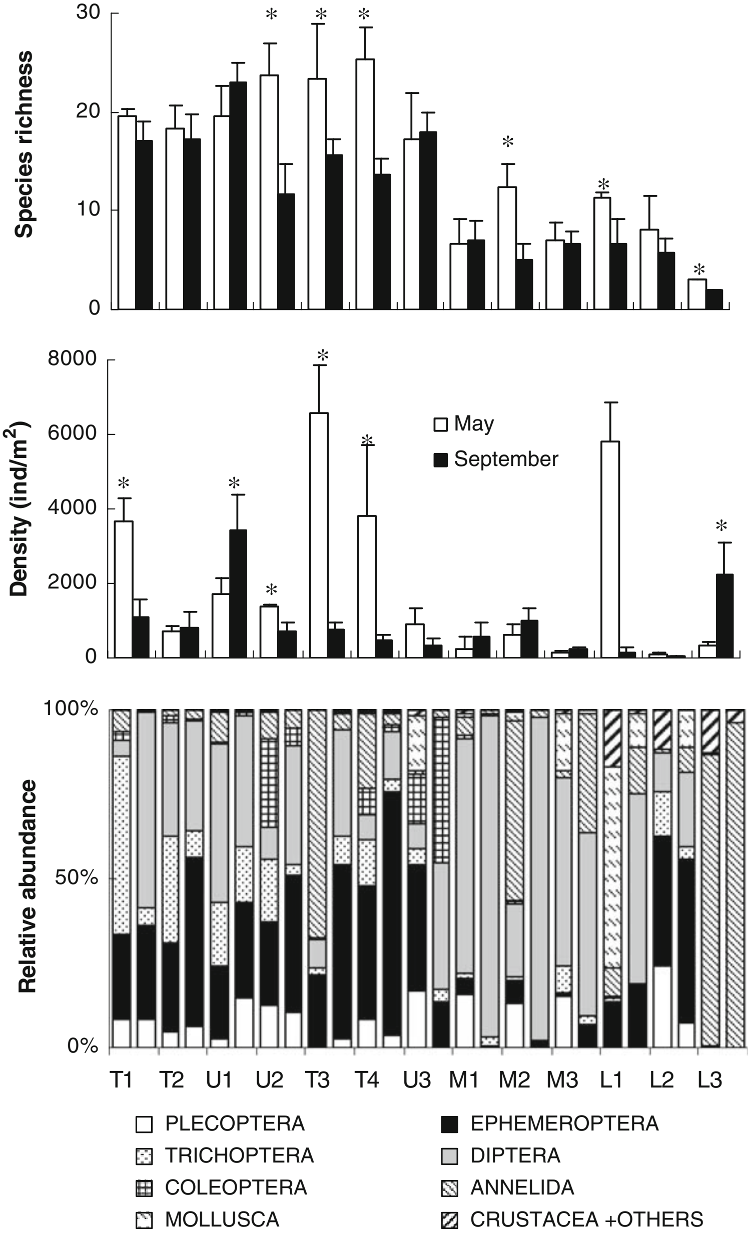


Fig. 5 Mean variation in species richness, density and relative abundance of benthos before (May 2004) and after (September 2004) the flooding (highest historical peak in last 50 years) in 13 sampling sites in the Chubut River basin, Patagonia, Argentina

(Fig. 5). On the other hand, density increased at sites U1, M1, M3 and L3, although the increases were significant only at U1 and L3. At U1 the increases were explained by the presence of the stoneflies *Limnoperla jaffueli*, *Potamoperla myrmidon* and a caddisfly *Brachysetodes major*, whereas at L3 by the tubificid *Limnodrilus* sp.

Table 3 Results of two-way ANOVA testing for dam effects on species richness, EPT richness, benthic densities and densities of Plecoptera, Ephemeroptera, Trichoptera and benthic organic matter

	Site $F_{(1,16)}$	Season $F_{(3,16)}$	Site × Season $F_{(3,52)}$
Species richness	ns	10.6***	ns
EPT richness	16.1**	11.7***	ns
Total density	29.6***	15.3**	18.1***
Plecoptera density	203.3***	48.8***	47.3 ***
Ephemeroptera density	ns	68***	219**
Trichoptera density	ns	81.6***	31.6***
POM	51.9***	3.7*	3.7*

Variables log (x + 1) transformed

$n = 12$; * $\leq P < 0.05$, ** $P < 0.01$, *** $P = 0.001$

Effects of regulation

Several post-impoundment changes in environmental parameters were observed when comparing mean values for M3 (non-regulated) with L1 (regulated). Thus, NO_3, SRP and chlorophyll *a* increased below the dam, whereas NH_4, TP, and TSS decreased (Fig. 4; Table 1). Benthic organic matter was significantly higher at M3 than L1 regardless of the season ($F_{(1,16)} = 51.9$, $P < 0.0001$).

Two-way ANOVA indicated significant effects of regulation on macroinvertebrate communities with total density being higher and Plecoptera density lower at regulated site L1 than at non-regulated site M3 (Table 3). Despite species richness being higher at L1 than M3, differences were not significant ($F_{(1,16)} = 4.08$, $P = 0.06$). However, EPT richness was significantly higher al M3 than L1 ($F_{(1,16)} = 16.1$, $P < 0.001$).

Macroinvertebrates and environmental relationships

Results of the CCA (first three axes) are summarized in Table 4 and shown in Fig. 6. The environmental variables selected in the analysis are represented in the biplot by arrows, which point in the direction of maximum change in the value of the associated variable (Fig. 6). The species-environmental correlations were: 0.95, 0.84 and 0.89 for the first, second, and third axes, respectively (Table 4), indicating a strong relationship with the environmental variables selected. Monte Carlo tests were significant for all axes considered (Table 4).

The strongest explanatory factors were physical and chemical variables, but only 25.5% of variation in the species data was accounted for by the environmental variables measured (Table 4). CCA axis 1 reflected the distribution of species and sites along the longitudinal gradient of the river. Elevation and TSS had the strongest correlations with axis 1, and total alkalinity, NH_4, SRP and TN were also correlated with this axis. These latter environmental variables are associated with land use (livestock, agriculture). Variables most strongly related to axis 2 were chlorophyll *a*, water velocity and POM. Samples taken at the upper basin sites were located at the negative end of axis 1, whereas those from the middle and lower basin sites were at the positive end (Fig. 6). Other significant variables were TSS and discharge. Sites and months having higher flows and high TSS values were positioned in the lower right quadrant, whereas sites and months with low discharge and TSS were in the upper left quadrant. Samples from the regulated section of the river (except L2M) were in the upper right quadrant; these sites had the highest SRP and chlorophyll *a* values.

Table 4 Eigenvalues and correlation of standardized environmental variables with the first three CCA axes

Axis	CCA1	CCA 2	CCA3
Eigenvalue	0.352	0.210	0.152
Species-environmental correlations	0.955	0.841	0.895
Cumulative percentage variance			
Of species data	12.5	20.0	25.5
Of species-environmental relation	27.6	44.1	56.0
Correlations			
Total alkalinity (TA)	0.55	0.09	−0.26
Total suspended solids (TSS)	0.65	−0.31	0.03
Ammonia (NH_4)	0.53	−0.09	−0.25
Total nitrogen (TN)	0.40	0.06	0.19
Soluble reactive phosphorus (SRP)	0.46	0.25	0.10
Chlorophyll *a*	0.17	0.42	0.29
Altitude	−0.88	−0.16	−0.09
Depth	0.25	0.05	0.64
Velocity	−0.04	−0.32	0.24
Water temperature	0.23	−0.24	−0.03
Particulate organic matter (POM)	−0.28	−0.32	0.34
Discharge	0.44	−0.08	0.61

Test of significance of first canonical axis: F = 5.018, $P < 0.001$

Test of significance of all canonical axes: F = 2.429, $P < 0.001$

Figure 6b shows the location of invertebrate assemblages along the same gradients. *Gundlachia concentrica* (Bivalvia), *Lymnaea diaphana* (Gastropoda), *Phreodrilus* sp. (Oligochaeta), *Oxyethira bidentata* (Hydroptilidae) and *Orthocladiinae* sp. either peaked, or were found only at regulated site L1. *Polypedilum* sp. (Chironomidae) was also present at L2. Most species that were common at middle basin sites were positioned in the lower right quadrant and included *Lopescladius* sp. (Chironomidae), *Smicridea dithyra* (Hydropsychidae) and *Traverella* sp. (Leptophlebiidae).

The gripopterygids *Aubertoperla illiesi* and *Notoperla magnaspina*, a hydropsychid, *Smicridea* sp., the leptophlebiid *Nousia maculata* and *Podonominae* sp. (Chironomidae) were at the negative end of axis 1 and were more common in high elevation, fast-flowing water. A caddisfly assemblage comprising *Brachysetodes major*, *Parasericostoma ovale* and *Neotrichia* sp. that peaked at U1 was located in the lower left quadrant, whereas *Hemiosus dejeani* (Coleoptera), *Notoperlopsis femina* (Gripopterygidae) and *Nousia delicata* (Leptophlebiidae), which had peaks of abundance in tributaries T3 and T4, were in the upper left quadrant.

Discussion

Results of this study demonstrated that the Chubut is a complex river whose biotic community was strongly related to landscape features. However, it was difficult to distinguish clearly between the effects of natural and anthropogenic disturbances. Whereas the river has a distinct longitudinal gradient in elevation, and hydro-geological features have a strong influence on benthos communities, my analysis suggests that river regulation and changes in the catchment activities also influenced the abundance and distribution of benthic invertebrates by affecting discharge and introducing fine sediments (sand and clays).

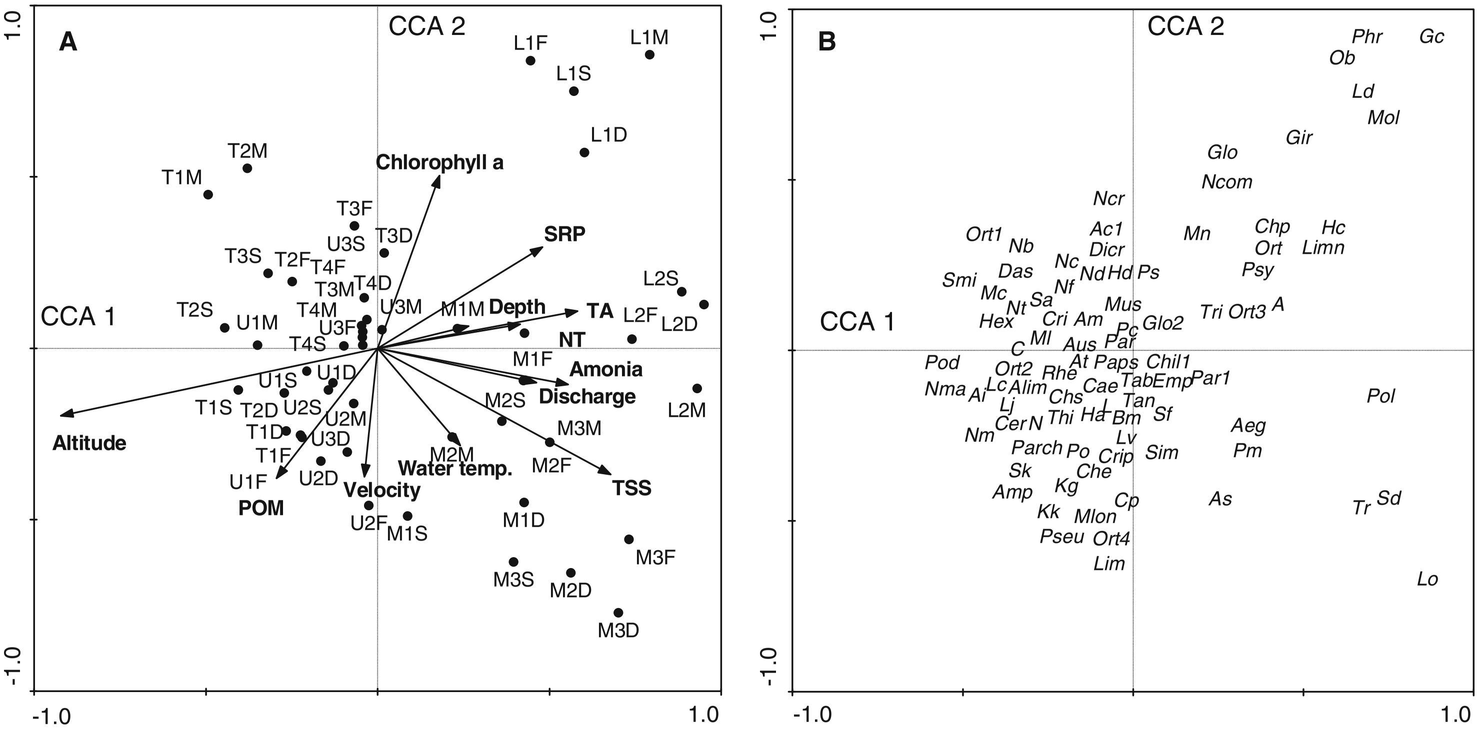


Fig. 6 (**a**) Biplot of the Chubut River sampling sites and environmental variables in relation to the first ordination axes of CCA. Analysis carried out on abundance data (94 macroinvertebrate species). Codes of sites in Table 1. Dates: F: February; M: May, S: September and D: December. (**b**) Ordination of macroinvertebrate species with regards to the first environmental axes of CCA. Codes of species in Table 2

As in earlier studies in Patagonia (Miserendino and Pizzolón 2000, 2004) benthic assemblage composition was determined primarily by altitude, gradient, river size and related attributes, and secondarily by river regulation. Other variables highlighted by the ordination were physico-chemical parameters, especially those associated with land use in the basin. In temperate catchments, concentrations of TN, nitrate, phosphorus, major anions and cations are often good indicators of land degradation (Sponseller et al. 2001; Hall et al. 2001) and as in some other arid and semiarid areas (Marshall et al. 2006), geological factors resulted in high TSS and TP values in the middle basin of the Chubut River. However, in the middle basin conductivity and nutrient concentrations, especially those of ammonia and TP, were two to three times higher than in the upper basin, probably as a consequence of cattle raising land use along this part of the river.

The longitudinal pattern of species richness displayed in the Chubut River resembles that observed in other large rivers in Patagonia. Petersen and Sangfors (1991) showed a strong change in benthic community richness across the altitudinal gradient in the Bio Bio (Chile) and Wais (1990) reported a decrease in species richness from the upper to the lower basin in the Negro River (Patagonia, Argentina), with maximum richness at the middle basin. In spite of those obvious similarities between the Negro and Chubut River, Plecoptera, Baetidae and Trichoptera, were absent in the lower Negro River basin (Bonetto and Wais 1995). A series of artificial reservoirs placed on the main tributaries at the middle basin, plus a higher agricultural development could explain these faunal discontinuities.

An interesting finding of the present study is that the main channel sites on the Chubut upper basin supported a higher number of species than the tributaries, being similar to medium size piedmont rivers intensively sampled (Miserendino and Pizzolón 2000). Collier and Lill (2008) observed an increase in diversity at main channel sites with distance down river in a large New Zealand watercourse, most likely as a consequence of interplay between habitat patchiness and successional and hydrogeomorphic processes influencing macroinvertebrate community. In the middle Chubut river basin where turbidity and flood disturbance were high, benthic density was low as found below a tributary of the Colorado River in arid Arizona (Shaver et al. 1997, Stevens et al. 1997). In contrast, the upper main river channel and its tributaries had a more abundant benthic fauna and twice the number of species found in the middle basin. These upper sites had higher water velocity, lower TSS, greater amounts of POM, and by inference, greater environmental heterogeneity.

Several insect taxa (*Caenis* sp., *Traverella* sp., *Potamoperla myrmidon*, *Paratrichocladius* sp2) characteristic of the Chubut middle basin were small sized with short life cycles, distinctive traits of species able to live in frequently disturbed systems. Mellado et al. (2007) identified the traits for species associated with natural disturbed semi-arid areas which contrasted with those in more stable and favourable environments as in upland forested areas. Among biological features that reduce the impact of environmental fluctuations they mentioned: small body size and many generations per year.

Disturbances, notably flooding, have an important role in regulating the distribution, abundance and coexistence of macroinvertebrates (Resh et al. 1988). Significant reductions in macroinvertebrate density have been recorded after scouring floods (Scrimgeour and Winterbourn 1989; Robinson et al. 2004) and in the present study the response of macroinvertebrate community to the flood was most severe in the non-turbid, upper main river and tributaries where benthos community was dominated by the most sensitive EPT species. Kaller and Hartman (2004) reported a strong reduction in EPT richness after fine sediment increases on bottom substrates in Appalachian streams. In our study, during September, tons of sediments washed downstream during the flood were present in the middle basin floodplain, many trees were dislodged from the river corridor, and trunks, branches and debris blocked some upper basin channels. Furthermore, large new gravel bars were seen in upper sections of the river and some sand deposits remained on the streambed and in the riparian corridor for over 3 months. Not unexpectedly, this extreme flood also resulted in a reduction in the density and species richness of the macroinvertebrate community, especially in the upper basin and headwater tributaries. Strong discharges in mountain rivers in Patagonia, including those rivers having little to moderate development in their basin (ej: incipient forestry and land-use practices), resulted in high suspended sediment loads altering benthos assemblages (Miserendino and Pizzolón 2003).

Even at regulated site L1 1 km below the Florentino Ameghino Dam the fauna was strongly affected, with mayflies decreasing in abundance, dramatically, and caddisflies that had been associated with aquatic plants disappearing. Many of these losses in fauna below the dam were likely a consequence of increase bed scouring as demonstrated elsewhere by Cereghino and Lavandier (1998) and Collier (2002). It is well known that impoundments can have strong effects on ecological processes and macroinvertebrate communities downstream of a dam (Ward 1992), and the serial discontinuity concept (Ward and Stanford 1982) predicted that reservoirs located in the lower reaches of river systems would increase biotic diversity below them. Florentino Ameghino Dam did not have a significant effect on species richness, but at least five insect species were no longer present 1 km below the dam and others were reduced in abundance compared with upstream sites. Furthermore, some like the leptophlebiid mayfly *Traverella* sp. increased in abundance again further down-river as did another leptophlebiid *Deleatidium* sp. in a regulated New Zealand river (Collier 2002). In contrast, the hydropsychid *S. dithyra* disappeared below the dam consistent with the findings of other workers that many species of temperate Hydropsychidae are affected negatively by the presence of hypolimnetic release dams (Hauer and Stanford 1991; García de Jalón et al. 1994). Riverine species favoured by regulation often have short life cycles (Cortes et al. 2002; Cereghino et al. 2002) and is likely the case for the baetid mayfly *Americabaetis* sp., which increased numerically below the dam. *Americabaetis* species have a multivoltine life cycle with short summer and autumn generations as reported by Corigliano et al. (2001).

Although macroinvertebrate density is often reduced below reservoirs (García de Jalón et al. 1994), it can also be higher (Munn and Brusven 1991; Fjellheim 1997), or show little change (Harding 1992). One reason for the significant increase in benthos density recorded below Florentino Ameghino Dam is likely to have been the decrease in suspended solids, which would have favoured colonization by primary producers (bryophytes, algae) in the more transparent water (Ward and Stanford 1994). In turn, this can be expected to have advantaged the algal scrapers *Chilina patagonica* and *Lymnaea diaphana* and species associated with aquatic vegetation such as the hydroptilids *O. bidentata* and *M. neotropicalis*.

Overall, the lower basin was the most modified section of the Chubut through a combination of agricultural development including irrigation, urbanization and river regulation, which have led to changes in nutrient concentrations, turbidity and in benthic community composition and abundance. This is consistent with Sastre et al. (1997) findings, who reported a gradient of eutrophication in the lower part of Chubut as revealed by physicochemical features and phytoplankton composition. Large rivers in temperate areas play several ecological functions and sustain multiple activities, but sometimes there is not a responsible use of aquatic resources (Buijse et al. 2005; Mellado et al. 2007). The results of this study should be considered by management authorities in the future, since new hydroelectric developments are projected on forested low-order watercourses in the cordillera, and also a series of large dams in a large turbid river on the Plateau. These projects would affect physico-chemical conditions and benthos below these structures. This needs to be understood by managers and planners in order to minimize environmental damage and maximize benefits to the diverse human and other communities dependent on these rivers. Jointly with these considerations, other aspects should be taken into account, like presence and position of cities; land use history and degree of development in the basin.

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