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Nutrient uptake in a stream affected by hydropower plants: comparison between stream channels and diversion canals

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Response to Reviewers:	Dear Michael, We have followed carefully the comments made by you, Hervé and referee #1 to our ms. The only point in which we did no make so is in Line 295. The referee noticed a disagreement between text and table. The table was wrong, so instead of correcting the text we corrected the table.

	We hope the ms is now ready for publication. Thank you very much for your effort Arturo and Eugénia

Nutrient uptake in a stream affected by hydropower plants: comparison between stream channels and diversion canals

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Abstract

Small hydropower plants divert part of the water from wide and physically complex stream channels with active hyporheic areas to narrow and hydraulically simple concrete canals, and thus, might affect nutrient dynamics. We compared nutrient uptake in diversion canals and in stream channels in the Leitzaran Stream (Basque Country, northern Spain). We hypothesized that simple morphology in diversion canals will result in lower nutrient uptake in canals than in stream channels.

Periphytic chlorophyll and biomass did not differ significantly between reach types. Water was significantly deeper and faster in canals than in stream channels, but the transient storage zone did not differ significantly between reach types. There were no significant differences between uptake length for neither phosphate nor ammonium between reach types. Uptake length in both stream channels and diversion canals decreased with discharge, in a pattern similar to that previously described for pristine rivers across the world. Uptake velocity and uptake rate for phosphate did not differ significantly between reach types, but in the case of ammonium both retention metrics were significantly larger in the diversion canals. Results suggest that although hydropower schemes have minor effects on nutrient retention, these depend on the proportion of flow diverted.

Key Words: hydropower plant, stream, nitrogen, phosphorus, uptake, hydromorphology, water diversion

Introduction

Hydropower plants cause profound effects on river ecosystems by damming, reducing flow in natural stream channels, and creating new water flow paths through man-made side canals. Dams constitute barriers along the river continuum, which alter the downstream flux of water, sediments, nutrients and organic matter, and the movement of organisms (Ward & Stanford, 1979). This in turn affects the channel morphology, community structure, and functioning of stream ecosystems (Graf, 1999; Petts, 1984; Ward et al., 1999; Elosegi et al., 2010). In addition, water diversion into artificial diversion canals reduces in-stream water flow, and thus modifies stream hydraulics and habitat characteristics affecting both invertebrates and fish communities (Armitage & Petts, 1992; Hax & Golladay, 1998; Murchie et al., 2008). There is less information on the effect of water diversion on stream ecosystem functioning, but impacts are likely, as both channel morphology and hydraulics exert a strong influence on ecosystem processes (Uehlinger, 2000; Hall et al. 2002; Sweeney et al. 2004; Elosegi et al. 2011). Finally, diversion canals can also be habitats for some organisms and play a role in the transport and processing of nutrients and organic matter, thus influencing ecosystem functioning of stream networks. However, there is little information on how diversion canals compare to stream channels regarding transport, retention and transformation of materials.

One of the ecosystem processes likely to vary between stream channels and man-made canals is nutrient uptake, because it is highly dependent on the interaction between hydrologic retention and both chemical and biological uptake (Valett et al., 1996) and these characteristics differ between both reach types. Diversion canals are morphologically more constrained and homogenous than natural river channels. Since they are often lined with concrete, they lack hyporheic zone, which is an active component of river ecosystems (Boulton et al., 1998). Furthermore, because diversion canals are managed to avoid flow obstructions, accumulation of sediments and organic matter is rare. Therefore, it is expected that the diversion canals have faster water velocity, less turbulence, and lower sediment-water interactions compared to the stream channels. All these physical characteristics suggest nutrient uptake would be lower in diversion canals than in stream channels (Mulholland et al. 1985; Gücker and Boëchat 2004;

Roberts et al. 2007). Differences in nutrient uptake between canals and channels may in turn have implications for nutrient dynamics at the network scale in streams affected by hydropower plants.

In the present study we compared nutrient uptake in two reach types: diversion canals and stream channels. We selected 5 canal-stream reach pairs downstream from water diversion dams, and an additional unregulated stream reach upstream from a dam. We hypothesized that channel form is an important factor controlling nutrient dynamics because it regulates interactions between water and bioreactive substrata. Therefore, we predict that simple morphology in diversion canals will result in lower nutrient uptake than in stream channels.

Methods

Study site

The Leitzaran is a 42 km-long stream that drains a 114.5 km^2 catchment (Fig. 1). Eighty five percent of the catchment area is dominated by siliceous geology, mostly carboniferous slate and sandstone. The stream is steep, sinuous, and runs along heavily incised meanders in a region with mountains higher than 1000 m a.s.l. located very close to the sea. The climate of the region is humid oceanic, with an average annual precipitation over 1500 mm and mean monthly temperatures ranging from 8.4 ºC in January to 20.7 ºC in August. Sixty six percent of the catchment is covered by conifer plantations (*Pinus radiata* up to 400-500 m a.s.l., *Larix kaempferi* at higher altitudes, and some sparse stands of *Pseudotsuga menziesii*), 18% is covered by native deciduous forests of oak (*Quercus robur*), beech (*Fagus sylvatica*), birch (*Betula* spp.), chestnut (*Corylus avellana*) and alder (*Alnus glutinosa*). The rest of the catchment (16%) consists of pasture land, meadows and few patches of arable land.

Near the headwaters of the Leitzaran there are two towns: Leitza and Areso (Fig. 1). Leitza has 3200 inhabitants, a large paper factory, some smaller factories, and many farms with sheep and cattle. The wastewater from Leitza receives secondary treatment before it is delivered into the stream. Areso has 290 inhabitants, mostly devoted to farming and forestry activities. Four km downstream from Leitza and Areso the Leitzaran Stream enters the province of Guipuscoa. At this location, the average concentrations of nitrate (NO_3^--N), ammonium (NH_4^+-N), and phosphate (PO_4^{3-}-P) are relatively high (1.37, 0.10 and 0.05 mg L^{-1}, respectively); however, invertebrate-based biotic indices indicate excellent water quality (Government of Navarre, 2005). Downstream from this point, the Leitzaran Stream runs for 30 km along a scarcely populated valley that is protected under the legal figure of Protected Biotope before it joins the Oria river. Nutrient concentrations tend to decrease along this reach.

Along the Leitzaran Stream there are 6 hydropower plants and 8 diversion dams, which are mostly concentrated in the lower 30 km of the stream (Fig. 1). Along this part, stream hydrology is highly influenced by the operation of these plants. Seventy percent of the stream length is affected by water diversion into canals, which run in parallel to the stream channel until they release the water at downstream locations, and an additional 4.1% is affected by water impoundments generated by dams. In this study, we selected 5 sites located at diversion dams (Fig. 1). One site was located in a headwater tributary (Franki) and the rest of sites were arranged along the main stem of the Leitzaran Stream (Plazaola, Mustar, Ameraun and Bertxin). Characteristics of each hydropower plant are shown in Table 1. Water concessions to hydropower companies (Table 1) are set to maintain environmental stream flows below the dams except at Franki and Plazaola, which are older concessions.

At each site we selected a reach in the stream (below the dam) and another reach in the diversion canal that runs in parallel to the stream reach (Table 2). At Franki, an additional reach was selected upstream from the dam and used as a reference for unregulated flow conditions. The diversion canal from Ameraun returns its water to the stream at a site located below Bertxin (i.e., the next sampling site). Therefore, stream discharge at Bertxin is affected by water abstraction from both the Bertxin and Ameraun canals (Fig. 1).

Field and laboratory procedures

The study was done between the 15th and 19th of May 2006. On each day, we sampled sequentially both the canal and stream reaches of a study site, so that the delay between both additions was typically less than 2 hours. At each reach we measured stream nutrient (i.e., NH_4^+-N and PO_4^{3-}-P) uptake using the pulse nutrient addition technique (Wilcock et al., 2002). We used this method because high discharge, especially in the canals, precluded the application of the more widely used constant-rate addition technique (Webster & Valett, 2006). Nevertheless, Powers et al. (2009) have recently shown that the two methods provide comparable results of nutrient uptake metrics. On each addition, 20-50 L of a solution containing NH_4Cl and $Na(H_2PO_4)\cdot H_2O$ as nutrient sources, and NaCl as a hydrologic tracer (Bencala et al. 1987) were added to the stream or canal in a single pulse at the head of the reach, in a place were fast mixing with stream water was ensured. In the case of the canals, we took advantage of the strong turbulence in the transition between the weir and the canal. The amount of reagents in the solution was set to target a 3-fold increase in background nutrient concentration at the peak of the pulse. Conductivity was automatically recorded at the downstream end of the reach every 5 s from the beginning of the addition pulse until conductivity returned to pre-addition values using a conductivity meter (WTW 330) connected to a data logger (Campbell CR 510). Water samples were collected in 250 mL acid-washed plastic bottles every 10-60 s at the bottom of the reach over the conductivity-pulse passage. Samples were stored on ice, transported to the laboratory, filtered through pre-ashed fiberglass filters (Whatman GF/F), and frozen until analysis. Concentrations of PO_4^{3-}-P and NH_4^+-N were analyzed manually and using TRAACS 800 autoanalyzer, respectively, following standard colorimetric methods (APHA, 1998).

Additionally, reach morphology was described by means of 10 regularly spaced transects, across which measurements were recorded at 0.5 - 1 m intervals. At each transect, we measured wetted width (w, m), water depth (h, m), percentage coverage of substrate types (silt, sand, gravel, pebble, cobble, boulder or bedrock), presence of wood and leaf litter, and canopy cover (measured as the vertical projection of leaf shade). We also measured water temperature, pH and oxygen concentration (WTW field probes). To estimate the accumulated radiation reaching the reach during the addition experiments, we corrected radiation data provided by the Meteorological Survey of the Basque Government for the shade produced by the canopy cover on each reach. The light attenuation was estimated using the ratios calculated by Izagirre and Elosegi (2004) at a full-canopy site with summer foliage.

At each reach we also collected periphyton samples to estimate biomass and pigment content. In the stream reaches, ten cobbles were collected at random, an area of 18.6 cm^2 was scraped from each cobble using scalpels and toothbrushes, and periphyton samples were collected with Pasteur pipettes. In the canal reaches, 10 samples were collected from the bottom and side-walls of the canal with a modified syringe (Biggs & Kilroy, 2000). All periphyton samples were stored in 50 mL plastic containers, brought to the laboratory on ice and kept frozen until analysis. After thawing, samples were homogenized with a domestic blender. One sub-sample was used to determine biomass as ash-free dry mass (AFDM) after drying at 105 ºC for 24 h and ashing at 500 ºC for 4 h. Another sub-sample was used to measure chlorophyll *a* spectrophotometrically after extraction in hot ethanol (Sartory & Grobbelaar, 1984).

Calculation of hydraulic parameters

Several hydraulic parameters were estimated from the time-conductivity curves obtained during the nutrient addition pulse at the end of the reach. Average water velocity (v, m s^{-1}) was calculated dividing reach length by the time elapsed between the addition and the conductivity peak (i.e., mean travel time). Discharge (Q, L s^{-1}) was estimated based on a mass balance approach using conductivity data as a surrogate of the chloride concentration. Briefly, discharge was the result of multiplying the volume of the added solution (L) by its conductivity (µS cm^{-1}) and dividing it by the integrated area of the conductivity curve above ambient conductivity levels (µS s cm^{-1}). Parameters to characterize the water transient storage along each study reach were estimated from the conductivity data by a one-dimensional solute transport model with inflow and storage (OTIS, Runkel, 1998). Estimated parameters from the model were a) the cross-sectional area of the wetted channel (A, m^2), b) the storage zone cross-sectional area

(A_s, m^2), and c) the water exchange rate from free flowing water to transient storage zone (k_1, s^{-1}). To allow comparison among reaches, A_s was normalized by A (i.e., A_s/A ratio). This ratio was used to estimate the water exchange rate from transient storage zone to free flowing water (k_2, s^{-1}) using the equation:

$$\frac{A_s}{A} = \frac{k_1}{k_2}$$

Calculation of nutrient uptake metrics

Three uptake metrics for both NH_4^+-N and PO_4^{3-}-P were estimated using nutrient concentration data from the pulse additions: uptake length (S_w, m), uptake velocity (V_f, mm min^{-1}) and uptake rate at ambient levels (U, μg m^{-2} s^{-1}). S_w is the average distance travelled by a nutrient molecule before being removed from the water column (Newbold et al. 1981), and reflects nutrient uptake efficiency in terms of nutrient removal relative to nutrient flux. V_f is the velocity at which a molecule moves from the water column to the stream bed, and it is an index of the biological nutrient demand (Stream Solute Workshop, 1990). U is the mass of nutrient taken per unit of stream bottom area and unit of time, and indicates the stream nutrient uptake capacity (Stream Solute Workshop, 1990).

To calculate nutrient uptake along the reach, we compared the nutrient concentrations measured at the bottom of the reach over the pulse passage to the nutrient concentrations predicted from the time-through curve of conductivity. We assumed predicted nutrient concentrations to be solely influenced by advection, dispersion and dilution, whereas observed nutrient concentrations were additionally subjected to biological or chemical uptake processes. Predicted concentrations were calculated using the following equation:

$$N_{t(pred)} = \frac{Cond_t - Cond_b}{Cond_i} \cdot N_i + N_b$$

where N_t and N_b are nutrient concentrations (mg L^{-1}) measured at time t and at background, respectively. This equation assumes that changes in background-corrected nutrient concentrations over time relative to the nutrient concentration of the added solution (N_i) are equal to changes in background-corrected conductivity ($Cond_t$ - $Cond_b$) over time relative to conductivity of the added solution ($Cond_i$). The total mass of nutrient added to the reach (M_i, mg) and the total mass of nutrients retrieved at the end of the reach (M_t, mg) were calculated as the integrated area of the background-corrected nutrient concentration-time curve (N_t, mg L^{-1} s^{-1}) multiplied by discharge (Q, L s^{-1}) using predicted and measured nutrient concentrations, respectively.

$$M_{i,t} = Q \int_0^{\infty} N_t dt$$

Based on these two values, we estimated the nutrient uptake rate coefficient (k_t, s^{-1}) following the exponential decay model (Martí and Sabater, 2009):

$$M_t = M_i e^{-k_t t_n}$$

where t_n is the mean water travel time (s) along the reach. The nutrient uptake metrics were derived from k_t using the following equations:

$$S_w = \frac{v}{k_t}$$

$$V_f = \frac{Q}{w\ S_w}$$

$$U_{amb} = \frac{N_b\ Q}{S_w\ w} = V_f\ N_b$$

For these calculations in the canals we used the wetted perimeter instead of the wetted width to account for the surface of the side walls.

Data analysis

We examined the normality of the variables by means of the Shapiro-Wilk test, and the homogeneity of variances by the Levene's statistic. In order to meet assumptions of normality, prior to the statistical analysis of data all variables were log-transformed. Differences in chlorophyll and benthic AFDM were analyzed by means of two-way ANOVA tests (stream site and reach type as factors). Student's t-tests for paired samples were used to compare data from all measured variables between stream and canal reaches.

We examined the relationships between nutrient uptake metrics and hydraulic variables, periphytic biomass, and nutrient concentrations using univariate lineal regression. Differences in regression models between stream and canals were analyzed using ANCOVA. In particular, we examined the relationships between a) S_w and Q, h and v, b) V_f and water transient storage parameters and nutrient concentrations, and c) U and periphytic biomass. The significance level for the tests was p=0.05. All statistical analyses were done using SPSS for Windows (version 12.0, SPSS Inc., Chicago).

Results

Chemical and biological characterization

Light levels during the addition were significantly higher at stream channels than at diversion canals (Student's paired t-test, t = 3.415, p = 0.027). Water temperature ranged from 11.1 to 18.2 ºC among sites, conductivity from 65.7 to 259.1 µS cm^{-1} and pH from 7.07 to 8.10 (Table 2). Dissolved oxygen concentration during the pulse additions ranged from 9.7 to 10.6 mg O_2 L^{-1}, which corresponds to 100 - 106% saturation. Concentration of nutrients was low to moderate, ranging from 0.004 to 0.060 mg L^{-1} for PO_4^{3-}-P, and from 0.008 to 0.044 mg L^{-1} for NH_4^+-N (Table 2). Neither nutrient followed any clear longitudinal pattern along the Leitzaran Stream. None of the variables described above showed any significant difference between the two reach types (Student's paired t-test, p > 0.05). Periphytic Chl *a* ranged from 2.4 to 120.5 mg m^{-2}, and biomass from 3.9 to 21.8 g AFDM m^{-2}. These two variables showed no clear patterns along the stream, and did not significantly differ between the two reach types nor among sites.

Morphology and hydraulics

The canals were more homogeneous than the stream reaches in terms of substrata. Canals were dominated by concrete, although the canal at Plazaola had a considerable accumulation of leaf litter. On the other hand, stream channels were dominated by cobble-boulder substrata (Table 3).

Total discharge (stream + canal) increased from 77.5 L s^{-1} at Franki to 870 L s^{-1} at Ameraun (Table 3). The decrease in Q observed at the most downstream site (Bertxin) is explained because the canal from Ameraun reverts its water downstream of Bertxin. At each site, the dams diverted more than 75% of the total stream discharge into the diversion canals, except at Bertxin (14%), because the hydropower plant was operating well below its full capacity. Streams were wider than canal reaches at all sites except Franki, where 99% of total discharge was diverted, leaving only a rivulet in the stream channel (Table 3). Mean water depth was below 20 cm at stream reaches and from 20 cm to 1 m at the canals, differences between reach types being statistically significant (paired Student's t-test, $t = -3.534$, $p = 0.024$). Water velocity ranged from 0.02 to 0.31 m s^{-1} in stream reaches and from 0.29 to 0.52 m s^{-1} in canal reaches, being significantly slower in the stream than in the canal reaches (paired Student's t-test, $t = -5.538$, $p = 0.005$).

Values of A were higher in the canals than in the stream reaches at all sites except Bertxin (Table 3). A was related to Q, but the relationship did not differ significantly between stream and canal reaches (ANCOVA). Taking all data together the relationship followed a potential model ($A = 0.0365\ Q^{0.565}$, $r^2 = 0.856$, $p < 0.001$). Reach types did not significantly differ in A_s (paired Student's t-test, $t = 1.749$, $p = 0.155$) nor in the A_s/A ratio (paired Student's t-test, $t = 2.342$, $p = 0.079$). This ratio was negatively related to Q but the relationship did not differ significantly between stream and canal reaches (ANCOVA). Taking all data together the relationship followed a logarithmic model ($A_s/A = 0.684 - 0.097\ \mathrm{Ln}\ Q$, $r^2 = 0.816$, $p < 0.001$). k_1 showed no significant differences between reach types, but k_2 was significantly higher in the canals than in the stream channels (paired Student's t-test, $t = -7.222$, $p = 0.002$).

Nutrient uptake

Values of S_w for PO_4^{3-}-P ranged from 14 to 195 m at stream reaches, including the upstream site at Franki, and from 97 to 577 m at canal reaches (Fig. 2). Contrary to our prediction, it was not significantly different between reach types (Table 4). S_w for PO_4^{3-} was positively related to water depth ($S_wP = 63.9 + 428$ h, $r^2 = 0.524$, $p = 0.012$). Values of V_f for PO_4^{3-}-P ranged from 6 to 20 mm min^{-1} at stream reaches, and from 6 to 97 mm min^{-1} at canal reaches (Fig. 2), and were not significantly different between reach types (Table 4). Values of U for PO_4^{3-}-P ranged from 1.2 to 12.5 µg m^{-2} s^{-1} at stream reaches and from 1.0 to 26.7 µg m^{-2} s^{-1} at canal reaches (Fig. 2); as with the other uptake metrics, differences were not statistically significant (Table 4). V_f and U for PO_4^{3-} were not significantly related to any of the independent variables considered.

S_w for NH_4^+-N ranged from 62 to 180 m in streams and from 52 to 532 in canal reaches (Fig. 2), and, as in the case for phosphate, showed no significant differences between reach types (Table 4). S_w for NH_4^+ was positively related to discharge ($S_wN = 89.6 + 0.463Q$, r^2 = 0,654, $p = 0.005$) and water depth ($S_wN = 68.1 + 372$ h, $r^2 = 0.69$, $p = 0.003$). V_f for NH_4^+-N ranged from 2 to 15 mm min^{-1} in stream reaches and from 12 to 58 mm min^{-1} in canals, being significantly higher in canal than in stream reaches (Table 4). Values of U for NH_4^+-N ranged from 0.7 to 8 µg m^{-2} s^{-1} in streams, and from 8 to 26 µg m^{-2} s^{-1} in canals, differences being statistically significant (Table 4). V_f and U for NH_4^+ were not significantly related to any of the independent variables considered.

Stream reaches consistently showed longer S_w values for NH_4^+ than for PO_4^{3-} (range of the S_w-N:S_w-P ratio 1.5 - 4.5) whereas no consistent pattern was found in the canals (range of the S_w-N:S_w-P ratio 0.5 - 1.7).

Discussion

Morphologically, diversion canals contrast sharply with stream channels, as they are narrower, deeper and have lower substrata heterogeneity. Contrasting with this apparent difference, our study showed only small hydraulic differences between diversion canals and stream channels. Water velocity in canals was much faster than in stream channels, but differences in other hydraulic variables were less consistent between reach types. This may be explained in part by differences in total discharge and in the fraction of water diverted among study sites. The active channel was in all cases wider in stream channels than in diversion canals. Nevertheless, changes in discharge in canals only affect water depth, whereas in stream channels affect both depth and wetted width, due to differences in shape of cross-sections (Jain, 2001). Therefore, when most water was diverted, like observed at Franki, the cross section was smaller in the stream than in the canal, whereas in cases where only a small fraction of the flow was diverted, like in Bertxin, the reverse was true.

Canals were characterized by smoother substrata than stream channels, and by reduced or absent hyporheos and dead zone storage. These features could result in smaller size of transient storage and lower water retention within the canal reaches, as both parameters are influenced by geomorphic complexity of the channel (Gooseff et al., 2007; Zarnetske et al., 2007). Nevertheless, and contrary to our predictions, the size of water transient storage and its exchange with free-flowing water in the Leitzaran did not consistently differ between reach types. The lack of consistent differences in hydraulic parameters between canal and stream reaches probably was not caused by uncertainty of the estimates, as estimated dispersion coefficients were below 0.20 m s^{-2}. We observed a negative relationship between the size of the transient storage (A_s/A) and discharge when pooling data from all sites together, in agreement with previous studies (Argerich et al., 2008). This relationship indicates that hydrology may override the effect of channel morphology on the variation of transient storage. In fact, at all the sites where a large fraction of the water was diverted (4 out of 5 sites) the transient storage size was larger at stream channels than at diversion canals. At Bertxin, where the canal diverted only 14% of the stream flow, the contrary was observed, but even there the transient storage size was not very large at the canal, probably limited by its low physical complexity. Other factors that may explain a lack of consistent differences could be associated with accumulation of benthic organic matter in the canals. Benthic organic matter is known to increase A_s/A in streams (Hart et al. 1999; Haggard and Storm 2003; Jin and Ward 2005; Argerich et al., 2008), and may also play a role in some of the diversion canals.

Contrary to our prediction, stream channels and canals did not differ in nutrient uptake efficiency. The nutrient uptake lengths measured along the Leitzaran Stream were in the order of few hundreds of metres, indicating relatively high nutrient uptake efficiency regardless of reach type. These values were similar to those published for headwater streams (e.g., Webster et al., 2003). In fact, the values measured in the Leitzaran fit within the relationship between uptake length and discharge described by Martí et al. (2004) from results compiled from the literature (Fig. 3). This provides further support to previous studies stating that discharge is the main factor controlling nutrient uptake efficiency in rivers (Butturini & Sabater 1998; Peterson et al. 2001). Considering data from the Leitzaran only, this relationship was significant for ammonium uptake length, but not for phosphate. However, phosphate uptake length was significantly related to depth, a variable directly linked to discharge. Therefore, it seems that hydrology overrides the effects of other variables, like physical channel complexity or the presence of hyporheos, thus, offering some clues to predict the nutrient uptake response of streams to variations in water diversion.

When uptake length values were corrected by discharge (i.e., estimated V_f), differences were significant between reach types for ammonium but not for phosphate. V_f-N values in the stream channels were similar to those reported in the literature for mountain streams (e.g., Hall et al. 2002; von Schiller et al. 2008), but were up to an order of magnitude higher in the canals. These differences were also observed for ammonium uptake rates. Other authors (e.g., Kent et al. 2005; Knap et al. 2009) have also shown fast nutrient retention in concrete-lined channels.

Abiotic sorption provides a potential explanation for the increased uptake in the canals (e.g., Boatman and Murray 1982; Triska et al. 1994), but biological activity could play a more crucial role. Primary producers show great affinity for dissolved nutrients (Webster et al. 2003) and affect uptake rates (Sabater et al. 2000; Mulholland et al. 2006). Canals have more stable substrate, more uniform current, and lower siltation (especially in the lateral walls) what would favour growth of primary producers such as filamentous green algae and mosses (Wood & Armitage 1997; Cardinale 2011). In fact, we observed that mosses covered most of the bottom and side walls of the studied canals. Some studies have highlighted that aquatic bryophytes have high capacity to retain nutrients (Mulholland et al. 2000), at least during some seasons (Steinman & Boston 1993).

In summary, our results show that the morphological contrast between stream channels and diversion canals do not result in consistent differences in transient storage and nutrient uptake efficiency. Instead, these variables seem to depend primarily on discharge, regardless of reach type. In addition, we found that canals had higher ammonium demand than expected. Therefore, the overall effect of hydropower plants on nutrient export from the stream-canal network can depend on operational decisions upon the proportion of water diverted into the canals.

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Table 1. Hydromorphological characteristics of the 5 hydropower plants where selected sites for this study were located (Franki, Plazaola, Mustar, Ameraun and Bertxin). Hydropower plants are arranged in the table following the downstream water flow. Dammed length corresponds to the length of the stream upstream from the dam subject to lentic conditions. Q= discharge.

Hydropower plant	Dam height (m)	Length of diversion canal (m)	Dammed length (m)	Mean Q in canals (L s^{-1})	Concession Q (L s^{-1})	Waterfall height (m)	Annual energy production (MWh)
Franki	1.5	1100	50	-	-	30	-
Plazaola	5.5	1200	100	928	400	130.7	3.0
Mustar	3.1	3150	225	186	2000	52	1.1
Ameraun	4.1	4150	150	955	3000	54	4.3
Bertxin	5.8	3245	475	453	1000	103	3.2

Table 2. Physical, chemical and biological characteristics measured in the canal and stream reaches of the 5 sites and in the reach upstream of the dam at Franki on the addition dates. Cond. = water conductivity. Chl *a* and AFDM are chlorophyll *a* and ash free dry mass, respectively, measured from stream cobbles or side-walls of the canals.

	Franki			Plazaola		Mustar		Ameraun		Bertxin	
	Upstream	Stream	Canal	Stream	Canal	Stream	Canal	Stream	Canal	Stream	Canal
Reach length (m)	65	8	95	83	180	95	130	99	108	89	59
Canopy cover (%)	82.00	82.00	77.27	82.00	48.45	74.32	82.00	51.07	71.60	55.08	22.24
Radiation (w m^{-2})	99.0	126.2	24.7	26.0	33.7	211.9	89.1	204.7	102.4	296.3	134.9
Water temp. (ºC)	12.2	12.0	11.1	14.2	14.2	16.0	15.1	18.2	15.8	16.8	16.5
Cond. (µS cm^{-1})	65.7	79.0	67.2	259.1	250.8	215.1	217.6	203.9	205.6	122.0	121.7
pH	7.07	-	-	7.80	-	7.83	-	8.10	-	7.48	-
Dissolved O_2 (mg L^{-1})	104	-	-	100.5	-	104.5	-	106	-	102.9	-
PO_4^{3-}-P (mg L^{-1})	0.010	0.029	0.011	0.050	0.060	0.011	0.016	0.034	0.034	0.007	0.004
NH_4^+-N (mg L^{-1})	-	0.020	0.044	0.039	0.036	0.009	0.008	0.039	0.036	-	0.028
Chl *a* (mg m^{-2})	26.9	2.4	120.5	85.8	20.4	22.6	-	88.7	16.1	29.7	30.4
AFDM (g m^{-2})	10.6	3.9	13.4	18.1	4.3	5.8	-	21.8	8.6	16.8	20.1

Table 3. Morphological and hydraulic parameters. Water transient storage zone parameters estimated using OTIS model in the canal and stream reaches of the five sites and upstream the dam at Franki at the addition dates.

	Franki			Plazaola		Mustar		Ameraun		Bertxin	
	Upstream	Stream	Canal	Stream	Canal	Stream	Canal	Stream	Canal	Stream	Canal
Clay (%)	0	0	0	0	0	0	0	0.9	0	0	0
Silt (%)	0	0	0	0.7	0	4.1	0	0	0	2.6	0
Sand (%)	16.0	0	9.3	3.4	0	0	0	2.8	0	0	0
Gravel (%)	8.0	14.3	0	10.2	0	15.5	0	10.4	0	8.8	0
Pebble (%)	8.0	0	2.3	10.2	0	0	0	16.9	0	0	0
Cobble (%)	22.0	28.6	0	23.8	0	34.5	0	42.5	0	28.1	0
Boulder (%)	12.0	22.7	0	29.9	0	30.4	0	16.0	0	33.8	0
Rock (%)	34.0	31.4	0	21.8	0	15.5	0	10.4	0	26.3	0
Concrete (%)	0	0	86.0	0	59.1	0	100	0	100	0	100
Wood (%)	0	0	0	0	0	0	0	0	0	0.4	0
Litter (%)	0	2.9	2.3	0	40.9	0	0	0	0	0	0
Q (L s^{-1})	77.5	0.8	76.2	139.1	496.4	201.1	645.5	79.7	789.9	381.5	61.6
% of total Q	100	1.0	99.0	21.9	78.11	23.8	76.3	9.2	90.8	86.1	13.9
Wetted width (m)	4.00	0.40	1.41	9.00	2.67	8.00	2.00	6.50	2.30	10.72	0.87
Depth (m)	0.16	0.04	0.26	0.17	0.96	0.20	0.80	0.09	0.90	0.21	0.19
Avg. velocity (m s^{-1})	0.17	0.02	0.33	0.14	0.29	0.31	0.52	0.15	0.51	0.22	0.37
A (m^2)	0.47	0.04	0.23	0.93	1.61	0.66	1.22	0.52	1.54	1.76	0.15
As (m^2)	0.12	0.03	0.03	0.18	0.22	0.23	0.07	0.10	0.02	0.27	0.03

As/A	0.25	0.77	0.13	0.19	0.14	0.35	0.05	0.18	0.01	0.15	0.19
k_1 (min^{-1})	0.18	0.20	0.20	0.12	0.36	0.33	0.24	0.09	0.09	0.12	1.71
k_2 (min^{-1})	0.71	0.26	1.53	0.62	2.63	0.94	4.50	0.49	9.22	0.80	9.20

Table 4. Mean values and standard deviation of uptake length (Sw), mass transfer coefficient (Vf) and ambient uptake rate (U) of PO_4^{3-}-P and NH^{4+}-N at the canal and stream reaches. Lowest row shows result of paired Student's t-test.

	PO_4^{3-}-P			NH_4^{+}-N		
	S_w (m)	V_f (mm min^{-1})	U (µg m^{-2} s^{-1})	S_w (m)	V_f (mm min^{-1})	U (µg m^{-2} s^{-1})
Stream	93.8 ± 68.6	12.12 ± 5.43	5.02 ± 4.33	146.5 ± 56.6	5.05 ± 2.89	2.02 ± 1.28
Canal	354.0 ± 235.5	32.98 ± 37.05	10.57 ± 10.31	284.1 ± 200.7	32.48 ± 22.82	12.82 ± 7.67
Paired Student t-test	t = -1.914 n.s.	t = -1.514 n.s.	t = -0.741 n.s.	t = -2.591 n.s.	t = -7.920 p = 0.004	t = -6.956 p = 0.006

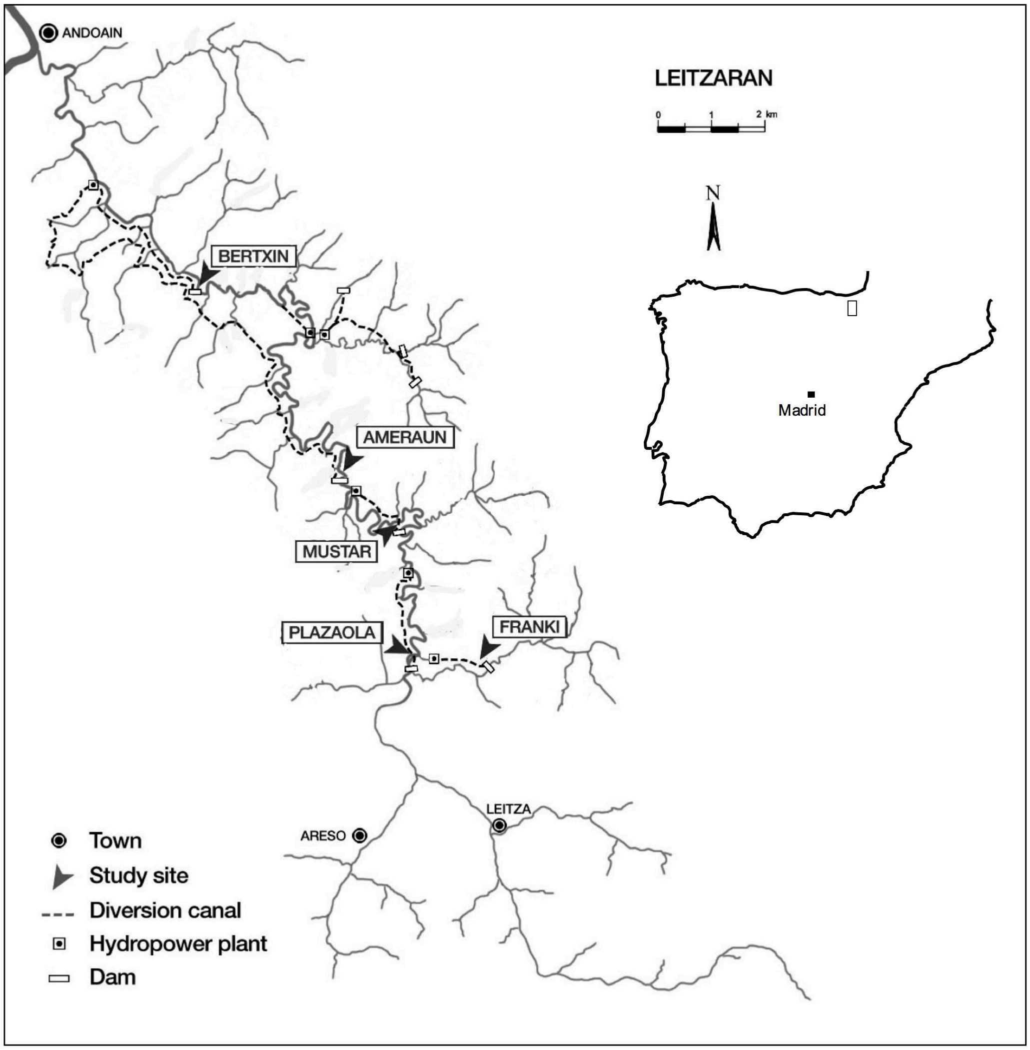

Figure 1. Leitzaran catchment, with the hydropower plants still operating and respective dam and diversion canals.

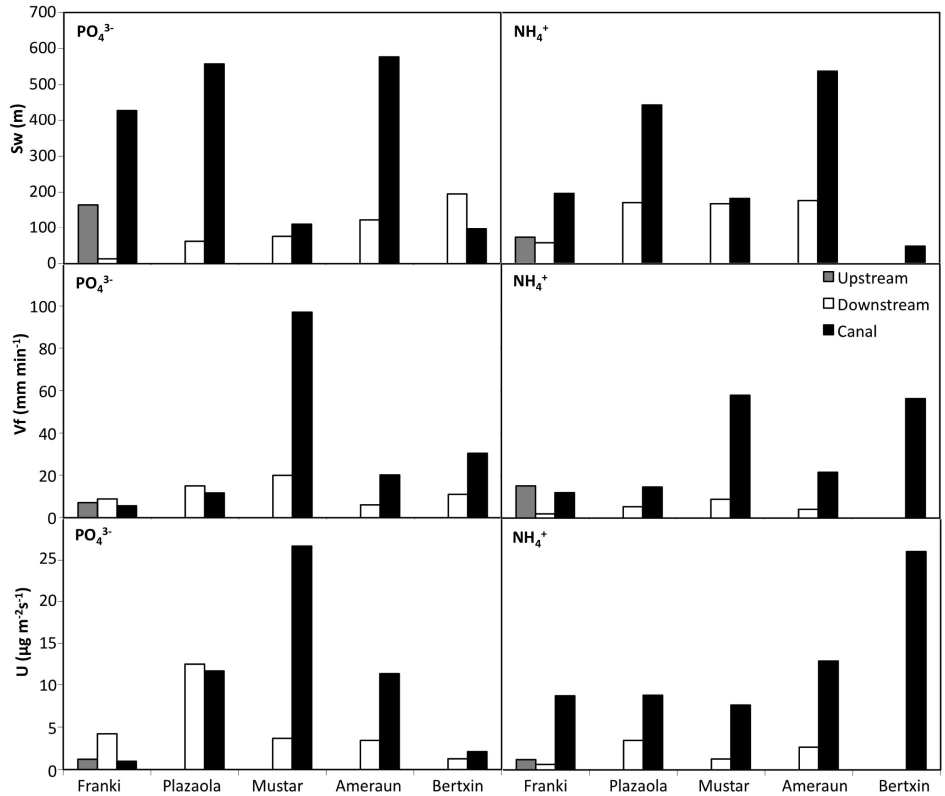

Figure 2. Parameters of nutrient retention, uptake length (S_w), mass transfer coefficient (V_f) and ambient uptake rate (U) of PO_4^{3-}-P and NH_4^+-N upstream from the dam (Franki), at stream channels below the dam and at diversion canals. Study sites are arranged in the x axis following the downstream flow. Ammonium data for Franki upstream and Bertxin stream not available.

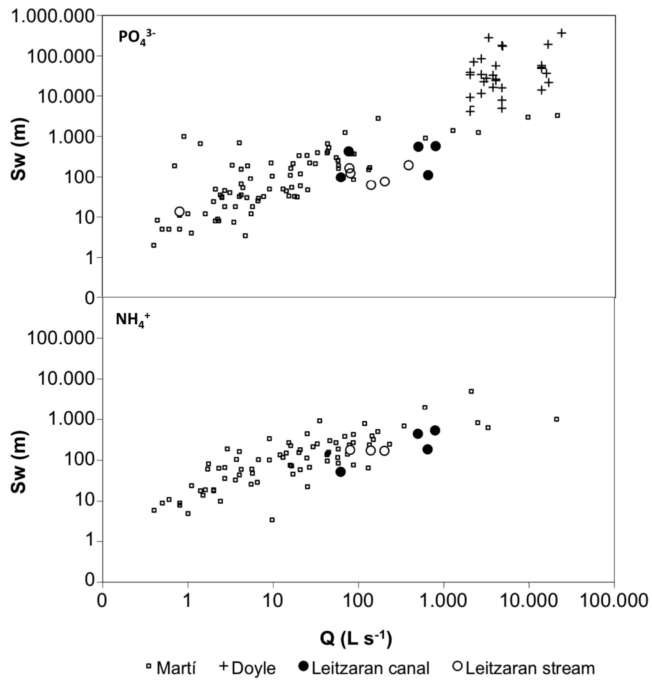

Figure 3. Comparison of uptake length for phosphate and ammonium in the present study with data from the literature, expanded from Martí et al. (2004) and values reported by Doyle et al. (2003) from the Koshkonong River.