

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

3

4 Oihana Izagirre¹, Alba Argerich², Eugènia Martí³ and Arturo Elosegí¹

5

6 ¹Department of Plant Biology and Ecology, Faculty of Science and Technology, the University of
7 the Basque Country, PO Box 644, 48080 Bilbao, Spain.

8 ²Forest Ecosystems and Society Department, Oregon State University, Corvallis, Oregon, USA

9 ³Biogeodynamics & Biodiversity Group, Centre d'Estudis Avançats de Blanes (CSIC), Accés a la
10 Cala St. Francesc 14, 17300 Blanes, Spain.

11

12 **Abstract**

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

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

29

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

32

33 **Introduction**

34 Hydropower plants cause profound effects on river ecosystems by damming, reducing
35 flow in natural stream channels, and creating new water flow paths through man-made side
36 canals. Dams constitute barriers along the river continuum, which alter the downstream flux of
37 water, sediments, nutrients and organic matter, and the movement of organisms (Ward &
38 Stanford, 1979). This in turn affects the channel morphology, community structure, and
39 functioning of stream ecosystems (Graf, 1999; Petts, 1984; Ward et al., 1999; Elosegi et al.,
40 2010). In addition, water diversion into artificial diversion canals reduces in-stream water flow,
41 and thus modifies stream hydraulics and habitat characteristics affecting both invertebrates and
42 fish communities (Armitage & Petts, 1992; Hax & Golladay, 1998; Murchie et al., 2008). There
43 is less information on the effect of water diversion on stream ecosystem functioning, but
44 impacts are likely, as both channel morphology and hydraulics exert a strong influence on
45 ecosystem processes (Uehlinger, 2000; Hall et al. 2002; Sweeney et al. 2004; Elosegi et al.
46 2011). Finally, diversion canals can also be habitats for some organisms and play a role in the
47 transport and processing of nutrients and organic matter, thus influencing ecosystem
48 functioning of stream networks. However, there is little information on how diversion canals
49 compare to stream channels regarding transport, retention and transformation of materials.

50

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

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

65

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

72

73 **Methods**

74

75 *Study site*

76 The Leitzarán is a 42 km-long stream that drains a 114.5 km² catchment (Fig. 1). Eighty
77 five percent of the catchment area is dominated by siliceous geology, mostly carboniferous slate
78 and sandstone. The stream is steep, sinuous, and runs along heavily incised meanders in a
79 region with mountains higher than 1000 m a.s.l. located very close to the sea. The climate of
80 the region is humid oceanic, with an average annual precipitation over 1500 mm and mean
81 monthly temperatures ranging from 8.4 °C in January to 20.7 °C in August. Sixty six percent of
82 the catchment is covered by conifer plantations (*Pinus radiata* up to 400-500 m a.s.l., *Larix*
83 *kaempferi* at higher altitudes, and some sparse stands of *Pseudotsuga menziesii*), 18% is
84 covered by native deciduous forests of oak (*Quercus robur*), beech (*Fagus sylvatica*), birch
85 (*Betula* spp.), chestnut (*Corylus avellana*) and alder (*Alnus glutinosa*). The rest of the
86 catchment (16%) consists of pasture land, meadows and few patches of arable land.

87

88 Near the headwaters of the Leitzarán there are two towns: Leitza and Areso (Fig. 1).
89 Leitza has 3200 inhabitants, a large paper factory, some smaller factories, and many farms with

90 sheep and cattle. The wastewater from Leitza receives secondary treatment before it is
91 delivered into the stream. Areso has 290 inhabitants, mostly devoted to farming and forestry
92 activities. Four km downstream from Leitza and Areso the Leitzaran Stream enters the province
93 of Guipuscoa. At this location, the average concentrations of nitrate (NO_3^- -N), ammonium
94 (NH_4^+ -N), and phosphate (PO_4^{3-} -P) are relatively high (1.37, 0.10 and 0.05 mg L⁻¹,
95 respectively); however, invertebrate-based biotic indices indicate excellent water quality
96 (Government of Navarre, 2005). Downstream from this point, the Leitzaran Stream runs for 30
97 km along a scarcely populated valley that is protected under the legal figure of Protected
98 Biotope before it joins the Oria river. Nutrient concentrations tend to decrease along this reach.
99

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

111
112 At each site we selected a reach in the stream (below the dam) and another reach in the
113 diversion canal that runs in parallel to the stream reach (Table 2). At Franki, an additional reach
114 was selected upstream from the dam and used as a reference for unregulated flow conditions.
115 The diversion canal from Ameraun returns its water to the stream at a site located below
116 Bertxin (i.e., the next sampling site). Therefore, stream discharge at Bertxin is affected by
117 water abstraction from both the Bertxin and Ameraun canals (Fig. 1).

118

119 *Field and laboratory procedures*

120 The study was done between the 15th and 19th of May 2006. On each day, we sampled
121 sequentially both the canal and stream reaches of a study site, so that the delay between both
122 additions was typically less than 2 hours. At each reach we measured stream nutrient (i.e.,
123 $\text{NH}_4^+\text{-N}$ and $\text{PO}_4^{3-}\text{-P}$) uptake using the pulse nutrient addition technique (Wilcock et al., 2002).
124 We used this method because high discharge, especially in the canals, precluded the application
125 of the more widely used constant-rate addition technique (Webster & Valett, 2006).
126 Nevertheless, Powers et al. (2009) have recently shown that the two methods provide
127 comparable results of nutrient uptake metrics. On each addition, 20-50 L of a solution
128 containing NH_4Cl and $\text{Na}(\text{H}_2\text{PO}_4)\cdot\text{H}_2\text{O}$ as nutrient sources, and NaCl as a hydrologic tracer
129 (Bencala et al. 1987) were added to the stream or canal in a single pulse at the head of the
130 reach, in a place where fast mixing with stream water was ensured. In the case of the canals, we
131 took advantage of the strong turbulence in the transition between the weir and the canal. The
132 amount of reagents in the solution was set to target a 3-fold increase in background nutrient
133 concentration at the peak of the pulse. Conductivity was automatically recorded at the
134 downstream end of the reach every 5 s from the beginning of the addition pulse until
135 conductivity returned to pre-addition values using a conductivity meter (WTW 330) connected
136 to a data logger (Campbell CR 510). Water samples were collected in 250 mL acid-washed
137 plastic bottles every 10-60 s at the bottom of the reach over the conductivity-pulse passage.
138 Samples were stored on ice, transported to the laboratory, filtered through pre-ashed fiberglass
139 filters (Whatman GF/F), and frozen until analysis. Concentrations of $\text{PO}_4^{3-}\text{-P}$ and $\text{NH}_4^+\text{-N}$ were
140 analyzed manually and using TRAACS 800 autoanalyzer, respectively, following standard
141 colorimetric methods (APHA, 1998).

142

143 Additionally, reach morphology was described by means of 10 regularly spaced transects,
144 across which measurements were recorded at 0.5 - 1 m intervals. At each transect, we
145 measured wetted width (w , m), water depth (h , m), percentage coverage of substrate types
146 (silt, sand, gravel, pebble, cobble, boulder or bedrock), presence of wood and leaf litter, and
147 canopy cover (measured as the vertical projection of leaf shade). We also measured water

148 temperature, pH and oxygen concentration (WTW field probes). To estimate the accumulated
149 radiation reaching the reach during the addition experiments, we corrected radiation data
150 provided by the Meteorological Survey of the Basque Government for the shade produced by
151 the canopy cover on each reach. The light attenuation was estimated using the ratios calculated
152 by Izagirre and Elosegi (2004) at a full-canopy site with summer foliage.

153

154 At each reach we also collected periphyton samples to estimate biomass and pigment
155 content. In the stream reaches, ten cobbles were collected at random, an area of 18.6 cm² was
156 scraped from each cobble using scalpels and toothbrushes, and periphyton samples were
157 collected with Pasteur pipettes. In the canal reaches, 10 samples were collected from the
158 bottom and side-walls of the canal with a modified syringe (Biggs & Kilroy, 2000). All periphyton
159 samples were stored in 50 mL plastic containers, brought to the laboratory on ice and kept
160 frozen until analysis. After thawing, samples were homogenized with a domestic blender. One
161 sub-sample was used to determine biomass as ash-free dry mass (AFDM) after drying at 105 °C
162 for 24 h and ashing at 500 °C for 4 h. Another sub-sample was used to measure chlorophyll *a*
163 spectrophotometrically after extraction in hot ethanol (Sartory & Grobbelaar, 1984).

164

165 *Calculation of hydraulic parameters*

166 Several hydraulic parameters were estimated from the time-conductivity curves obtained
167 during the nutrient addition pulse at the end of the reach. Average water velocity (v , m s⁻¹) was
168 calculated dividing reach length by the time elapsed between the addition and the conductivity
169 peak (i.e., mean travel time). Discharge (Q , L s⁻¹) was estimated based on a mass balance
170 approach using conductivity data as a surrogate of the chloride concentration. Briefly, discharge
171 was the result of multiplying the volume of the added solution (L) by its conductivity ($\mu\text{S cm}^{-1}$)
172 and dividing it by the integrated area of the conductivity curve above ambient conductivity
173 levels ($\mu\text{S s cm}^{-1}$). Parameters to characterize the water transient storage along each study
174 reach were estimated from the conductivity data by a one-dimensional solute transport model
175 with inflow and storage (OTIS, Runkel, 1998). Estimated parameters from the model were a)
176 the cross-sectional area of the wetted channel (A , m²), b) the storage zone cross-sectional area

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

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

182

183 *Calculation of nutrient uptake metrics*

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

193

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

200

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

202

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

$$212 \quad M_{i,t} = Q \int_0^{\infty} N_t dt$$

213

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

$$216 \quad M_t = M_i e^{-k_t t_n}$$

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

$$219 \quad S_w = \frac{v}{k_t}$$

$$220 \quad V_f = \frac{Q}{w S_w}$$

$$221 \quad U_{amb} = \frac{N_b Q}{S_w w} = V_f N_b$$

222

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

225

226 *Data analysis*

227 We examined the normality of the variables by means of the Shapiro-Wilk test, and the
 228 homogeneity of variances by the Levene's statistic. In order to meet assumptions of normality,

229 prior to the statistical analysis of data all variables were log-transformed. Differences in
230 chlorophyll and benthic AFDM were analyzed by means of two-way ANOVA tests (stream site
231 and reach type as factors). Student's t-tests for paired samples were used to compare data
232 from all measured variables between stream and canal reaches.

233

234 We examined the relationships between nutrient uptake metrics and hydraulic variables,
235 periphytic biomass, and nutrient concentrations using univariate lineal regression. Differences in
236 regression models between stream and canals were analyzed using ANCOVA. In particular, we
237 examined the relationships between a) S_w and Q , h and v , b) V_f and water transient storage
238 parameters and nutrient concentrations, and c) U and periphytic biomass. The significance level
239 for the tests was $p=0.05$. All statistical analyses were done using SPSS for Windows (version
240 12.0, SPSS Inc., Chicago).

241

242

243 **Results**

244 *Chemical and biological characterization*

245 Light levels during the addition were significantly higher at stream channels than at
246 diversion canals (Student's paired t-test, $t = 3.415$, $p = 0.027$). Water temperature ranged from
247 11.1 to 18.2 °C among sites, conductivity from 65.7 to 259.1 $\mu\text{S cm}^{-1}$ and pH from 7.07 to 8.10
248 (Table 2). Dissolved oxygen concentration during the pulse additions ranged from 9.7 to 10.6
249 $\text{mg O}_2 \text{ L}^{-1}$, which corresponds to 100 - 106% saturation. Concentration of nutrients was low to
250 moderate, ranging from 0.004 to 0.060 mg L^{-1} for $\text{PO}_4^{3-}\text{-P}$, and from 0.008 to 0.044 mg L^{-1} for
251 $\text{NH}_4^+\text{-N}$ (Table 2). Neither nutrient followed any clear longitudinal pattern along the Leitzaran
252 Stream. None of the variables described above showed any significant difference between the
253 two reach types (Student's paired t-test, $p > 0.05$). Periphytic Chl a ranged from 2.4 to 120.5
254 mg m^{-2} , and biomass from 3.9 to 21.8 g AFDM m^{-2} . These two variables showed no clear
255 patterns along the stream, and did not significantly differ between the two reach types nor
256 among sites.

257

258 *Morphology and hydraulics*

259 The canals were more homogeneous than the stream reaches in terms of substrata.

260 Canals were dominated by concrete, although the canal at Plazaola had a considerable
261 accumulation of leaf litter. On the other hand, stream channels were dominated by cobble-
262 boulder substrata (Table 3).

263

264 Total discharge (stream + canal) increased from 77.5 L s⁻¹ at Franki to 870 L s⁻¹ at
265 Ameraun (Table 3). The decrease in Q observed at the most downstream site (Bertxin) is
266 explained because the canal from Ameraun reverts its water downstream of Bertxin. At each
267 site, the dams diverted more than 75% of the total stream discharge into the diversion canals,
268 except at Bertxin (14%), because the hydropower plant was operating well below its full
269 capacity. Streams were wider than canal reaches at all sites except Franki, where 99% of total
270 discharge was diverted, leaving only a rivulet in the stream channel (Table 3). Mean water
271 depth was below 20 cm at stream reaches and from 20 cm to 1 m at the canals, differences
272 between reach types being statistically significant (paired Student's t-test, $t = -3.534$, $p =$
273 0.024). Water velocity ranged from 0.02 to 0.31 m s⁻¹ in stream reaches and from 0.29 to 0.52
274 m s⁻¹ in canal reaches, being significantly slower in the stream than in the canal reaches (paired
275 Student's t-test, $t = -5.538$, $p = 0.005$).

276

277 Values of A were higher in the canals than in the stream reaches at all sites except
278 Bertxin (Table 3). A was related to Q, but the relationship did not differ significantly between
279 stream and canal reaches (ANCOVA). Taking all data together the relationship followed a
280 potential model ($A = 0.0365 Q^{0.565}$, $r^2 = 0.856$, $p < 0.001$). Reach types did not significantly
281 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
282 t-test, $t = 2.342$, $p = 0.079$). This ratio was negatively related to Q but the relationship did not
283 differ significantly between stream and canal reaches (ANCOVA). Taking all data together the
284 relationship followed a logarithmic model ($A_s/A = 0.684 - 0.097 \ln Q$, $r^2 = 0.816$, $p < 0.001$). k_1
285 showed no significant differences between reach types, but k_2 was significantly higher in the
286 canals than in the stream channels (paired Student's t-test, $t = -7.222$, $p = 0.002$).

287

288 *Nutrient uptake*

289 Values of S_w for $\text{PO}_4^{3-}\text{-P}$ ranged from 14 to 195 m at stream reaches, including the
290 upstream site at Franki, and from 97 to 577 m at canal reaches (Fig. 2). Contrary to our
291 prediction, it was not significantly different between reach types (Table 4). S_w for PO_4^{3-} was
292 positively related to water depth ($S_w\text{P} = 63.9 + 428 h$, $r^2 = 0.524$, $p = 0.012$). Values of V_f for
293 $\text{PO}_4^{3-}\text{-P}$ ranged from 6 to 20 mm min^{-1} at stream reaches, and from 6 to 97 mm min^{-1} at canal
294 reaches (Fig. 2), and were not significantly different between reach types (Table 4). Values of U
295 for $\text{PO}_4^{3-}\text{-P}$ ranged from 1.2 to 12.5 $\mu\text{g m}^{-2} \text{s}^{-1}$ at stream reaches and from 1.0 to 26.7 $\mu\text{g m}^{-2} \text{s}^{-1}$
296 at canal reaches (Fig. 2); as with the other uptake metrics, differences were not statistically
297 significant (Table 4). V_f and U for PO_4^{3-} were not significantly related to any of the independent
298 variables considered.

299

300 S_w for $\text{NH}_4^+\text{-N}$ ranged from 62 to 180 m in streams and from 52 to 532 in canal reaches
301 (Fig. 2), and, as in the case for phosphate, showed no significant differences between reach
302 types (Table 4). S_w for NH_4^+ was positively related to discharge ($S_w\text{N} = 89.6 + 0.463Q$, $r^2 =$
303 0.654 , $p = 0.005$) and water depth ($S_w\text{N} = 68.1 + 372 h$, $r^2 = 0.69$, $p = 0.003$). V_f for $\text{NH}_4^+\text{-N}$
304 ranged from 2 to 15 mm min^{-1} in stream reaches and from 12 to 58 mm min^{-1} in canals, being
305 significantly higher in canal than in stream reaches (Table 4). Values of U for $\text{NH}_4^+\text{-N}$ ranged
306 from 0.7 to 8 $\mu\text{g m}^{-2} \text{s}^{-1}$ in streams, and from 8 to 26 $\mu\text{g m}^{-2} \text{s}^{-1}$ in canals, differences being
307 statistically significant (Table 4). V_f and U for NH_4^+ were not significantly related to any of the
308 independent variables considered.

309

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

313

314

315

316 **Discussion**

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

329

330 Canals were characterized by smoother substrata than stream channels, and by reduced
331 or absent hyporheos and dead zone storage. These features could result in smaller size of
332 transient storage and lower water retention within the canal reaches, as both parameters are
333 influenced by geomorphic complexity of the channel (Gooseff et al., 2007; Zarnetske et al.,
334 2007). Nevertheless, and contrary to our predictions, the size of water transient storage and its
335 exchange with free-flowing water in the Leitzaran did not consistently differ between reach
336 types. The lack of consistent differences in hydraulic parameters between canal and stream
337 reaches probably was not caused by uncertainty of the estimates, as estimated dispersion
338 coefficients were below 0.20 m s^{-2} . We observed a negative relationship between the size of the
339 transient storage (A_s/A) and discharge when pooling data from all sites together, in agreement
340 with previous studies (Argerich et al., 2008). This relationship indicates that hydrology may
341 override the effect of channel morphology on the variation of transient storage. In fact, at all
342 the sites where a large fraction of the water was diverted (4 out of 5 sites) the transient
343 storage size was larger at stream channels than at diversion canals. At Bertxin, where the canal

344 diverted only 14% of the stream flow, the contrary was observed, but even there the transient
345 storage size was not very large at the canal, probably limited by its low physical complexity.
346 Other factors that may explain a lack of consistent differences could be associated with
347 accumulation of benthic organic matter in the canals. Benthic organic matter is known to
348 increase A_b/A in streams (Hart et al. 1999; Haggard and Storm 2003; Jin and Ward 2005;
349 Argerich et al., 2008), and may also play a role in some of the diversion canals.

350

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

365

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

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

382

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

390

391 **Acknowledgements**

392 This research has been funded by the Spanish Department of Science and Technology,
393 the University of the Basque Country, and the European Regional Development Fund, through
394 projects 9/UPV00118.310-14476/2002 and BOS2003-04466. The authors want to thank Félix
395 Izco and Patxi Tamés (Province Government of Guipuscoa), for continuous support. Oihana
396 Izagirre did this work thanks to a pre-doctoral grant by the Basque Government.

397

398 **References**

399 APHA, 1998. *Standard methods for the examination of water and wastewater*. 20th edition.

400 American Public Health Association, Washington, D.C.

401 Argerich, A., E. Martí, F. Sabater, M. Ribot, D. von Schiller & J. L. Riera, 2008. Combined effects
402 of leaf litter inputs and a flood on nutrient retention in a Mediterranean mountain
403 stream during fall. *Limnology and Oceanography* 53: 631-641.

404 Armitage, P.D. & G. E. Petts, 1992. Biotic score and prediction to assess the effects of water
405 abstractions on rivermacroinvertebrates for conservation purposes. *Aquatic*
406 *Conservation: Marine and Freshwater Ecosystems* 2: 1-17.

407 Bencala, K.E., D. M. McKnight & G. W. Zellweger, 1987. Evaluation of natural tracers in an
408 acidic and metal-rich stream. *Water Resources Research* 23: 827-836.

409 Biggs, B. J. F. & C. Kilroy, 2000. Stream periphyton monitoring manual. New Zealand Ministry
410 for the Environment/ NIWA, Christchurch, New Zealand.

411 Boatman, C. D. & J. W. Murray, 1982. Modeling exchangeable NH_4^+ adsorption in marine-
412 sediments - process and controls of adsorption. *Limnology and Oceanography* 27: 99-
413 110.

414 Boulton, A. J., S. Findlay, P. Marmonier, E. H. Stanley & H. M. Vallet, 1998. The functional
415 significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and*
416 *Systematics* 29: 59-81.

417 Butturini, A. & F. Sabater, 1998. Ammonium and phosphate retention in a Mediterranean
418 stream: hydrological versus temperature control. *Canadian Journal of Fisheries and*
419 *Aquatic Sciences* 55: 1938-1945.

420 Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. *Nature*
421 472: 86-89.

422 Elosegi, A., J. R. Díez & M. Mutz, 2010. Effects of hydromorphological integrity on biodiversity
423 and functioning of river ecosystems. *Hydrobiologia* 657: 199-215.

424 Elosegi, A., L. Flores & J. R. Díez, 2011. The importance of local processes on habitat
425 characteristics: a Basque stream case study. *Limnetica* 30: 183-196.

- 426 Gooseff, M. N., R. O. Hall & J. L. Tank, 2007. Relating transient storage to channel complexity
427 in streams of varying land use in Jackson Hole, Wyoming. *Water Resources Research*
428 43. DOI: 10.1029/2005WR004626
- 429 Government of Navarre, 2005. Estudio de determinación de índices bióticos en 87 puntos de los
430 ríos de Navarra. Government of Navarre, Pamplona, Spain.
- 431 Graf, W. L., 1999. Dam nation: A geographic census of American dams and their large-scale
432 hydrologic impacts. *Water Resources Research* 35: 1305-1311.
- 433 Gücker, B & I. G. Boëchat, 2004. Stream morphology controls ammonium retention in tropical
434 headwaters. *Ecology* 85: 2818-2827.
- 435 Haggard, B. E. & D. E. Storm, 2003. Effect of leaf litter on phosphorus retention and
436 hydrological properties at a first order stream in northeast Oklahoma, USA. *Journal of*
437 *Freshwater Ecology* 18: 557-565
- 438 Hall, R. O., E. S. Bernhardt & G. E. Likens, 2002. Relating nutrient uptake with transient storage
439 in forested mountain streams. *Limnology and Oceanography* 47: 255-265.
- 440 Hart, D. R., P. J. Mulholland, E. R. Marzolf, D. L. DeAngelis & S. P. Hendricks, 1999.
441 Relationships between hydraulic parameters in a small stream under varying flow and
442 seasonal condition. *Hydrological Processes* 13: 1497-1510
- 443 Hax, C. L. & S. W. Golladay, 1998. The effects of a man-made flow disturbance on
444 macroinvertebrate communities of a north Texas prairie stream. *American Midland*
445 *Naturalist* 139: 210-223.
- 446 Izagirre, O. & A. Elosegi, 2004. Environmental control of seasonal and inter-annual variations of
447 periphytic biomass in a north Iberian stream. *Annales de Limnologie* 41: 35-46.
- 448 Jain, S. C., 2001. *Open-channel flow*. Wiley.

- 449 Jin, H. S. & G. M. Ward, 2005. Hydraulic characteristics of a small Coastal Plain stream of the
450 southeastern United States: effects of hydrology and season. *Hydrological Processes*
451 19: 4147-4160.
- 452 Kent, R., K. Belitz & C.A. Burton, 2005. Algal productivity and nitrate assimilation in an effluent
453 dominated concrete lined stream. *Journal American Water Resources Association* 41:
454 1109-1128.
- 455 Knapp, C.W., W.K. Dodds, K.C. Wilson, J.M. O'Brien & D.W. Graham, 2009. Biogeography of
456 denitrification genes in a highly homogenous urban stream. *Environmental Science and*
457 *Technology* 43: 4273-4279.
- 458 Martí, E. & F. Sabater, 2009. Retención de nutrientes en ecosistemas fluviales. In *Conceptos y*
459 *técnicas en ecología fluvial*, Elosegi A and Sabater S (eds), Fundación BBVA, Bilbao,
460 España.
- 461 Martí, E., J. Aumatell, L. Godé, M. Poch & F. Sabater, 2004. Nutrient retention efficiency in
462 streams receiving inputs from wastewater treatment plants. *Journal of Environmental*
463 *Quality* 33: 285-293.
- 464 Murchie, K. J., K. P. E. Hair, C. E. Pullen, T. D. Redpath, H. R. Stephens & S. J. Cooke, 2008.
465 Fish response to modified flow regimes in regulated rivers: research methods, effects
466 and opportunities. *River Research and Applications* 24: 197-217
- 467 Mulholland, P. J., J. D. Newbold, J. W. Elwood & J. R. Webster, 1985. Phosphorus spiralling in a
468 woodland stream: Seasonal variations. *Ecology* 66: 1012-1023.
- 469 Mulholland, P. J., J. L. Tank, D M. Sanzone, W. M. Wollheim, B. J. Peterson, J. R. Webster & J.
470 L. Meyer, 2000. Nitrogen cycling in a forest stream determined by a ¹⁵N tracer addition.
471 *Ecological Monographs* 70: 471-493.

472 Mulholland, P. J., S. A. Thomas, H. M. Valett, J. R. Webster & J. Beaulieu, 2006. Effects of light
473 on nitrate uptake in small forested streams: diurnal and day-to-day variations. *Journal*
474 *of the North American Benthological Society* 25: 583-595.

475 Newbold, J. D., J. W. Elwood, R. V. O'Neil & W. Van Winkle, 1981. Measuring nutrient spiraling
476 in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 860-863.

477 Peterson, B. J., W. Wolheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, N. B.
478 Grimm, E. Martí, W. B. Bowden, H.M. Vallet, A. E. Hershey, W.B. McDowell, W.K.
479 Dodds, S. K. Hamilton, S.V. Gregory & D. J. D'Angelo, 2001. Control of nitrogen export
480 from watersheds by headwater streams. *Science* 292: 86-90.

481 Petts, G. E., 1984. *Impounded rivers – perspectives for ecological management*. John Wiley
482 and Sons: Chichester, UK.

483 Powers, S. M., E. H. Stanley & N. R. Lottig, 2009. Quantifying phosphorus uptake using pulse
484 and steady-state approaches in streams. *Limnology and Oceanography Methods* 7: 498-
485 508.

486 Roberts, B. J., P. J. Mulholland & A. N. Houser, 2007. Effects of upland disturbance and
487 instream restoration on hydrodynamics and ammonium uptake in headwater streams.
488 *Journal of the North American Benthological Society* 26: 38-53.

489 Runkel, R. L., 1998. One-dimensional transport with inflow and storage (OTIS): A solute
490 transport model for streams and rivers. U.S. Geological Survey Water-Resources
491 Investigation Report 98-4018, Denver, CO.

492 Sabater, F., A. Buturini, E. Martí, I. Muñoz, A. Romani, J. Wray & S. Sabater, 2000. Effects of
493 riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of*
494 *the North American Benthological Society* 19: 609-620.

495 Sartory, D. P. & J. E. Grobbelaar, 1984. Extraction of chlorophyll *a* from freshwater
496 phytoplankton for spectrophotometric analysis. *Hydrobiologia* 114: 177-187.

- 497 Steinman, A. D. & H.L. Boston, 1993. The ecological role of aquatic bryophytes in a woodland
498 stream. *Journal of the North American Benthological Society* 12: 17-26.
- 499 Stream Solute Workshop, 1990. Concepts and methods for assessing solute dynamics in stream
500 ecosystems. *Journal of the North American Benthological Society* 9: 95-119.
- 501 Sweeney, B. W., T. L. Bott, J. K. Jackson, L. A. Kaplan, J. D. Newbold, L. J. Standley, W. C.
502 Hession & R. J. Horwitz, 2004. Riparian deforestation, stream narrowing, and loss of
503 ecosystem services. *Proceedings of the National Academy of Sciences* 101: 14132-
504 14137.
- 505 Triska, F. J., A. P. Jackman, J. H. Duff & R. J. Avanzino. 1994. Ammonium sorption to channel
506 and riparian sediments - a transient storage pool for dissolved inorganic nitrogen.
507 *Biogeochemistry* 26: 67-83.
- 508 Uehlinger, U., 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river
509 system. *Freshwater Biology* 45: 319-332.
- 510 Valett, H. M., J. A. Morice, C. N. Dahm & M. E. Campana, 1996. Parent lithology, surface-
511 groundwater exchange, and nitrate retention in headwater streams. *Limnology and*
512 *Oceanography* 41: 333-345.
- 513 von Schiller, D., E. Martí, J. L. Riera, M. Ribot, J. C. Marks & F. Sabater. 2008. Influence of land
514 use on stream ecosystem function in a Mediterranean catchment. *Freshwater Biology*
515 53: 2600-2612.
- 516 Ward, J. V. & J. A. Stanford (eds), 1979. *The ecology of regulated streams*. Plenum Press: New
517 York, NY.
- 518 Webster, J. R. & M. H. Valett, 2006. Solute dynamics. In *Methods in stream ecology*, F. R.
519 Hauer and G. A. Lamberti (eds), Academic Press, San Diego, California.
- 520 Webster, J. R., P. J. Mulholland, J. L. Tank, H. M. Valett, W. K. Dodds, B. J. Peterson, W. B.
521 Bowden, C. N. Dahm, S. Findlay, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L.

522 Johnson, E. Martí, W. H. McDowell, J. L. Meyer, D. D. Morrall, S. A. Thomas & W. M.
523 Wollheim, 2003. Factors affecting ammonium uptake in streams – an interbiome
524 perspective. *Freshwater Biology* 48: 1329-1352.

525 Wilcock, R. J., M. R. Scarsbrook, K. J. Costley & J. W. Nagels, 2002. Controlled release
526 experiments to determine the effects of shade and plants on nutrient retention in a
527 lowland stream. *Hydrobiologia* 485: 153-169.

528 Wood, P. J. & P. D. Armitage, 1997. Biological effects of fine sediment in the lotic environment.
529 *Environmental Management* 21: 203-217.

530 Zarnetske, J. P., M. N. Gooseff, T. R. Brosten, J. H. Bradford, J. P. McNamara & W. B. Bowden,
531 2007. Transient storage as a function of geomorphology, discharge, and permafrost
532 active layer conditions in Arctic tundra streams. *Water Resources Research*, 43. DOI:
533 10.1029/2005WR004816.

534

535

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. (°C)	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 <i>a</i> (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 (S_w), mass transfer coefficient (V_f) 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 ($\mu\text{g m}^{-2} \text{s}^{-1}$)	S_w (m)	V_f (mm min ⁻¹)	U ($\mu\text{g m}^{-2} \text{s}^{-1}$)
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	t = -1.514	t = -0.741	t = -2.591	t = -7.920	t = -6.956
	n.s.	n.s.	n.s.	n.s.	p = 0.004	p = 0.006

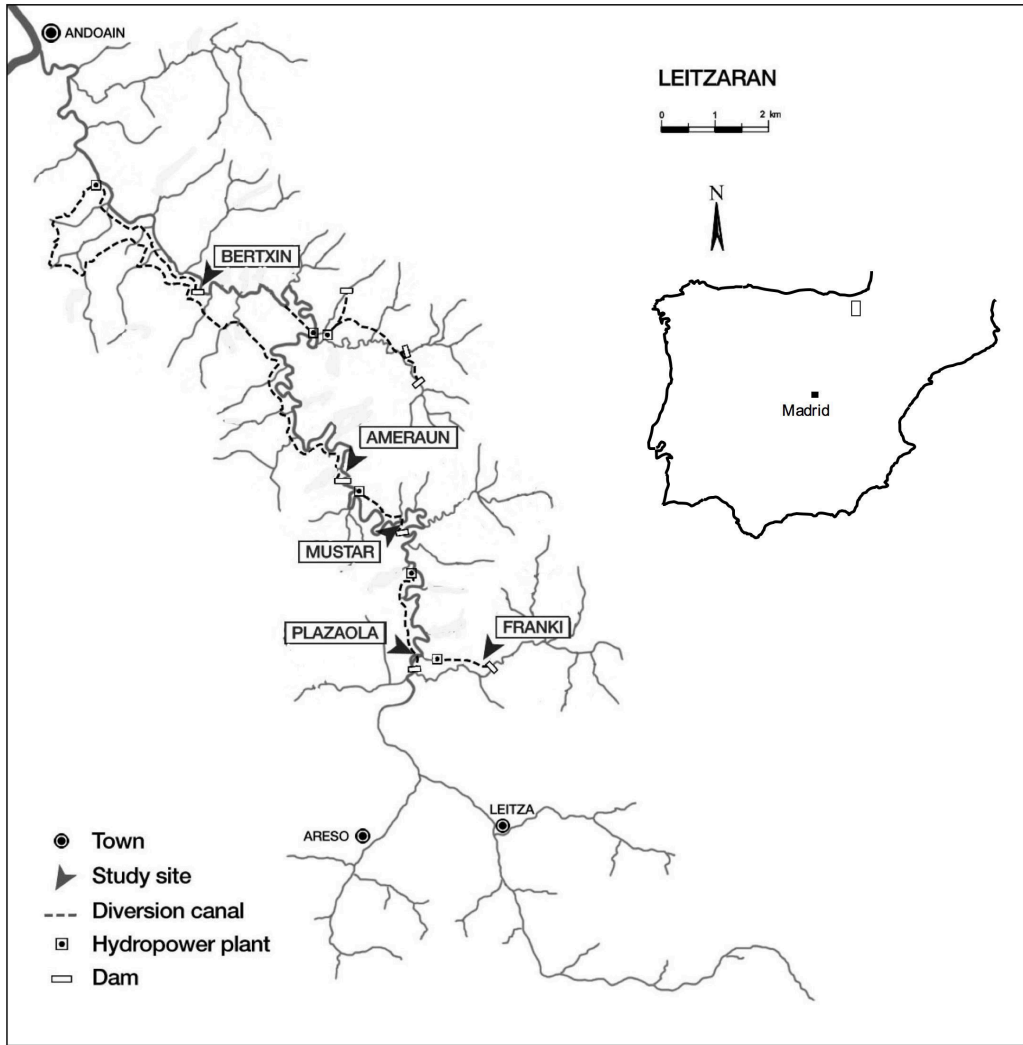


Figure 1. Leitzaran catchment, with the hydropower plants still operating and respective dam and diversion canals.

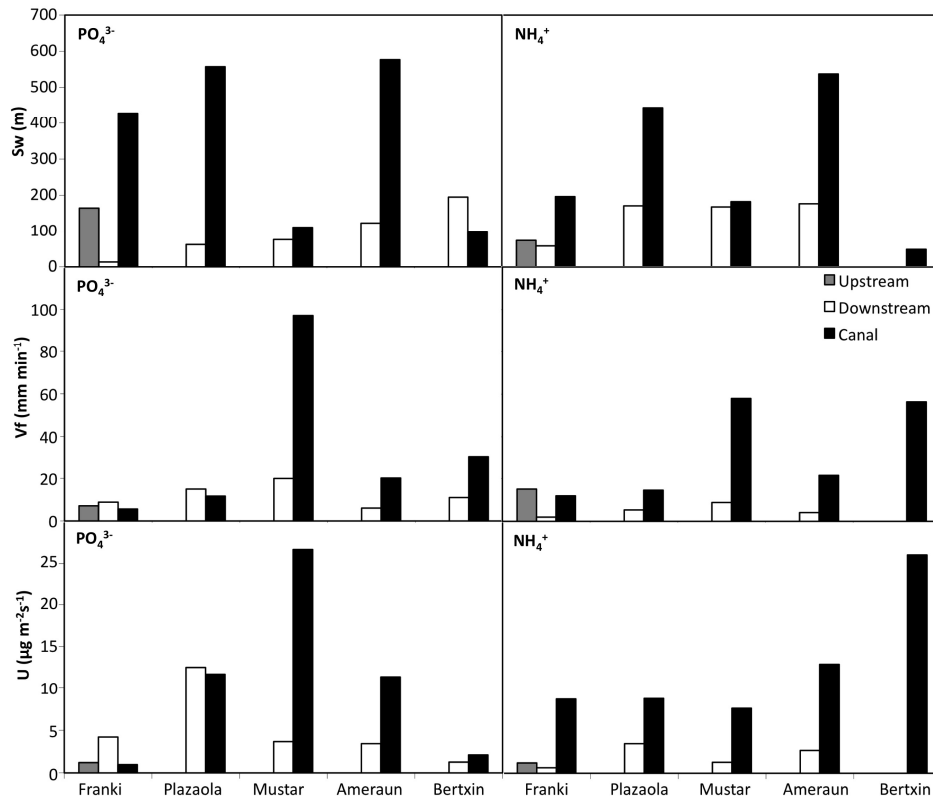


Figure 2. Parameters of nutrient retention, uptake length (S_w), mass transfer coefficient (V_f) and ambient uptake rate (U) of PO_4^{3-} -P and NH_4^+ -N upstream from the dam (Franki), at stream channels below the dam and at diversion canals. Study sites are arranged in the x axis following the downstream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

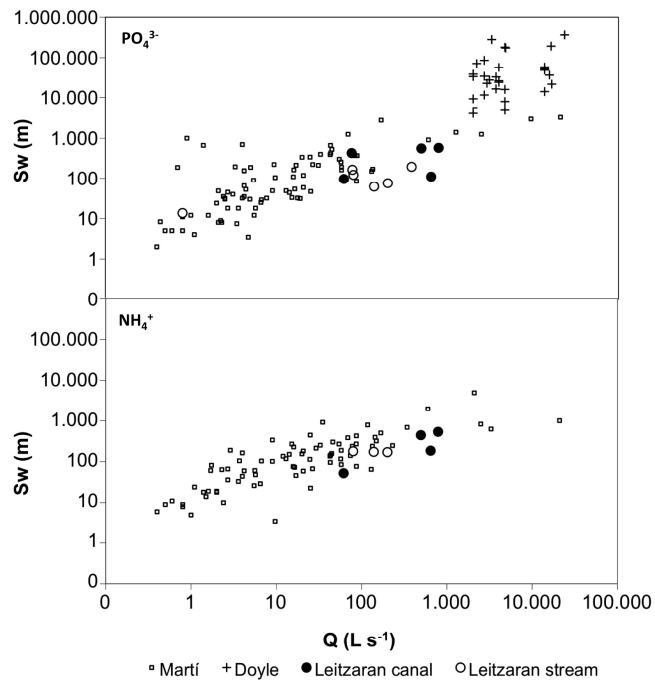


Figure 3. Comparison of uptake length for phosphate and ammonium in the present study with data from the literature, expanded from Martí et al. (2004) and values reported by Doyle et al. (2003) from the Koshkonong River.