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Regulation causes nitrogen cycling discontinuities in Mediterranean rivers

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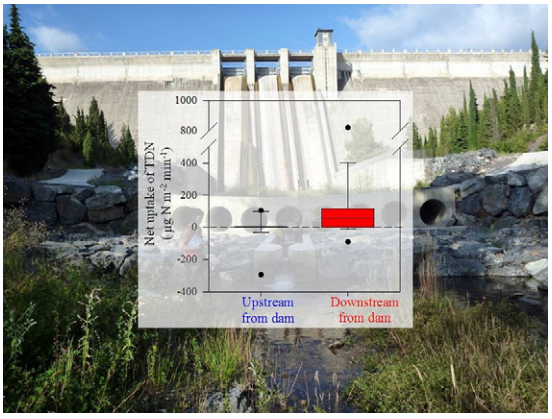
HIGHLIGHTS

- Whole-reach net uptake of dissolved nitrogen (N) increases downstream from dams.
- Hydromorphological stability and high organic matter and metabolism foster N uptake.
- River reaches below dams may constitute relevant N cycling discontinuities.

GRAPHICAL ABSTRACT



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ABSTRACT

River regulation has fundamentally altered large sections of the world's river networks. The effects of dams on the structural properties of downstream reaches are well documented, but less is known about their effect on river ecosystem processes. We investigated the effect of dams on river nutrient cycling by comparing net uptake of total dissolved nitrogen (TDN), phosphorus (TDP) and organic carbon (DOC) in river reaches located upstream and downstream from three reservoir systems in the Ebro River basin (NE Iberian Peninsula). Increased hydromorphological stability, organic matter standing stocks and ecosystem metabolism below dams enhanced the whole-reach net uptake of TDN, but not that of TDP or DOC. Upstream from dams, river reaches tended to be at biogeochemical equilibrium (uptake ≈ release) for all nutrients, whereas river reaches below dams acted as net sinks of TDN. Overall, our results suggest that flow regulation by dams may cause relevant N cycling discontinuities in rivers. Higher net N uptake capacity below dams could lead to reduced N export to downstream ecosystems. Incorporating these discontinuities could significantly improve predictive models of N cycling and transport in complex river networks.

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1. Introduction

Human needs, including drinking water supply, irrigation, flood control and hydropower, have fostered the construction of dams along river networks worldwide (Lehner et al., 2011). Today, more than 25% of the global river flow is dammed or diverted (Vörösmarty et al., 2010). Around 50,000 large dams (defined as more than 15 m in height) and over 800,000 smaller ones are in operation, and more are still being constructed (Nilsson et al., 2005; Zarfl et al., 2015). Dams have become common features in many landscapes, and have fundamentally altered large sections of the world 's river networks (Graf, 1999). The Mediterranean region is especially abundant in dams because of the high water demand and dry climatic conditions (Nilsson et al., 2005). In particular, the Iberian Peninsula hosts ~20% of the European reservoirs and has the largest number of dams per inhabitant and per land area in the world (Léonard and Crouzet, 1999).

The serial discontinuity concept (SDC) (Ward and Stanford, 1983) recognizes that dams and associated reservoirs create breaks or discontinuities in the river continuum. Dams affect structural properties of downstream reaches, reducing flood frequency (Haxton and Findlay, 2008; Poff et al., 1997), simplifying channel geomorphology (Graf, 2006; Petts and Gurnell, 2005), reducing sediment load (Tena et al., 2011; Xu et al., 2006), and altering water chemistry (Friedl and Wüest, 2002; Humborg et al., 1997) and temperature (Olden and Naiman, 2010; Preece and Jones, 2002). These changes alter community composition (Haxton and Findlay, 2008), and increase biofilm biomass below dams (Ponsatí et al., 2014). Additional impacts include changes in growth, foraging, reproduction, and migration of aquatic species (Johnson et al., 2008; Murchie et al., 2008). The impact seems to be directly related to the degree of flow alteration, which in its turn is related, among other factors, to the reservoir age and dam size as well as to the regional climate (Poff and Zimmerman, 2010).

Less is known about the effect of dams on river ecosystem processes, despite their inherent importance to ecosystem services that rivers provide (Wilson and Carpenter, 1999). Dams can affect organic matter decomposition (Arroita et al., 2015; Casas et al., 2000; Mendoza-Lera et al., 2012), ecosystem metabolism (Aristi et al., 2014; Uehlinger et al., 2003) or biofilm functioning (Munn and Brusven, 2004; Ponsatí et al., 2014). Particular attention needs to be given to nutrient cycling in rivers and how much it is affected by the presence of dams. The SDC proposes that river nutrient cycling will be strongly altered by dams, especially in low to mid-order streams (Ward and Stanford, 1983), even though empirical evidence of such a pattern is not strong. To our knowledge, no studies have specifically investigated the effect of dams on nutrient cycling in rivers. However, some studies conducted in lake outlets show that the combined effects of stable benthic habitat and lake-derived source-waters may result in high in-stream uptake of phosphorus (P) and low in-stream uptake of nitrogen (N) (Arp and Baker, 2007; Hall and Tank, 2003; Hall et al., 2002).

Discontinuities in nutrient cycling are important to be understood, since they reflect changes in nutrient retention, removal, and transport which ultimately may affect nutrient loading and eutrophication of freshwater and coastal ecosystems (Alexander et al., 2000; Mulholland et al., 2008). Noteworthy, results from most river nutrient cycling studies are derived from estimates of gross nutrient uptake (i.e. immobilization of nutrients from the water column) which may overestimate the net influence of streams on nutrient downstream export because they do not take into account the release of immobilized nutrients to the water column (Brookshire et al., 2009; Newbold et al., 1982; Roberts and Mulholland, 2007). Release processes (e.g. mineralization, nitrification, desorption), however, can be relevant in streams, and may counterbalance to some extent nutrient immobilization processes (e.g. assimilation, denitrification, and adsorption), or even result in a net downstream release of nutrients (von Schiller et al., 2015). Therefore, measurements of net nutrient uptake provide a more accurate information on actual nutrient export from a given river reach and on the relevance of in-stream processes at catchment scale (Bernal et al., 2012).

To examine the effect of dams on river nutrient cycling, we compared net uptake of dissolved nitrogen (N), phosphorus (P) and organic carbon (DOC) between river reaches located upstream and downstream from three reservoir systems. We predicted that the net uptake of downstream reaches would be increased with respect to upstream reaches because of higher hydromorphological stability, larger organic matter standing stocks and increased biological activity below dams. In the case our prediction is true, incorporating these alterations could significantly improve predictive models of biogeochemical cycling and transport in complex river networks.

2. Materials and methods

2.1. Study sites

We sampled reaches upstream (control) and downstream (impact) from reservoirs in three rivers within the Ebro River catchment (NE Iberian Peninsula; Fig. 1). The Cinca River drains a 9000-km^2 limestone-dominated catchment in the Central Pyrenees. Precipitation averages ~800 mm and tends to be greater in winter, although discharge peaks in late spring and early summer with the thaw (Beguería et al., 2003). Two successive large reservoirs, Mediano and El Grado, with a storage capacity of 436 and 399 hm^3, respectively, separate the control and impact reaches. The Montsant River and the Siurana River drain smaller (170 and 347 km^2, respectively) limestone-dominated catchments. Their climate is strongly Mediterranean, with an average annual precipitation of ~600 mm, 80% of it falling from October to April (Candela et al., 2012). The Margalef reservoir (3 hm^3) and the Siurana reservoir (12 hm^3) separate the control and impact reaches in the Montsant River and the Siurana River, respectively.

The studied reservoirs differ in their hydrological operation. Those in the Cinca River are subject to important water abstraction, which is diverted for irrigation and hydropower, whereas no significant abstraction occurs either in the Margalef or in the Siurana reservoirs. All studied reservoirs release deep water, which depending on the period, varies from epilimnetic to hypolimnetic. All have set environmental flows, defined as 10% of the seasonal average. The regulation capacity (i.e. the ratio between river annual discharge and reservoir storage capacity) is 0.46 year^{-1} in the Siurana River, 1.75 year^{-1} in the Cinca River and 3.64 year^{-1} in the Montsant River (Aristi et al., 2014).

The length of selected reaches ranged from 500 to 2500 m. The control and impact reaches were as close as possible to the reservoir inlet and outlet, respectively. No lateral surface-water inputs were present along the reaches. For measurements, we placed 6 equidistant transects along each reach. We performed three sampling campaigns at different hydrological periods: summer and autumn of 2011, and winter of 2012. Because the control reach of the Montsant River was dry in summer 2011, we performed the sampling campaign in May 2012, just before the summer drought.

2.2. Hydrogeomorphological characteristics

We obtained daily means of water level for the Cinca and Siurana rivers from the water agencies (Confederación Hidrográfica del Ebro, and Agència Catalana de l'Aigua, respectively). For the Montsant, we calibrated precipitation data (Servei Metereològic de Catalunya) against a pressure transducer (Levelloger LCT F100/M30 and Barologger LT F15/M5, Solinst, Georgetown, USA) installed in the river during the study. We assessed disturbance by extreme flow events on the basis of incipient movement of streambed particles (Leopold et al., 1964). Once at each site, we determined the size distribution of 150 stones collected randomly in the wet channel following the method by Wolman (1954). We established the discharge thresholds for initiation of sediment motion and for disruption of riverbed based on a comparison

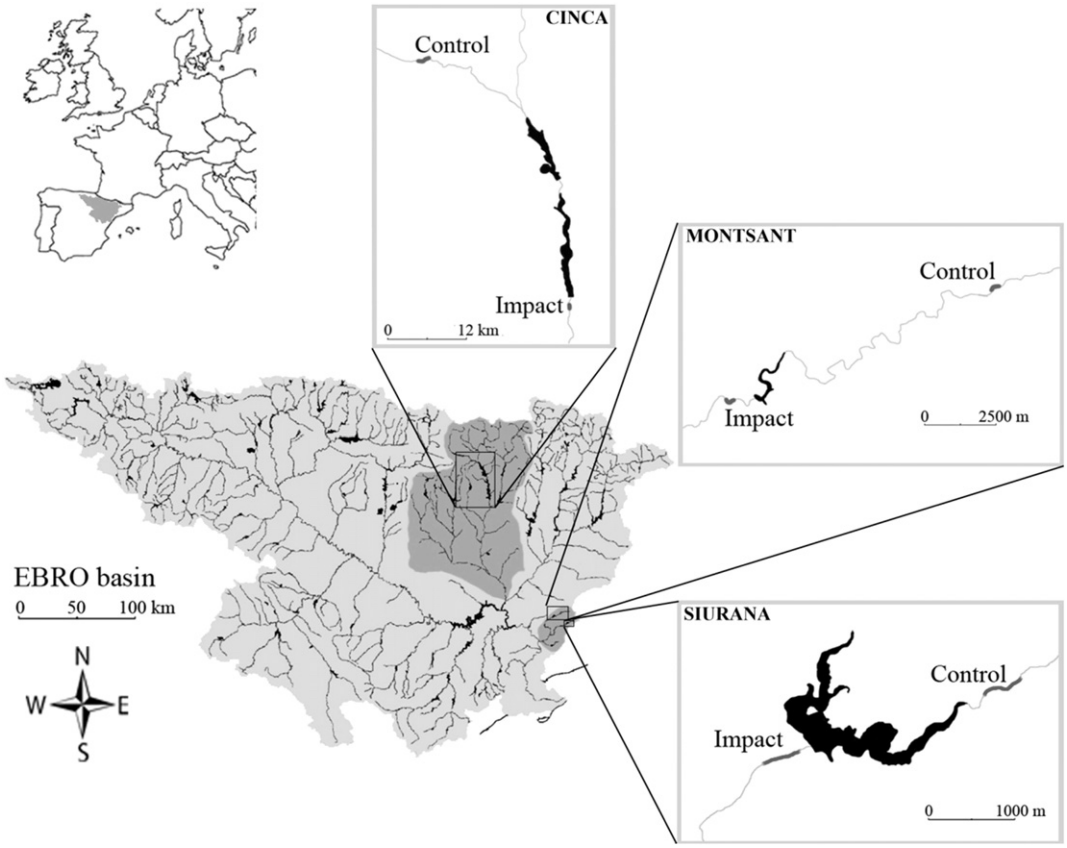

Fig. 1. Geographical location of the sampling sites in the three studied rivers within the Ebro River catchment.

between actual and critical dimensionless shear stress, calculated from water depth, channel slope, riverbed material density and mean grain diameter (Acuña et al., 2007). We assessed riverbed stability according to the time elapsed since the last sediment-moving flood (moderate flood, ST-1) and to the time elapsed since the last riverbed-disrupting flood (severe flood, ST-2).

On each sampling date, we measured the wetted width, water depth, water velocity and discharge at each transect with an acoustic Doppler velocity meter (Flow Tracker, Handheld-ADVr, Sontek Corporation, San Diego, CA, USA). Additionally, we calculated the mean light irradiance for each reach and season from solar radiation and canopy cover. We estimated the canopy cover by taking photographs along the reach with a digital camera with fisheye lens (E171-A Nikon-8 mm, Nikon D3000, Nikon Corporation, Tokyo, Japan). We obtained the received solar radiation (W m^{-2} h^{-1}) from the closest meteorological station and applied it to the obtained proportion of radiation for each moment of the day calculated with the software HemiView 2.1 (Dynamax Inc., Houston, TX, USA).

2.3. Organic matter, algal biomass and ecosystem metabolism

We determined the concentration of suspended particulate organic matter (SPOM) by taking three water samples (2 L) at each transect and filtering them through pre-ashed and pre-weighed glass fiber filters (Whatman GF/F, Whatman International, Maidstone, UK). At each transect, we also took five replicates of benthic particulate organic matter (BPOM), including live biomass and detritus, with Surber nets (0.09 m^2 of sampling surface, 0.2 mm mesh size). We froze filters and benthic samples for transport. Once in the laboratory, we dried (70 °C, 72 h), weighed, ashed (500 °C, 5 h) and reweighed them to estimate ash-free dry mass. Additionally, at each transect, we took four biofilms samples for chlorophyll-a (Chl-a) measurements. For each sample, we scrapped the light-exposed sides of three to four cobbles in a known volume of filtered river water and froze aliquots at −20 °C until analysis. We estimated the scraped surface by covering stones with aluminum foil of known density and later converting from aluminum weight to surface area. In the laboratory, we extracted Chl-a with acetone 90% v/v overnight at 4 °C and quantified spectrophotometrically (Shimadzu UV1800, Shimadzu Corporation, Kyoto, Japan) after filtration (Whatman GF/C fibreglass filters) of the extract (Jeffrey and Humphrey, 1975).

We calculated metabolism from diel DO changes by the two-station method, except in the Siurana control reach in summer and winter, where unreliable results forced us to use the single-station method (Reichert et al., 2009). We recorded temperature and DO at 10-min intervals at the upstream and downstream ends of each reach with optical oxygen probes (YSI 6150 connected to YSI 600 OMS; YSI Corporation, Yellow Springs, OH, USA). We estimated reaeration coefficients with the night-time method (Hornberger and Kelly, 1975) using the first 5 h after sunset. We calculated the nominal travel time of water measuring with a bromide sensor (WTW Br 800, WTW, Weilheim, Germany) the time between the peaks of the two breakthrough curves at the upstream and downstream stations after a slug addition of bromide (Hubbard et al., 1982). We calculated ecosystem respiration (ER) as the sum of net DO production rate during the dark period and respiration values during the light period. Gross primary production (GPP) was the sum of net metabolism rate during the light period and respiration rates during the light period. We calculated net ecosystem metabolism (NEM) as the sum of GPP and ER.

2.4. Water physico-chemical characteristics

We followed a Lagrangian approach (Writer et al., 2011) to sample the same parcel of water as it moved downstream at the thalweg of each transect along the reach two times per day (midnight and noon). For this purpose, we used the nominal travel times estimated with the

slug additions of bromide. We measured water temperature, conductivity, dissolved oxygen (DO) and pH with hand-held probes (WTW multiline 3310, WTW, Weilheim, Germany; YSI ProODO handled, YSI Inc., Yellow Springs, OH, USA). In parallel, we collected water samples and filtered them through glass fiber filters (Whatman GF/F) into plastic bottles and froze them at −20 °C until analysis. We determined the concentration of total dissolved phosphorus (TDP) after acid digestion colorimetrically using a Smartchem 140 spectrophotometer (Alliance-AMS, Frepillon, France). We determined DOC and TDN concentrations on a Shimadzu TOC-V CSH coupled to a TNM-1 module (Shimadzu Corporation, Kyoto, Japan).

2.5. Whole-reach net uptake

For each sampling date and time of the day (noon and midnight), we calculated the net uptake (U_{net}) of TDN, TDP and DOC from the longitudinal variation in ambient concentration along the reach following the spiraling method (von Schiller et al., 2011). The spiraling method has a number of advantages compared to the more commonly used mass-balance method (e.g. Roberts and Mulholland, 2007) and other alternative methods (e.g. Heffernan and Cohen, 2010; Hensley et al., 2014). For further details on the advantages, assumptions, limitations and a sensitivity analysis of the spiraling method see von Schiller et al. (2011) and von Schiller et al. (2015). First, we estimated the net uptake coefficient per unit of reach length (k_{net}, in m^{-1}) using the 1st-order equation

$$C_x = C_{top}\left(\frac{Cl_x}{Cl_{top}}\right)e^{-k_{net}x} \quad (1)$$

where C is river-water ambient nutrient concentration (in μg N L^{-1}, μg P L^{-1}, or μg C L^{-1}) and Cl is ambient river-water chloride concentration (in μg L^{-1}) at the top of the reach (top) and at each sampling location along the reach (x, in m). We calculated k_{net} and its 95% confidence interval (CI) from the regression between the natural logarithm of the river-water nutrient concentration corrected by chloride concentration and the downstream distance (x) after linearizing Eq. (1). Then, we calculated U_{net} based on the equation

$$U_{net} = (QC_{Avg}k_{net})/w \quad (2)$$

where Q is the average discharge, C_{Avg} is the average ambient nutrient concentration in river water and w is the average wetted width from the 6 sampling locations along the reach. U_{net} integrates nutrient uptake and release processes occurring along the reach and can be positive (uptake > release), negative (uptake < release) or 0 (uptake = release) depending on the value of k_{net}. We estimated an upper and lower limit of U_{net} based on the 95% CI of k_{net}. We assumed that U_{net} was indistinguishable from 0 (uptake ≈ release) when its 95% CI contained 0 (von Schiller et al., 2011).

2.6. Statistical analyses

We tested differences in hydrogeomorphology, POM, Chl-a and metabolism variables using generalized linear models (GLMs) with River (3 levels: Cinca, Montsant and Siurana), Season (3 levels: autumn, winter and summer) and Reach (2 levels: control and impact) as independent factors. For water physico-chemical variables and whole-reach net uptake, we added Time of the day (2 levels: midnight and noon) as independent factor to the GLMs. Interactions were not considered due to the low number of values. When the effect of a factor was statistically significant, we applied the post hoc Tukey test to identify differences between levels of that factor. We performed Pearson-moment correlations to examine relationships between whole-reach net uptake and metabolism variables. All statistical analyses were done with the software Statistica (version 6.0; StatSoft, Tulsa, Oklahoma, USA). In all cases, differences were considered significant if $p < 0.05$.

3. Results

3.1. Hydromorphological characteristics

Dams increased downstream hydrological stability, mainly by reducing the frequency of moderate floods. The time since the last moderate flood (ST-1) was consistently higher in impact than in control reaches (Table 1). Yet, there were no differences between reaches in the time since the last severe flood (ST-2; Table 1). Instead, there were differences among seasons in ST-2, with higher values in winter than in summer (Table 1). Mean discharge, water velocity, width and depth measured during the sampling campaigns differed among rivers, with generally higher values in the Cinca than in the Montsant and Siurana rivers (Table 1). There were no consistent differences in hydraulics between control and impact reaches, with reduced values below the dam in the Cinca, increased values in the Montsant, and no major effect in the Siurana (Table 1). Light irradiance was generally higher in control than in impact reaches (Table 1), because reaches below dams tended to be incised and single-channel with a larger riparian cover, whereas controls tended to be braided reaches running across a wide active channel. In addition, light irradiance followed seasonal and phenological changes, with highest values in summer, medium values in winter and lowest values in autumn (Table 1).

3.2. Organic matter, algal biomass and ecosystem metabolism

Organic matter standing stocks and epilithic algal biomass increased consistently below dams (Table 2). BPOM, SPOM and Chl-a were on average 2.1-, 2.0- and 8.1-fold higher, respectively, in impact than in control reaches (Table 2). Only BPOM showed differences among rivers, being higher in the Montsant than in the Cinca and Siurana rivers (Table 2). Most BPOM in control reaches was a combination of allochthonous detritus (leaves and wood) coming from upstream and lateral sources and relatively thin epilithic biofilms. In contrast, impact reaches did not receive any significant BPOM inputs from upstream as a result of the presence of dams, and the accumulated BPOM consisted mainly of live authochthonous biomass (macrophytes and thick epilithic biofilms) and a mixed detritus of decomposing authochthonous plants and allocthonous lateral inputs. Differences in organic matter standing stocks and algal biomass were reflected in changes in ecosystem metabolism upstream and downstream from dams. GPP and ER were on average 1.8-fold higher in impact than in control reaches, whereas NEM showed no differences upstream and downstream from dams (Table 2). Among the metabolism variables, only GPP showed a consistent seasonal pattern with higher values in summer than in the other seasons (Table 2). We found significant correlations between ER and GPP ($r = -0.76$, $p < 0.001$, $n = 18$) and between ER and NEM ($r = +0.83$, $p < 0.001$ $n = 18$).

3.3. Water physico-chemical characteristics

Dams had only a minor effect on the water physico-chemical variables (Table 3). Water temperature, conductivity, DO and pH showed no differences upstream and downstream from dams (Table 3). Among these variables, only DO and pH showed slightly higher but statistically significant average values at noon than at midnight (Table 3). Average temperature and pH were highest in summer, whereas conductivity was highest in autumn and DO in winter (Table 3). Conductivity and pH also showed differences among rivers, with the highest conductivity in Siurana and the highest pH in Cinca (Table 3).

The effect of dams on dissolved nutrient concentrations was only evident for TDP, but not for TDN and DOC (Table 3). The TDP concentration was on average 1.8-fold higher in control than in impact reaches,

Table 1
Hydrogeomorphological characteristics at each study site during the samplings. Numbers are the mean value for the whole study reach. The p-values of the factor main-effects in the general linear models (GLMs) are shown in the lower part of the table; significant effects ($p < 0.05$) are marked in bold.

River	Season	Reach	ST-1 d	ST-2 d	Discharge L s^{-1}	Velocity m s^{-1}	Width m	Depth m	Light W m^{-2} h^{-1}
Cinca	Summer	Control	14	38	1464	0.23	19.3	0.26	18894
		Impact	452	1200	185	0.13	5.5	0.23	21135
	Autumn	Control	1	5	2549	0.32	27.3	0.30	1842
		Impact	519	1267	231	0.22	0.4	0.24	2420
	Winter	Control	73	90	1398	0.23	22.7	0.26	8412
		Impact	612	1360	180	0.18	4.3	0.24	10111
Montsant	Summer	Control	238	243	5	0.13	0.2	0.25	21141
		Impact	246	246	9	0.26	0.4	0.23	13659
	Autumn	Control	98	343	28	0.05	0.4	0.19	6608
		Impact	346	346	14	0.07	2.9	0.13	2435
	Winter	Control	28	47	23	0.11	0.7	0.11	13624
		Impact	421	421	25	0.08	1.9	0.20	5662
Surana	Summer	Control	134	138	82	0.02	3.7	0.08	23799
		Impact	142	142	220	0.05	1.4	0.18	16717
	Autumn	Control	233	237	8	0.12	2.2	0.09	6973
		Impact	241	241	20	0.05	1.8	0.17	1185
	Winter	Control	96	340	11	0.10	0.8	0.13	10494
		Impact	344	344	30	0.07	2.2	0.15	2150
GLM	River effect		0.216	0.230	**0.022**	**0.005**	**0.009**	**0.002**	0.902
	Season effect		0.106	**0.046**	0.763	0.962	0.978	0.694	<**0.001**
	Reach effect		**0.022**	0.120	0.068	0.490	0.052	0.549	**0.016**

ST-1 = Time elapsed since the last moderate flood; ST-2 = Time elapsed since the last severe flood.

whereas the concentrations of TDN and DOC did not differ between upstream and downstream reaches. The concentrations of TDN, TDP and DOC showed marked differences among rivers, with the Montsant River showing on average the highest concentrations (Table 3). There were no significant differences between midnight and noon concentrations for any nutrient (Table 3).

3.4. Whole-reach net uptake

Among all nutrients, only the net uptake of TDN differed significantly between reaches located upstream and downstream from the dams (Table 4; Fig. 2). U_{net}-TDN was higher in impact (mean ± SE = 117.2 ± 11.7 μg N m^{-2} min^{-1}) than in control reaches (mean ± SE = −0.02 ± 4.54 μg N m^{-2} min^{-1}). In addition, U_{net}-TDN in control reaches was = 0 (i.e. no net uptake or release) in 72% of the cases, whereas in impact reaches it was = 0 in only 33% of the cases. In contrast, U_{net}-TDP and U_{net}-DOC did not differ upstream and downstream from the dams. U_{net}-TDP was close to 0 in both control (mean ± SE = 0.7 ± 0.3 μg P m^{-2} min^{-1}) and impact reaches (mean ± SE = 0.008 ± 0.002 μg P m^{-2} min^{-1}). U_{net}-DOC tended to be higher in impact (mean ± SE = 64.0 ± 0.8 μg C m^{-2} min^{-1}) than in control reaches (mean ± SE = 4.9 ± 9.0 μg C m^{-2} min^{-1}), but the high variability made this difference statistically not significant. Both U_{net}-TDP and U_{net}-DOC were = 0 in >72% of the cases in control and impact reaches. The whole-reach net uptake of all nutrients showed no consistent differences between midnight and noon or among rivers and seasons (Table 4).

Table 2
Particulate organic matter, epilithic algal biomass and ecosystem metabolism at each study site during the samplings. Numbers are the mean value for the whole study reach. The p-values of the factor main-effects in the general linear models (GLMs) are shown in the lower part of the table; significant effects ($p < 0.05$) are marked in bold.

River	Season	Reach	BPOM g m^{-2}	SPOM mg L^{-1}	Chl-a μg cm^{-2}	GPP g O_2 m^{-2} d^{-1}	ER g O_2 m^{-2} d^{-1}	NEM g O_2 m^{-2} d^{-1}
Cinca	Summer	Control	27.27	0.70	2.69	3.27	-1.70	1.56
		Impact	47.63	0.71	8.58	6.00	-8.61	-2.61
	Autumn	Control	13.15	0.40	1.12	0.91	-4.62	-3.72
		Impact	92.66	1.28	16.46	2.56	-6.99	-4.43
	Winter	Control	8.64	0.76	0.88	0.69	-3.09	-2.41
		Impact	59.20	0.74	16.51	1.32	-4.53	-3.21
Montsant	Summer	Control	118.42	0.65	1.70	4.29	-7.52	-3.22
		Impact	224.28	1.05	16.02	3.96	-10.16	-6.20
	Autumn	Control	327.04	0.70	1.36	1.06	-4.75	-3.70
		Impact	216.25	1.80	16.29	1.29	-3.15	-1.86
	Winter	Control	155.18	0.47	2.98	1.52	-2.15	-0.63
		Impact	247.39	0.62	30.83	1.89	-4.34	-2.45
Surana	Summer	Control	13.33	0.71	2.66	0.65	-1.42	-0.77
		Impact	169.13	0.96	11.32	2.60	-3.40	-0.80
	Autumn	Control	28.48	0.69	8.70	0.68	-1.27	-0.59
		Impact	146.88	2.26	32.05	1.06	-2.01	-0.96
	Winter	Control	15.64	0.67	0.91	0.26	-1.47	-1.21
		Impact	281.17	1.78	38.73	2.78	-6.22	-3.44
GLM	River effect		**0.002**	0.188	0.151	0.149	0.108	0.271
	Season effect		0.609	0.184	0.143	**0.004**	0.307	0.873
	Reach effect		**0.017**	**0.005**	<**0.001**	**0.034**	**0.039**	0.161

BPOM = Benthic particulate organic matter; SPOM = Suspended particulate organic matter; Chl-a = chlorophyll-a
GPP = Gross primary production; ER = Ecosystem respiration; NEM = Net ecosystem metabolism

Table 3
Water physico-chemical characteristics at each study site during the samplings. Numbers are the mean value (midnight value/noon value) for the whole study reach. The p-values of the factor main-effects in the general linear models (GLMs) are shown in the lower part of the table; significant effects ($p < 0.05$) are marked in bold.

River	Season	Reach	Temperature °C	Conductivity µS cm^{-1}	DO mg L^{-1}	pH -	NO_3^- mg N L^{-1}	NH_4^+ mg N L^{-1}	TDN mg N L^{-1}	PO_4^{3-} mg P L^{-1}	TDP mg P L^{-1}	DOC mg C L^{-1}
Cinca	Summer	Control	17.7 (17.5/17.9)	323 (320-325)	9.0 (8.5/9.4)	8.80 (8.62-8.97)	0.253 (0.245/0.262)	0.023 (0.013/0.033)	0.279 (0.262/0.295)	0.004 (0.003-0.004)	0.006 (0.004/0.009)	0.106 (0.105/0.107)
		Impact	22.1 (22.0/22.2)	288 (291/284)	8.4 (7.6/9.2)	8.60 (8.60-8.60)	0.124 (0.131/0.117)	0.016 (0.015/0.017)	0.246 (0.269/0.224)	0.002 (0.002/0.002)	0.007 (0.009/0.004)	0.446 (0.780/0.111)
	Autumn	Control	7.1 (6.3/7.8)	311 (312/310)	11.6 (11.4/11.9)	8.30 (8.26/8.34)	0.198 (0.208/0.189)	0.008 (0.008/0.008)	0.282 (0.284/0.281)	0.003 (0.003/0.003)	0.004 (0.005/0.004)	0.136 (0.141/0.130)
		Impact	8.5 (8.2/8.8)	386 (397/375)	10.6 (10.3/10.9)	8.25 (8.22/8.28)	0.280 (0.259/0.301)	0.031 (0.029/0.032)	0.393 (0.379/0.407)	0.003 (0.003/0.003)	0.005 (0.006/0.004)	0.114 (0.114/0.114)
	Winter	Control	3.3 (2.8/3.9)	314 (314/314)	12.3 (12.2/12.4)	8.36 (8.33/8.39)	0.258 (0.240/0.276)	0.004 (0.004/0.004)	0.289 (0.275/0.303)	0.002 (0.002/0.002)	0.006 (0.004/0.008)	0.228 (0.129/0.237)
		Impact	3.5 (3.1/3.9)	369 (369/369)	13.0 (12.7/13.3)	8.29 (8.27/8.32)	0.288 (0.299/0.276)	0.004 (0.004/0.004)	0.341 (0.323/0.359)	0.002 (0.002/0.002)	0.004 (0.004/0.004)	0.767 (0.748/0.786)
Montsant	Summer	Control	15.1 (14.7/15.6)	362 (366/359)	9.5 (8.2/10.8)	8.54 (8.23/8.85)	0.011 (0.012/0.011)	0.008 (0.008/0.008)	0.164 (0.167/0.161)	0.017 (0.017/0.016)	0.024 (0.0026/0.023)	1.978 (2.002/1.954)
		Impact	15.1 (14.9/15.4)	395 (400/390)	9.6 (8.4/10.8)	8.32 (8.18/8.46)	0.603 (0.625/0.582)	0.008 (0.008/0.008)	0.826 (0.846/0.806)	0.004 (0.004/0.004)	0.008 (0.009/0.007)	3.148 (3.143/3.153)
	Autumn	Control	13.6 (13.0/14.3)	769 (767/770)	8.6 (8.3/8.9)	7.79 (7.77/7.80)	2.419 (2.123/2.716)	0.016 (0.015/0.018)	3.065 (2.786/3.344)	0.023 (0.023/0.024)	0.023 (0.023/0.024)	6.841 (6.887/6.795)
		Impact	12.1 (12.3/11.9)	400 (400/400)	9.6 (9.1/10.1)	7.99 (7.98/8.01)	0.384 (0.365/0.404)	0.006 (0.006/0.007)	0.576 (0.577/0.575)	0.007 (0.006/0.008)	0.007 (0.006/0.008)	2.589 (2.586/2.529)
	Winter	Control	3.2 (2.6/3.7)	486 (486/486)	12.7 (12.2/13.3)	8.24 (8.14/8.33)	0.462 (0.459/0.466)	0.008 (0.008/0.008)	0.589 (0.588/0.590)	0.011 (0.011/0.012)	0.017 (0.017/0.017)	1.259 (1.224/1.294)
		Impact	3.5 (3.7/3.4)	446 (444/447)	12.7 (11.8/13.6)	8.27 (8.20/8.35)	0.855 (0.835/0.874)	0.013 (0.010/0.016)	1.018 (1.016/1.020)	0.004 (0.004/0.004)	0.004 (0.004/0.004)	2.511 (2.539/2.484)
Surana	Summer	Control	23.4 (22.6/24.2)	646 (645/647)	7.7 (7.5/7.8)	8.30 (8.24/8.36)	0.141 (0.148/0.133)	0.018 (0.020/0.017)	0.226 (0.238/0.215)	0.007 (0.007/0.007)	0.010 (0.011/0.010)	0.743 (0.674/0.813)
		Impact	14.7 (14.5/14.9)	635 (636/634)	9.1 (8.8/9.5)	8.32 (8.28/8.36)	0.096 (0.098/0.093)	0.016 (0.012/0.020)	0.285 (0.281/0.288)	0.003 (0.002/0.005)	0.010 (0.010/0.010)	2.176 (2.412/1.940)
	Autumn	Control	11.8 (11.3/12.3)	703 (705/701)	10.9 (10.8/11.0)	8.23 (8.25/8.22)	0.393 (0.378/0.408)	0.016 (0.012/0.019)	0.409 (0.392/0.427)	0.003 (0.003/0.002)	0.005 (0.006-0.004)	0.117 (0.113/0.120)
		Impact	10.4 (9.7/11.2)	626 (626/626)	10.5 (10.1/11.0)	8.18 (8.20/8.16)	0.295 (0.292/0.299)	0.038 (0.047/0.030)	0.359 (0.347/0.370)	0.004 (0.003/0.005)	0.005 (0.004/0.006)	2.587 (2.625/2.548)
	Winter	Control	3.3 (2.8/3.8)	705 (706/704)	12.5 12.5/12.5)	8.26 (8.24/8.27)	0.279 (0.286/0.273)	0.010 (0.009/0.010)	0.354 (0.353/0.355)	0.004 (0.004/0.004)	0.005 (0.005/0.005)	0.547 (0.527/0.567)
		Impact	5.4 (4.6/6.1)	595 (598/591)	12.0 (11.5/12.5)	8.26 (8.21/8.30)	0.038 (0.046/0.031)	0.016 (0.015/0.018)	0.203 (0.201/0.204)	0.004 (0.005/0.004)	0.007 (0.007/0.007)	2.032 (1.947/2.116)
GLM	River effect		0.515	**<0.001**	0.519	**0.001**	**0.006**	**0.034**	**0.003**	**<0.001**	**<0.001**	**<0.001**
	Season effect		**<0.001**	**0.030**	**<0.001**	**<0.001**	0.060	**0.017**	0.083	0.193	0.113	0.231
	Reach effect		0.682	0.053	0.774	0.480	0.296	0.132	0.405	**0.001**	**0.002**	0.237
	Time of the day effect		0.363	0.917	**0.003**	**0.022**	0.809	0.499	0.849	0.797	0.834	0.901

DO = Dissolved oxygen; NO_3^- = Nitrate; NH_4^+ = Ammonium; TDN = Total dissoved nitrogen; PO_4^{3-} = Phosphate; TDP = Total dissolved phosphorus; DOC = Dissolved organic carbon

Table 4
Whole-reach net uptake (U_{net}) of total dissolved nitrogen (TDN), phosphorus (TDP) and organic carbon (DOC) at each study site during the samplings. Numbers are the mean value (midnight value/noon value) for the whole study reach. The p-values of the factor main-effects in the general linear models (GLMs) are shown in the lower part of the table; significant effects ($p < 0.05$) are marked in bold.

River	Season	Reach	U_{net}-TDN		U_{net}-TDP		U_{net}-DOC	
			μg N m^{-2} min^{-1}		μg P m^{-2} min^{-1}		μg C m^{-2} min^{-1}	
Cinca	Summer	Control	0	(0/0)	9.5	(0/19.0)	26.8	(0/53.6)
		Impact	220.9	(349.4/92.6)	0	(0/0)	330.7	(661/0.4)
	Autumn	Control	0	(0/0)	0.1	(0/0.2)	0	(0/0)
		Impact	-44.6	(0/-89.2)	0	(0/0)	0	(0/0)
	Winter	Control	0	(0/0)	0	(0/0)	0	(0/0)
		Impact	177.5	(0/355.0)	0.1	(0.1/0)	0	(0/0)
Montsant	Summer	Control	0.0	(0/0)	0	(0/0)	0	(0/0)
		Impact	410.4	(820.8/0)	0	(0/0)	0	(0/0)
	Autumn	Control	-147.2	(-294.5/0)	0	(0/0)	0	(0/0)
		Impact	103.5	(100.0/107.0)	0	(0/0)	158.2	(147.4/169.0)
	Winter	Control	91.2	(77.6/104.8)	0	(0/0)	0	(0/0)
		Impact	0.0	(0/0)	0	(0/0)	0	(0/0)
Surana	Summer	Control	0.0	(0/0)	0	(0/0)	14.8	(0/29.6)
		Impact	55.2	(46.1/64.3)	0	(0/0)	87.3	(174.6/0)
	Autumn	Control	48.9	(0/97.9)	-2.3	(-4.4/-0.05)	2.5	(5.1/0)
		Impact	74.0	(0/148.0)	0	(0/0)	0	(0/0)
	Winter	Control	6.9	(13.8/0)	-1.0	(-2.1/0)	0	(0/0)
		Impact	57.7	(64.8/50.6)	0	(0/0)	0	(0/0)
GLM	River effect		0.867		0.249		0.644	
	Season effect		0.283		0.283		0.271	
	Reach effect		**0.041**		0.523		0.134	
	Time of the day effect		0.804		0.195		0.295	

There were no significant correlations between U_{net}-TDN, U_{net}-TDP and U_{net}-DOC ($p > 0.721$), except for a positive correlation between U_{net}-TDN and U_{net}-DOC when we only considered U_{net}-values ≠ 0 (i.e. net uptake or release) (Fig. 3). In addition, U_{net}-TDN was significantly correlated with ER and marginally significantly with GPP (Fig. 4). There was higher U_{net}-TDN with higher ecosystem respiration (lower ER values) and higher GPP, suggesting a coupling between ecosystem metabolism and net uptake of N. In both cases, the highest U_{net}-TDN values occurred in impact reaches and were coincident with the lowest ER and the highest GPP values. U_{net}-TDP showed no significant correlation with metabolism variables ($p > 0.010$). U_{net}-DOC showed a significant correlation with GPP ($r = 0.56$, $p = 0.015$, $n = 18$), but the correlation was no longer significant ($r = 0.01$, $p = 0.977$, $n = 17$) when an outlier with unusually high U_{net}-DOC and GPP values (impact reach of the Cinca River in summer) was removed.

4. Discussion

The presence of dams enhanced hydromorphological stability, the accumulation of organic matter and ecosystem metabolism in downstream reaches. Flow regulation also altered river nutrient cycling by increasing the whole-reach net uptake of dissolved N, but not of dissolved P or C. The reaches located upstream from dams were close to biogeochemical equilibrium with no significant net uptake of dissolved TDN, TDP or DOC, whereas reaches located downstream from dams acted as net sinks of TDN. However, dams did not interfere in the uptake of TDP and DOC that remained similar between upstream and downstream reaches.

Reservoirs are particularly efficient in removing P (Harrison et al., 2010), thus, streams below reservoirs can show a tendency towards P limitation (i.e. low N:P ratios as in our case). As a result, in river reaches located below reservoirs we would expect higher demand for P than for N. In line with this expectation, results from studies on the effects of lakes show a tendency for increased P uptake and reduced N uptake in lake outlets. For instance, Arp and Baker (2007) showed no nitrate uptake but high phosphate uptake at lake outlets, what they attributed to the combined effects of stable hydrology and lake-derived source-waters on the nutrient requirements of biological communities. Similarly, Hall et al. (2002) reported one of the highest uptakes of phosphate in a lake outlet from a set of 13 reaches, whereas Hall and Tank (2003) measured the lowest uptake of nitrate at a lake outlet compared with the other 10 streams in their study. In contrast to results from streams below lakes, we observed increased N uptake and no changes in P uptake below reservoirs. In the absence of more empirical evidence, these apparently contradictory results suggest that differences in the functioning of reservoirs and lakes could differently influence downstream nutrient cycling. For instance, nutrient removal tends to be higher in reservoirs compared to lakes (Harrison et al., 2009), and river reaches below reservoirs are exposed to deep water releases (Friedl and Wüest, 2002) and strong hydromorphological modifications (Graf, 2006). Moreover, while results from lake outlets (Arp and Baker, 2007; Hall and Tank, 2003; Hall et al., 2002) were derived from estimates of gross nutrient uptake, our results were derived from estimates of net nutrient uptake. Gross nutrient uptake approximates nutrient demand, whereas net nutrient uptake is the balance between gross nutrient uptake and release (von Schiller et al., 2015). Thus, high gross uptake as a result of high demand may be counterbalanced by high release. This could at least partially explain the lack of difference in net P uptake between our control and impact reaches as well as the differences observed between the results from lake outlets (i.e. gross uptake estimates) and results from our study (i.e. net uptake estimates). Unfortunately, we did not measure gross uptake of nutrients in addition to net uptake; thus, we were not able to establish the magnitude of gross uptake in comparison to release in our study reaches. Furthermore, the lack of difference in P uptake between our control and impact reaches could also have been influenced by the low TDP concentrations (except in the control of the Montsant River), which may have caused P limitation and high P recycling in biofilms upstream and downstream from dams (Ponsatí et al., 2014).

In the absence of studies that have measured net uptake of TDN in rivers, studies on the net uptake of dissolved inorganic nitrogen (DIN) provide evidence on the net capacity of rivers to take up N. For instance, Roberts and Mulholland (2007) reported an average DIN net uptake close to 0 and values ranging from −6.2 to 36 μg N m^{-2} min^{-1} from a North American forested headwater stream investigated over a whole year. Bernal et al. (2012) measured net uptake of DIN in two headwater streams in the Iberian Peninsula over two years and also reported an average DIN net uptake close to zero but with a wider range (−207.6 to 340.5 μg N m^{-2} min^{-1}). In these headwater streams,

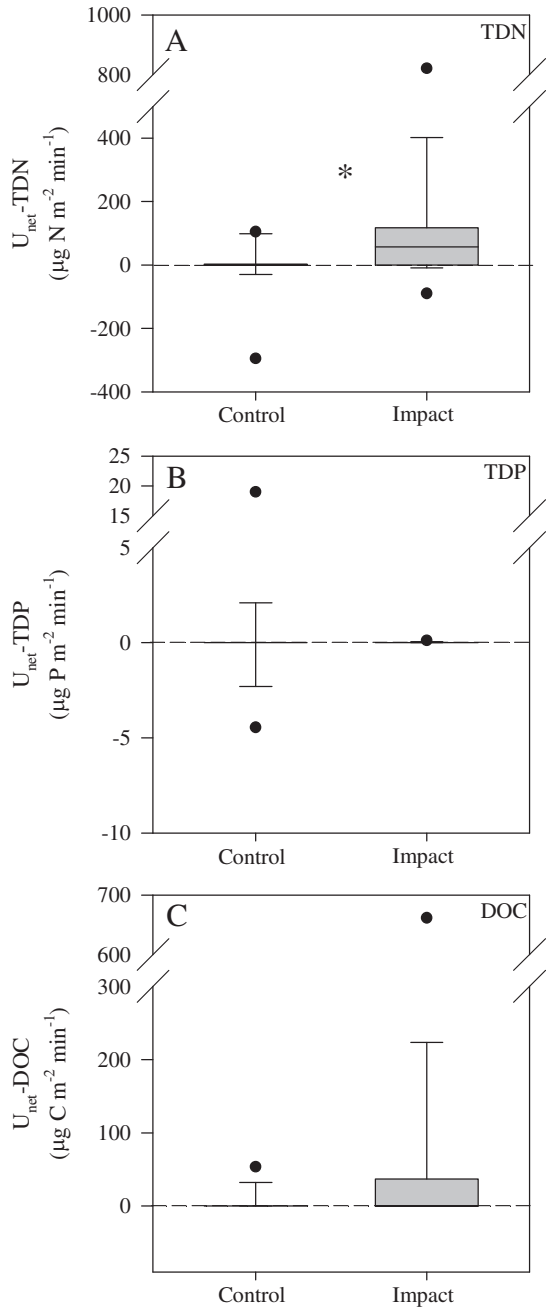

Fig. 2. Whole-reach net uptake (U_{net}) of total dissolved nitrogen (TDN; panel A), total dissolved phosphorus (TDP; panel B) and total dissolved organic carbon (DOC; panel C) in the river reaches located upstream (control) and downstream (impact) from the dams. Box plots display the 10th, 25th, 50th, 75th, and 90th percentiles and outliers. The asterisk indicates significant difference as reported in Table 4.

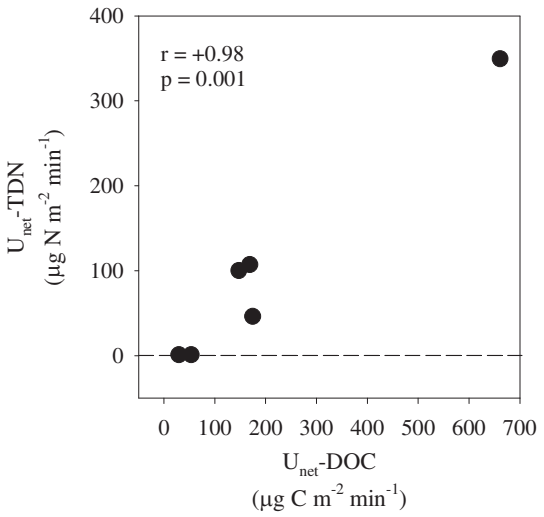

Fig. 3. Relationship between the net uptake of total dissolved nitrogen (U_{net}-TDN) and the net uptake of dissolved organic carbon (U_{net}-DOC) when only U_{net}-values ≠ 0 (i.e. net uptake or release) are considered. The results from the Pearson-moment correlation are shown.

biogeochemical equilibrium ($U_{net} \sim 0$) dominated most of the time similarly as it happened in our control reaches (Bernal et al., 2012; Roberts and Mulholland, 2007). In contrast, in our impact reaches net uptake of TDN was ≠ 0 in two thirds of the cases and the average value was relatively high (mean ± SE = 117.2 ± 11.7; range = −89.2–820.8 μg N m^{-2} min^{-1}). In addition to the influence of high metabolic fluxes (see below), the high uptake of N measured in our impact reaches may be partially explained by the fact that net uptake of TDN includes the cycling of dissolved organic nitrogen (DON) in addition to that of DIN (Brookshire et al., 2005). In this sense, DON accounted on average for 30% of TDN in the impact reaches (von Schiller et al., unpublished data). Unfortunately, we were not able to distinguish how much DIN vs. DON contributed to N cycling in the investigated river reaches. Furthermore, we should take into account that net uptake in our study was only measured three times in each reach and during periods of base flow. Net uptake could be strongly altered during flood periods or just after floods (Grimm, 1987; Marti et al., 1997).

Metabolic fluxes were correlated with the net uptake of TDN. There was higher U_{net}-TDN at higher ecosystem respiration (lower ER values) and higher GPP. This coupling was driven by the high values of ER, GPP and U_{net}-TDN in impact reaches. In a parallel study, Aristi et al. (2014) showed increased metabolic fluxes downstream from the dam as a result of higher hydromorphological stability and accumulation of organic matter and algal biomass. Here, we show that enhanced metabolism below dams also enhances the net uptake of TDN. Several studies have found a positive relationship between metabolic variables and gross N uptake (e.g. Fellows et al., 2006; Hall and Tank, 2003; Valett et al., 2008). Our study adds to the lower number of studies that have reported a relationship between metabolism and net N uptake (e.g. Heffernan and Cohen, 2010; Heffernan et al., 2010).

To examine the relative contribution of autotrophs and heterotrophs to assimilatory N uptake, we estimated the N demand by autotrophops and heterotrophs based on the approach used by Hall and Tank (2003). Predicted N demand was derived from metabolism assuming a respiratory quotient = 1 and a molar C:N = 20. We assumed net autotrophic production to be 0.5 × GPP, and we used a moderate heterotrophic growth efficiency (0.2) to estimate heterotrophic production. The predicted autotrophic vs. heterotrophic N demand ratio was 1.2 ± 0.2 (mean ± SE, n = 17; the control reach of Cinca River in summer with a ratio = 90.6 was excluded). The ratio was similar between control (1.0 ± 0.2) and impact reaches (1.3 ± 0.2). Viewed with caution, our results suggest that autotrophs and heterotrophs contributed similarly to assimilatory N uptake in the study reaches, and that this relative contribution did not vary significantly between reaches located upstream and downstream from dams. We did not investigate the primary uptake compartments responsible for N uptake; however, a parallel study by Ponsatí et al. (2014) observed increased photoautotrophic and heterotrophic activity in epilithic biofilms downstream from the dams, indicating that this compartment may be a key driver of N uptake in the investigated river reaches. Moreover, the positive correlation between U_{net}-TDN and U_{net}-DOC when we considered U_{net}-values ≠ 0 suggests that coupled DOC and TDN uptake by heterotrophs could have been important during some periods. Nonetheless, dissimilatory N uptake via denitrification could also have significantly contributed to N removal, especially below dams where positive net N uptake was frequent.

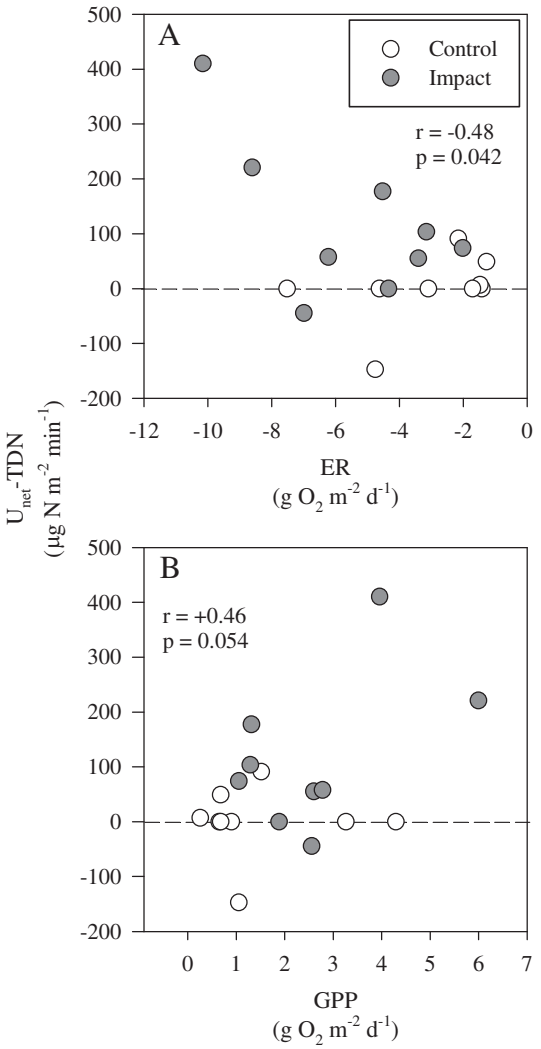

Fig. 4. Relationships of the net uptake of total dissolved nitrogen (U_{net}-TDN; mean of noon and midnight values for each date and reach) with ecosystem respiration (ER; panel A) and gross primary production (GPP; panel B) in the river reaches located upstream (Control) and downstream (Impact) from the dams. Results from Pearson-moment correlations are shown in each panel.

Indeed, in spring-fed rivers, which similarly to our impact reaches also have stable hydromorphological conditions and high metabolic activity, dissimilatory N uptake via denitrification was the predominant mechanism of N removal despite high N demand by autotrophs and heterotrophs (Heffernan et al., 2010). Unfortunately, in our study we did not directly measure denitrification, and our data (i.e. net N uptake estimates) did not allow us to reliably estimate the magnitude and relative importance of assimilatory vs. dissimilatory N uptake.

Diurnal changes (i.e. midnight vs. noon) observed in some variables (i.e. DO, pH) were not reflected in diurnal changes in nutrient cycling. As such, there were no differences in net uptake for TDN, TDP or DOC between midnight and noon samplings. Because primary production is dependent on the light presence, this observation supports the fact that despite the dominance of net heterotrophy (GPP < ER) autotrophic and heterotrophic processes contributed similarly to nutrient uptake in the investigated river reaches (Fellows et al., 2006). Our result are sustained by results from other streams that have found differences in gross uptake of N and P between day and night only during periods of net autotrophy (Mulholland et al., 2006). Nonetheless, we should be cautious in interpreting midnight-noon differences as the best proxies for diel variability in uptake because maximum and minimum values can occur at other moments of the day (Heffernan and Cohen, 2010).

5. Conclusions

Hydrologic regulation by dams in Mediterranean rivers enhances hydromorphological stability, organic matter accumulation and metabolic fluxes, thereby increasing the net uptake capacity of dissolved N downstream. Consequently, not only reservoirs themselves, but also river reaches located downstream from their dams may constitute relevant N cycling discontinuities along regulated river networks. Our results suggest that higher net N uptake capacity in river reaches below dams could lead to less N exported to downstream systems. How far this effect extends downstream along the rivers and over wider geographical scales remains to be investigated. Incorporating these discontinuities could significantly improve predictive models of N cycling and transport in complex river networks.

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