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Phosphorus use by planktonic communities in a large regulated Mediterranean river

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ABSTRACT

The regulation of large rivers to meet human requirements (e.g. hydroelectricity production, flood prevention, recreation activities) alters the longitudinal distribution of plankton communities and may affect their capacity to use nutrients and organic matter. Here we analyzed phosphorus (P) availability and use by phytoplankton and bacterioplankton in 6 upstream and 5 downstream sites from a reservoir system in the Ebro River (N Spain). Alkaline phosphatase activity (APA) was related to nutrient availability and biomass of both phytoplankton and bacterioplankton. During dry periods phytoplankton and bacterioplankton APA was inversely correlated to P availability in the water, but these patterns became less clear during wet periods. The phosphorus-APA patterns were more consistent in the upstream sites and especially during dry periods. Although phytoplankton APA was 6–40 times greater than that of bacterioplankton, APA per unit of biomass suggested that bacterioplankton was more efficient at utilizing dissolved organic phosphorus (DOP) in the upstream section during dry periods. Imbalanced N:P ratios in the particulate (N:P ranging 133–170) and dissolved (N:P ranging 301–819) water fractions confirmed the strong P limitation in these upstream communities. The phosphorus-APA patterns were weaker in the downstream section and during wet periods. The reservoirs caused a change in the downstream dynamics, where bacterioplankton biomass was positively correlated to APA but APA per unit of biomass decreased. Our findings reveal that river regulation drives changes in plankton use of organic phosphorus, especially during extreme dry periods.

1. Introduction

The dynamics of phytoplankton and bacterioplankton largely determine organic matter production and nutrient recycling in large rivers (Findlay and Sinsabaugh, 1999; Vis et al., 2007; Ochs et al., 2010). Riverine plankton tends to increase from mid-to-low river sections as a result of the slowing down of water flow (Wehr and Descy, 1998). These longitudinal patterns are stronger during periods of low discharge, especially if they coincide with periods of high temperature and light availability, all of which stimulate phytoplankton (Vis et al., 2007). During wet periods, greater discharge tends to shorten water residence times resulting in dilution of biomass along the river (Salmaso and Zignin, 2010). These spatial and temporal patterns are subjected to considerable alterations in regulated rivers (Rodrigues et al., 2009; Bi et al., 2010). Reservoirs along the river course affect the structure and functioning of plankton communities (Bi et al., 2010; Wuang et al., 2011). In the Ebro River, three large reservoirs (Mequinenza, Ribaroja and Flix) located in the final section of the river decrease the water residence time in the downstream section by nearly 2 days (Sanchez-Cabeza and Pujol, 1999), and cause nutrient retention (especially nitrate; Roura, 2004). Lower phytoplankton densities and chlorophyll concentration after the reservoirs are probably related with these hydrological and chemical differences caused by the reservoirs (Sabater et al., 2008).

Riverine phytoplankton and bacterioplankton exert a large influence on dissolved organic matter (DOM) overall contributing to nutrient recycling (Findlay and Sinsabaugh, 1999). Phytoplankton and bacterioplankton can meet their needs for phosphorus by the uptake of dissolved forms (mostly in form of phosphate) through the cell membranes. When ambient phosphate concentrations are depleted, micro-organisms may obtain P through extracellular decomposition of dissolved organic phosphorus compounds (Chróst and Overbeck, 1987). Phytoplankton and bacterioplankton alike have the capacity to produce extracellular enzymes that degrade organic matter, namely Alkaline Phosphatase Activity (APA) in the case of organic phosphorus compounds (Litchman and Nguyen, 2008). While most research into planktonic APA has been conducted in lentic environments (Rose and Axler, 1998; Sereda et al., 2011), including reservoirs (Giraudet et al., 1999; Nedoma et al., 2006), river plankton have received less attention (Wilczek et al., 2007; Rees et al., 2009). APA synthesis is promoted by low concentrations of dissolved inorganic phosphorus (DIP; Chróst and Overbeck, 1987) or by high

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concentrations of dissolved organic phosphorus (DOP; Dyhrman and Ruttenberg, 2006).

Phytoplankton often dominates the uptake of dissolved phosphorus although in cases of very low concentration bacterioplankton, which have a greater affinity for phosphate, can be more active (Cotner and Wetzel, 1992; Currie and Kalff, 1984a, 1984b). The larger surface-to-volume ratio of bacterial cells could explain their higher nutrient uptake efficiency, but the higher efficiency of bacterioplankton is not universal, since there are also large colony-forming bacteria whose affinities are not higher than those of phytoplankton (e.g. Løvdal et al., 2007). The present study aims to investigate the effect of reservoirs in the downstream use of DOP by plankton communities, as well as the effect on the respective DOP utilization by phytoplankton and bacterioplankton in different hydrological periods.

We conducted a three-year observational study on the relationship between phosphorus availability and use (APA) by phytoplankton and bacterioplankton communities in two river sections of the Ebro River which are separated by reservoirs. We predicted stronger phosphorus-APA relationships and greater APA efficiencies (that is the APA per unit of microbial biomass) in the upstream reservoirs section, where plankton densities are expected to be greater. Conversely, reservoirs contribution to plankton dilution may reduce APA expression in the downstream section. These foreseen differences between sections may increase during dry periods, when low flows would enhance the hydro-chemical and biological differences between sections separated by reservoirs. We also expected that bacterioplankton could dominate P uptake and utilization during dry periods, and that the DOP utilization was more balanced between plankton groups in wet periods. The Ebro River provides a range of conditions in which to test these hypotheses (Sabater et al., 2008); plankton development and activity show a marked seasonal pattern which is accentuated during extreme dry periods.

2. Materials and methods

2.1. Study area

The Ebro is the largest river in the Iberian Peninsula draining to the Mediterranean Sea. It drains a basin of 85,000 km^2 forming a complex network (a total of 347 streams), encompassing a variety of climate and land uses (Sabater et al., 2009). The Ebro basin has mostly a Mediterranean climate with continental characteristics, these becoming semi-arid in the center, while climate is oceanic at the western extreme. Long periods of low precipitation are common in the summer and higher rainfall occurs in spring and autumn. The mean water discharge at the Ebro River mouth is 380 $m^3\ s^{-1}$ (average daily data from 1953 to 2008) but is highly variable (382 $m^3\ s^{-1}$, standard error).

The Ebro network is regulated by 187 reservoirs, which store 57% of the mean annual runoff (Sabater et al., 2009). The largest reservoirs are located in the mid-lower part of the main section of the river. The reservoirs of Mequinenza (1534 Mm^3 capacity), Ribaroja (210 Mm^3 capacity) and Flix (11 Mm^3 capacity) account for a total sediment retention of $7\times10^6\ t\ y^{-1}$, less than 1% of the original sediment load reaches the lower Ebro in present days (Batalla and Vericat, 2011). These reservoirs store the water from winter floods and produce increased baseflow in summer (used to irrigation), what reduces water residence time, alter the transport and quality of fine sediments (Vericat and Batalla, 2005), decrease conductivity and remove phosphorus and nitrate (Roura, 2004). All these effects drive to changes in the structure of phytoplankton communities (Sabater et al., 2008). The lower river section is also characterized by high macrophtyes proliferation (Batalla and Vericat, 2009) which compete with phytoplankton for P (Soley, unpublished data).

2.2. Sampling strategy

Twelve sites were sampled in the main mid-lower course of the Ebro River. Six sites (Zaragoza, Pina Ebro, Quinto, Zaida, Sástago, Escatrón) were located upstream of the Mequinenza, Ribaroja and Flix reservoirs, while five (Flix, Ascó, Mora Ebro, Benifallet, Xerta) were downstream and up to 30 km from the river mouth (Fig. 1). The intermediate site of Almatret, in the tail of the Ribaroja reservoir, was also included. At all these sites, water samples for chemical and biological analyses were collected on nine occasions during the hydrological periods from 2008 to 2010 (Fig. 1). Five of these periods were classified as dry periods (water flow $<100\ m^3\ s^{-1}$, at Zaragoza and Escatrón sites), and the other four as wet periods (water flow $>300\ m^3\ s^{-1}$, at the same sites). Daily water flow measurements were provided by the Ebro Basin Authority (CHE). Data were available for 2 sites upstream of the reservoirs (Zaragoza, Escatrón) and 2 below them (Ascó, Xerta) and were used to characterize the hydrological patterns in each river section.

Physical, chemical and biological parameters were analyzed in 300-m long reaches at all the sites. Three surface (5–40 cm depth) water samples per reach were collected 50–100 m apart by submerging 10-L polyethylene buckets held by a rope. Samples were taken from the river bank but reaching always the free water zone. Water temperature, conductivity and dissolved oxygen were determined in situ by means of field meters (Hach, Loveland, USA). Water samples were filtered in the field using portable filtration devices connected to a vacuum pressure pump (Millipore, USA) and supplied by a power generator (Honda, Japan). Low pressure was utilized for plankton filtration in order to prevent cell disruption.

Water was fractioned for chemical analysis and APA measurements, by filtering through Whatman GF/F filters (0.7 μm pore size). The filtrate was assumed to consist mainly of bacterioplankton, the fraction larger than 0.7 to include most phytoplankton and dead particulate material. APA incubations were performed in the non-filtered water samples (total or bulk activity) and in the water samples previously filtered by GF/F (activity <0.7 μm) immediately after sampling. Filtrated water samples and filters for the determination of the carbon (C), nitrogen (N), and phosphorus (P) content (>0.7 and <0.7 fractions) were preserved at 4 °C until they reached the laboratory and stored frozen (−20 °C) until analysis.

Subsamples for chlorophyll-*a* and bacterial density analyses were collected for each replicate water sample. Between 0.3 and 2 L of water per sample was passed through Whatman GF/F filters for chlorophyll-*a* analysis. Water was filtered until clogging. Filters were later wrapped in aluminum foil, preserved at 4 °C until arrival at the laboratory and frozen until analysis. Water samples for bacterial density were first filtered (Whatman GF/F) and 8-mL aliquots were preserved with 1% paraformaldehyde and 0.5% glutaraldehyde (final concentration) and then frozen at −80 °C until quantification.

2.3. Chemical analyses

Dissolved nutrient analysis was performed on thawed water samples that were further passed through Millipore Nylon Membrane filters (0.2-μm pore size) prior to analysis. Nitrate concentration was determined with an ion chromatograph Metrohm 716 Compact IC (Herisau, Switzerland). Ammonia was determined after the addition of sodium salicilate, sodium citrate and sodium nitroprussiate, and read spectrophotometrically at 690 nm (Hach Company, 1992). Soluble reactive phosphorus (SRP) was measured following Murphy and Riley (1962). Total dissolved nutrient concentrations were also estimated. Total carbon included dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) fractions which were measured using a total organic carbon analyzer (TOC-5000 Shimadzu, Japan). Total dissolved N and P were determined after alkaline digestion of the water samples (Grasshoff et al., 1983).