



Shifts of environmental and phytoplankton variables in a regulated river: A spatial-driven analysis

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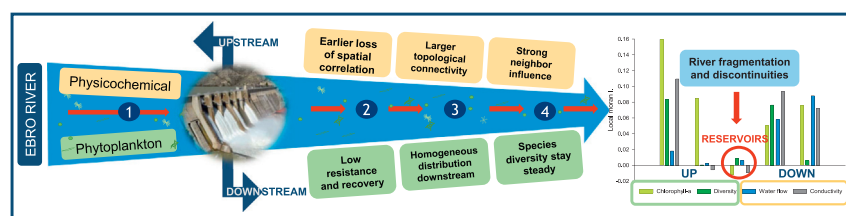
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HIGHLIGHTS

- Phytoplankton community structure and composition do not absorb reservoir impact.
- Phytoplankton and environmental variables show spatial discontinuities and river fragmentation.
- There is a strong neighbor influence on the longitudinal river dynamics of environmental variables.
- An adaptive response of the phytoplankton taxa and rapid colonization of opportunist species after reservoirs is observed.

GRAPHICAL ABSTRACT



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ABSTRACT

The longitudinal structure of the environmental and phytoplankton variables was investigated in the Ebro River (NE Spain), which is heavily affected by water abstraction and regulation. A first exploration indicated that the phytoplankton community did not resist the impact of reservoirs and barely recovered downstream of them. The spatial analysis showed that the responses of the phytoplankton and environmental variables were not uniform. The two set of variables revealed spatial variability discontinuities and river fragmentation upstream and downstream from the reservoirs. Reservoirs caused the replacement of spatially heterogeneous habitats by homogeneous spatially distributed water bodies, these new environmental conditions downstream benefiting the opportunist and cosmopolitan algal taxa. The application of a spatial auto-regression model to algal biomass (chlorophyll-*a*) permitted to capture the relevance and contribution of extra-local influences in the river ecosystem.

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1. Introduction

River networks have an asymmetrical configuration which determines unidirectional physical and chemical processes (Frissell et al., 1986). The imposed downstream direction in environmental conditions greatly determines the biological structure of river (Vannote et al., 1980; Wehr and Descy, 1998), though geomorphological complexity

configures non-linear connections (Delong and Thorp, 2006). So forth, neighboring sites are not independent one from the other, and this can be reflected both in the hydrological and environmental conditions as well as in the composition and relative abundance of biological assemblages (Amoros and Bornette, 2002; Tockner et al., 1999; Ward and Stanford, 1995). This complex pattern is further complicated when hydraulic infrastructures (dams, weirs, channels) occur in the river (Lobera et al., 2017). Largely regulated rivers show alterations of the water regime and its chemical quality, which affect biological assemblages (Dynesius and Nilsson, 1994; Nilsson et al., 2005). The

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regulation capacity of reservoirs is one of the strongest causes for river discontinuity (Ward and Stanford, 1983), but their impact on environmental and biological variables is not necessarily analogous (Bunn and Arthington, 2002). It is unknown yet if the ability to resist regulation effects, and the ability to recover after them, is parallel between ones and the others.

One of the most sensitive elements in large river ecosystems is phytoplankton. The phytoplankton community plays a central role as primary producers in the functioning of large rivers (Dale, 2001; Wehr and Descy, 1998). River phytoplankton occurs as a balance result of the advective forces occurring in flowing waters and the in situ population growth rates (Reynolds, 2006). In this delicate balance, river phytoplankton is affected both by local environmental factors (light and nutrient availability, water temperature, grazing pressure) as well as by the upstream influence of continuous seeding and hydrological and chemical conditions. Here we use the phytoplankton community composition and its associated biomass (planktonic chlorophyll-*a*) as the biological receptors to be tested in the river because of regulation, and compare their changes in structure with those occurring in the environmental variables.

In that context, the Ebro River offers a suitable case study to explore the spatial structure of an ecosystem impacted by man-made perturbation. The Ebro River is one of the largest rivers in the Iberian Peninsula, strongly regulated by dams since the 1940s'. Around 190 dams are spread across the whole basin, impounding 57% of the mean annual runoff (Romaní et al., 2011). The location of the three large reservoirs (Mequinenza, Ribarroja and Flix) in the middle-lower section of the river causes a large disruption to the sites downstream. These reservoirs cause water thermal alteration downstream (Prats et al., 2010), contribute to retain sediments (Batalla and Vericat, 2011), and disrupt the biogeochemical nutrients cycles and the phytoplankton community structure (Sabater et al., 2008; Tornes et al., 2014). Since the basin is subjected to multiple human activities which produce impacts like inorganic and organic pollution and water abstraction (Batalla et al., 2004; Lacorte et al., 2006; Navarro-Ortega and Barceló, 2011), effects might be complex on both water quality and phytoplankton assemblages. The size and position of these reservoirs offer a good setting for the analysis of the phytoplankton and environmental variables responses to the impact, showing in which way their respective spatial patterns differ or resemble.

In order to do so, we apply an analogous approach to that used on trophic webs and metapopulations analysis, able to deal with complex systems in which different constituents ("nodes") interact ("links") to each other (Nordstrom and Bonsdorff, 2017; Wallach et al., 2017). We use this as starting point to capture the river topology and connections among neighboring nodes, where variables were measured (monitoring sites) and the anthropogenic effects on this arrangement were evaluated by using appropriate tools commonly used in the spatial analysis (Fischer and Wang, 2011; Ginebreda et al., 2018). Whereas either time or spatial data series could be in principle equally used in autocorrelation modeling of phytoplankton indicators, their performance depends on (a) the connectivity and heterogeneity of the area under study, (b) the spatial and temporal scales of the variable considered and (c) the easiness of monitoring. Spatial autocorrelation works better on heterogeneous environments, and its analysis takes into account the connectivity (Dakos et al., 2010). On the other hand, the timescales that govern phytoplankton succession (weeks) require of an extensive monitoring effort far beyond the one required for a spatial study. Based on that, the spatial analysis approach is a convenient alternative to time series when available data are not sufficiently complete. In this paper we implement a method to analyze and compare the spatial patterns of environmental and biological variables in rivers systems submitted to regulation. The identification of 'stability' properties (resistance and resilience), and thus, the interpretation in terms of connectivity and longitudinal patterns are aimed to test the hypothesis that regulation produces uncoupled responses on the environmental and

phytoplankton variables, further compromising the ability of phytoplankton community to resist and recover. While the longitudinal dynamics of environmental variables supposedly has a strong neighbor influence, the response of phytoplankton is likely more complex as a result of conjoint local and extra-local influences. The spatial dimension may then provide understanding on how the different elements of river ecosystem respond to regulation.

2. Material and methods

2.1. Study area

The Ebro basin is located in the Northeastern part of the Iberian Peninsula occupying a total surface of 85,362 km². The main river is 910 km length and flows from the Cantabrian mountains to the Mediterranean sea (Romaní et al., 2011). In the Ebro mainstream there is a system of three consecutive large reservoirs, Mequinenza (1500 × 10⁶ m³), Ribarroja (210 × 10⁶ m³) and Flix (11 × 10⁶ m³) that regulate the hydrology of the lower part (Prats et al., 2010). These reservoirs cause major changes in the hydromorphological dynamics by altering floods peaks (López-Moreno et al., 2002) as well as by retaining sediments (Buendia et al., 2016).

2.2. Data collection

For this study we used data from several published studies (Artigas et al., 2012; Sabater et al., 2008; Tornes et al., 2014), as well as public data from the Confederación Hidrográfica del Ebro webpage (<http://www.chebro.es>). Using these sources, we selected data from twelve sites located in the mid-lower course from Zaragoza to the proximity of the river mouth (Fig. 1). Six of the sites (Zaragoza, EB01; Pina Ebro, EB02; Quinto, EB03; Zaida, EB04; Sástago, EB05; Escatrón, EB06) were located upstream of the Mequinenza, Ribarroja and Flix reservoirs. One site (Almatret, EB07) was placed between the first two dams, and the remaining five (Flix, EB08; Ascó, EB09; Móra d'Ebre, EB10; Benifallet, EB11; Xerta, EB12) were located downstream to the reservoirs.

We collected some data on abiotic and biotic variables to characterize the ecosystem response to regulation. Regarding biological variables, we used metrics on the phytoplankton biomass (biovolume and chlorophyll-*a* concentration) and community structure (Shannon-Wiener diversity, cell density). Both biovolume and chlorophyll-*a* concentration have been used as surrogate of biomass (Hillebrand et al., 1999); while the Shannon diversity index (*H'*) characterizes the taxonomic diversity in a community. The selected physical and chemical variables included water temperature, conductivity, water flow and nutrients. NH₄⁺ and NO₃⁻ were considered together as dissolved inorganic nitrogen (DIN), comparable to, soluble reactive phosphorus (SRP), Dissolved Inorganic Carbon (DIC), Dissolved Organic Carbon (DOC) and Dissolved Organic Nitrogen (DON).

Phytoplankton and environmental data covered eighteen sampling campaigns between 2008 and 2013. The dataset included samples from different hydrological conditions, low waters and high water periods, occurring in the river (Artigas et al., 2012). Therefore, the data we used accounted for 350 km of the main river axis over 5 years (Table S1a and b).

2.3. Data analysis

The sequence of analysis is summarized in Fig. 2. Briefly, the stress effect of reservoirs into phytoplankton was analyzed by means of two stability properties, i.e., resilience and resistance (Grimm and Wissel, 1997). These are dynamic properties largely dependent on the connections of the ecosystem (Pimm, 1984); resilience is the capacity of the system to return to a reference state after a disturbance, while resistance refers to staying essentially unchanged despite the perturbation

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