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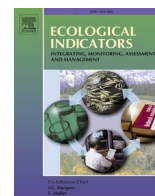
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## Original Articles

## Ecological consequences of consecutive river damming for three groups of bioindicators

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## ABSTRACT

We studied three commonly used bioindicator groups: phytoplankton, phytobenthos and benthic invertebrate communities' structure patterns in transitions between lotic and lentic habitats as consequences of two consecutive large dams constructed in the early twentieth century on the intermediate reach of a lowland river in Normandy (NW, France), the Selune. According to sampling station position along the river, including two in the two reservoir lakes, we defined three sorts of transitions, from upstream to downstream: lentic to lotic transition (hereafter len-lot), lentic to lentic transition (hereafter len-len), within the two reservoir lakes, and lentic to lotic transition (hereafter len-lot).

Lot-len transition, imposed by damming, and the recovery of lotic character of the river afterward dams, promoted different diversity patterns for the studied organisms' groups. Phytobenthos'  $\alpha$  diversity significantly increased in the len-lot transition, and the highest  $\beta$  diversity score was observed in the lot-len. Both, habitat conditions and spatial controls drove phytobenthos community structure. Benthic invertebrate community was mainly shaped by habitat conditions. Invertebrate's  $\alpha$  diversity significantly changed in the lot-len and len-lot transitions, with the  $\beta$  diversity score being the highest in the lot-len transition. Community's traits composition of invertebrates best fitted predictions on lotic- and lentic- type communities. Phytoplankton's  $\alpha$  diversity remained unchanged in the transitions and subsequently  $\beta$  diversity scores were low.

According to the results, we proposed three classes of organisms based on their response to river damming: i) organisms indifferent or tolerant to dams effect, like phytoplankton communities in this study, that were neither hampered by changes in water flow velocity, and did not display dispersal limitation neither; ii) organisms sensitive to habitat conditions shift but not limited in their dispersal capacity by the dam, like benthic invertebrates and phytobenthos in this study. Benthic invertebrate community and phytobenthos communities differed in their response likely due to their differential dispersal capabilities and niche breadth; iii) organisms limited in their dispersal by the dam, not represented in this study.

Riverine organisms best tracked transitions, while  $\beta$  diversity assessment revealed as the most useful metric to disentangle the relative contribution of dispersal limitation or habitat modification provoked by multiple dams.

### 1. Introduction

The River Continuum Concept proposes a framework for unregulated, free-running rivers, in which biological communities are structured as a function of longitudinal connectivity. Biological communities

are functionally linked by the materials non-consumed by the upstream communities and drifted downstream (RCC; Vannote et al., 1980). RCC predicts that diversity score peaks at intermediate order river reaches, and plankton develops in lowland river reaches (Vannote et al., 1980; Fig. 1A). However, the fragmentation of rivers by dams alters flow

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regime and discharge patterns, modifying thermal regimes and degrading habitats, thus altering ecological processes and native river diversity (Turgeon et al., 2019). Damming is a pervasive disturbance of lotic ecosystems worldwide and nearly 58,000 dams over 15 m height or impounding >3 million cubic meters are listed (ICOLD, 2020). The Serial Discontinuity Concept (SDC) modifies RCC predictions by considering abrupt lentic-lotic transitions when a river is dammed (Stanford and Ward, 2001). According to SDC, impoundments along river courses may cause the shift of river abiotic and biotic parameters towards headwaters or seaward conditions depending on the magnitude of the perturbation (Fig. 1A), but also on the location of the impoundment along the river profile (Poole, 2002).

The effect of such barriers on aquatic organisms in regulated rivers has been repeatedly reported for fishes (Turgeon et al., 2019) and invertebrates (Vinson, 2001). Additional dispersal alterations may also occur for primary producers: phytoplankton (Heino et al., 2015b; Qu et al., 2018), diatoms (Liu et al., 2013) and macrophytes (Jones et al., 2020).

In the present work, we studied community structure patterns of aquatic communities in multiple habitat transitions (lotic-lentic, lentic-lentic and lentic-lotic) as consequences of two consecutive large dams constructed in the early twentieth century on the intermediate reach of a lowland sixth order river. We focused on three different taxonomic groups with markedly different habitat requirements, dispersal capacities and functional roles. We aimed to study which of the selected groups better tracked ecological transitions in multi-dam systems in order to use it as an useful bioindicator. The first two groups are primary producers: phytoplankton, accounting for up to the half of the total primary production in aquatic ecosystem (Litchman & Klausmeier, 2008) and phytobenthos conforming biofilms, in which diatoms is one of the most important contributor to biodiversity in streams (Kelly et al., 2008). The third group comprises benthic invertebrates, which includes for both primary and secondary consumers. These 3 groups are recurrently used in bioassessment of aquatic ecosystems and their value as bioindicators of ecological state has widely demonstrated (Birk et al., 2012). But ecological consequences of multi-dam systems on the community structure of these three taxonomic groups have been seldom addressed in scientific literature.

Metacommunity theory depicts two main forces structuring

communities. Species sorting refers to environmental filtering driving community dissimilarity, and it is reflected by a gradual adaptation of instream communities to biotic interaction and the physico-chemical variables gradient along the river course, as predicted by the RCC. It is complemented by effective short-distance dispersal, the spatial contribution to community dissimilarity. Making that at reach-scale, closer communities are more ecologically similar than distant ones. Both, species sorting and dispersal, drive community structure promoting increases in  $\beta$  diversity, but their relative importance is expected to be altered in dammed rivers. This is firstly due to artificial dispersal limitation and to the abrupt changes in ecosystem conditions, from lotic to lentic conditions and from lentic to lotic again in the tailwaters, and secondly to specific dispersal capacity of each taxonomic group and their differential sensitivity to alterations (Astorga et al., 2012; Heino et al., 2015a). A higher contribution of nestedness component of  $\beta$  diversity denotes a pattern of species subset within richer and poorer sites due to species dispersal limitation and/or species response to abrupt environmental changes, while gradual environmental filtering is linked to species replacement, species turnover component of  $\beta$  diversity (Soininen et al., 2007).

We first hypothesized (H1) that the  $\alpha$  diversity pattern of the riverine organisms (macroinvertebrates and phytobenthos) greatly differs to phytoplankton  $\alpha$  diversity pattern due to consecutive damming (Fig. 1A; Table 1). Habitat modification from lotic to lentic conditions should limit riverine organism development, while favour phytoplankton. Furthermore, dams likely limit the dispersion of riverine organisms, while phytoplankton dispersion is not expected to be hampered by dams. According to SDC (Stanford and Ward, 2001; Ellis and Jones, 2013) consecutive dams (len-len transition) should additionally hamper riverine organisms dispersion. We expected that riverine organisms'  $\alpha$  diversity rises and recovers the level predicted by RCC, according to its longitudinal position, after the lentic to lotic transition. On the other hand, we expected that phytoplankton diversity drops (Fig. 1D), although drift from reservoirs assures higher diversity score than expected in unregulated river.

In dammed rivers, both dispersal limitation and dramatic shifts in habitat conditions occur, and the key question is how spatial or environmental forces control local communities shaping. So, concerning  $\beta$  diversity, we predicted (H2) that in the lotic-lentic and in the lentic to

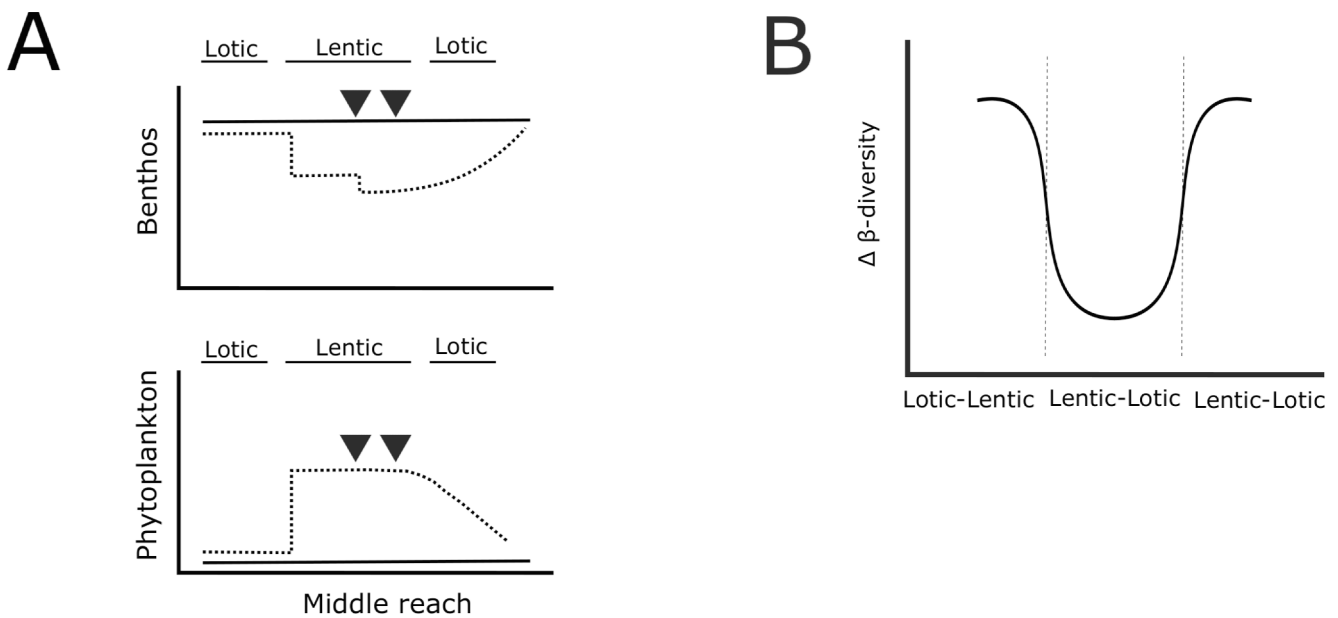


Fig. 1. A) First hypothesis prediction (dashed line): consecutive reduction of benthic organisms' diversity and increase of phytoplankton diversity due to the presence of two consecutive dams. Solid lines denote expected values according to RCC and inverted black triangles denote dams. B) Second hypothesis predictions:  $\beta$  diversity shifts in the lotic-lentic, lentic-lentic and lentic-lotic transitions.

**Table 1**

Summary of hypothesis and predictions of community patterns. Hypothesis 1 and 2 pay directly attention to diversity patterns in transitions and hypothesis 3 deals with community trait composition opposing lotic and lentic habitats.

		Lot-Len	Len-Len	Len-Lot
H1:	$\alpha$ diversity pattern in transitions greatly differs among phytoplankton and riverine organisms (phytobenthos + macroinvertebrate)			
	$\alpha$ diversity	Riverine organisms	Drop	Slight reduction
		Phytoplankton	Rise	No-change
H2:	Lot-Len	Len-Len	Len-Lot	Recovery to predicted by RCC
	• High $\beta$ diversity	• Low $\beta$ diversity	• High $\beta$ diversity (Lower increase of $\beta$ diversity in the case of phytoplankton)	Gradual drop
	• $\beta_{\text{nestedness}}$ priority	• $\beta_{\text{turnover}}$ priority	• $\beta_{\text{nestedness}}$ priority	
H3:	Traits proportions in community reflect the changes between lotic and lentic conditions			
	Lotic conditions (reduced in lentic environments):			
Benthic Diatoms	<ul style="list-style-type: none"> <li>• Pad attachment</li> <li>• Small size classes</li> <li>• Functional groups: low profile and motile</li> <li>• Solitary cells</li> </ul>			
Macroinvertebrate	<ul style="list-style-type: none"> <li>• Preferences: Medium to fast current Blocs and root substrate</li> <li>• Trophic guilds: Scrapers, shredders and other litter decomposers</li> </ul>			
Phytoplankton	<ul style="list-style-type: none"> <li>• Reynold's functional groups: D or J depending on turbidity</li> </ul>			

lotic transitions,  $\beta$  diversity will be high due to the  $\alpha$  diversity shifts predicted in our first hypothesis (Fig. 1B; Table 1). It is noteworthy that according to our first hypothesis, we expected for phytoplankton relatively low  $\beta$  diversity scores in len-lot because of phytoplankton drifting from the upstream reservoirs would homogenize community's composition in the reservoir and in the tailwaters (Fig. 1B; Table 1). Furthermore, we expected that nestedness  $\beta$  diversity component would rule over the turnover component in lot-len and len-lot transition due to abrupt change in habitat conditions and the barrier to dispersion that these sharp transitions represent. On the other hand in the len-len transition, we hypothesized that  $\beta$  diversity would be low, since no big  $\alpha$  diversity shifts are expected according to H1 (Fig. 1A). In this transition, we expected that turnover component  $\beta$  diversity gain importance because habitat conditions are quite similar between the two reservoirs and changes in  $\beta$  diversity would depend mainly on species substitution.

Trait-based approach offers a mechanistic alternative to taxonomy-based synecology studies that likely better characterizes habitat conditions (Statzner et al., 2004; Wu et al., 2019). We therefore hypothesized (H3) that the proportions of traits in communities will reflect straightforwardly the changes between lotic and lentic conditions (Table 1). Thus, we expected that the following traits would be selected in lotic habitats and would diminish significantly in lentic habitats: traits conferring capabilities to resist shear stress and flushing for benthic diatoms communities (Passy, 2007; Rimet and Bouchez, 2012); traits denoting preferences for medium to fast current velocity and for substrates like blocs and roots, and also trophic guilds linked to coarse plant material and phytobenthos feeding resources for invertebrates; and finally for phytoplankton, functional groups typical of shallow enriched habitats, also tolerant to flushing and turbidity (Reynolds et al., 2002; Table 1).

## 2. Material and methods

### 2.1. Geographical context and river description

The Selune River is located in Normandy (NW, France), in a temperate oceanic climate region. Average annual precipitation in the area is 800 mm (Saint-Hilaire-du Harcouët meteorological station, data from 1934 to 1989), evenly distributed throughout the year, being the rainiest month December (98.3 mm) and the driest July (55.2 mm). Mean annual temperature is 10 °C with an observed narrow temperature amplitude between winter (4.2 °C) and summer (16.6 °C). The river's source is located at 116 m asl, and after 91 km of gently slope

watercourse it runs into the Mont Saint Michel Bay after draining a watershed of 1,106 km<sup>2</sup>, mainly composed of schists and metamorphic rocks (Fig. 2A). The Selune River Basin lies in a patchy landscape with forests, pastures, and traditional extensive livestock farming.

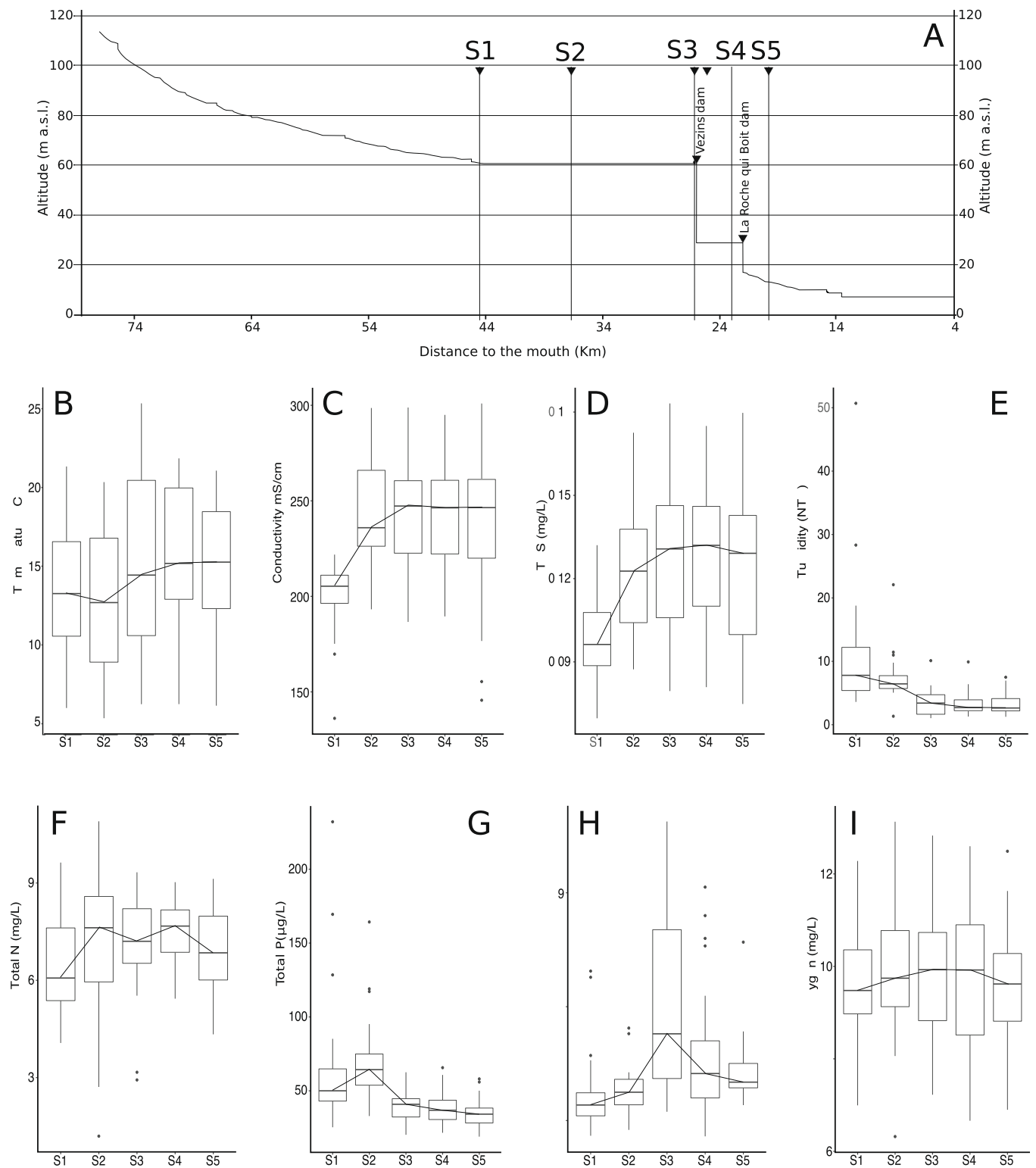
In 1919 a first hydropower dam, the Roche-qui-Boit Dam (16 m height), was built 26 km away from the Selune's mouth followed in 1932, by a second hydropower dam, the Vezins Dam (36 m height) located 4 km upstream. Vezins' water releases ran directly into La-Roche-qui-Boit Dam's reservoir, therefore conforming one continuous impoundment section in the river course of nearly 17 km long (Fig. 2A).

### 2.2. Sampling set-up and protocol

Five sampling stations were established. A first lotic station was located nearby the city of Saint-Hilaire-du-Harcouët (48° 34' 54.6''N, 1° 05' 35.44''W; from here on called S1) upstream all reservoirs. A second one was located in the upstream tail of the Vezins Dam reservoir at the Pont de la Republique (48° 33' 53.9''N, 1° 09' 2''W; from here on called S2), corresponding to a riverine or transitional zone still influenced by stream inflow. A third one, a lentic station, was located in the lake in the deepest part of the Vezins Dam's reservoir, just upstream the dam (48° 34' 36.9''N, 1° 13' 57.6''W; from here on called S3). The fourth station was located in the deepest part of the Roche-qui-Boit Dam's reservoir about 3 km downstream from S3 (48° 35' 58.3''N, 1° 15' 4.9''W; from here on called S4) and less than 1 km upstream the dam. Finally, a fifth lotic station, 4 km downstream the second dam, located nearby Signy's bridge (48° 35' 44.9''N, 1° 17' 35.9''W; from here on called S5). The water depth in the two river stations, S1 and S5, is fully wadable. For further details on sampling stations about morphological and physico-chemical characteristics see Fig. 2.

### 2.3. Physicochemical parameters

In the field, water chemistry was recorded monthly from September 2014 to October 2017 (except from December 2016 to February 2017) using a multiprobe Idronaut (Idronaut Ocean Seven 316Plus CTD, Milan, Italy) to assess temperature (°C), electrical conductivity ( $\mu\text{S}\cdot\text{cm}^{-1}$  corrected to 25 °C), dissolved oxygen content (% and  $\text{mg}\cdot\text{L}^{-1}$ ), turbidity (NTU), pH and TDS ( $\text{mg}\cdot\text{L}^{-1}$ ). The measures were taken in a continuous way from the bottom to the surface every 0.001 s. For the purpose of this work, for any given parameter all the measured values from the surface to 2 m depth were averaged in one single value by date. Furthermore, water samples were gathered at 1 m from surface in all stations and for



**Fig. 2.** A) Selune's river profile including dams and sampling stations positions (modified from [Artelia 2012](#)). B to I figures show box-plots (median + percentiles) of temperature, conductivity, total dissolved solids, turbidity, total N load, total P load, pH and Oxygen content respectively, measured in each sampling station.

deeper stations (S2, S3 and S4), at the euphotic depth (determined as 1% of Photosynthetic Active Radiation or PAR). Water was filtered (GF/C, 1.2 µm pore size, Whatman™, Maidstone, UK) in the field and kept chilled until stored at -20 °C at the lab until their analysis, except those dedicated to total nitrogen and total phosphorus analysis that were not filtered. Once at the lab, the nutrient contents total dissolved nitrogen (DN\_tot), total dissolved phosphorous (DN\_tot), nitrate (N\_NO3),

orthophosphate (P\_PO4), total nitrogen (TN\_Ntot) and total phosphorous (TP\_Ptot) were measured using an automated discrete photometry analyzer (Gallery™, Thermo Fisher Scientific, Waltham, USA) based on standard colorimetric methods.

## 2.4. Phytobenthos

Phytobenthos was collected four times in June and September 2015 and 2016 from artificial substrates placed in the middle of the river: glass slides (dimensions 30 cm × 10 cm) were left incubated for a month in the river, maintained vertically inside a perforated plastic box for fruit transportation, therefore allowing the water through-in flow. The plastic box was either fixed to the bottom of the Selune River (S1, S5), or fixed to buoys and placed one meter below the surface in the dams (S2, S3 and S4).

After one month of colonization, glass slides were removed from water and one of them, randomly selected, was scrapped with a razor blade to gather all the phytobenthos: each sample was then fixed in the field with lugol solution and stored in the dark at 4 °C until analysis. In the laboratory, phytobenthos' taxa identification and counting (individuals/cm<sup>2</sup>) was realized using a Nageotte counting chamber under an upright microscope (DM4000B, Leica Microsystems; at x630 magnification). Diatoms were identified and counted by the Bi-Eau consultancy (Angers, France). At least 400 individuals per sample were enumerated and identified to species taxonomic level in most of the cases.

Once the taxonomic list was established, we assigned traits values to each diatom taxa according to Rimet and Bouchez (2012), whenever the information was not available for a given taxa in the aforementioned publication we used Diatoms of North America data base (<https://diatoms.org/>), and sister species traits. From Rimet and Bouchez's (2012) work, we retained only the traits that potentially may be affected by current transitions: biovolume ( $\mu\text{m}^3$ ) with 5 size ranges (<100  $\mu\text{m}^3$ , 100–299  $\mu\text{m}^3$ , 300–599  $\mu\text{m}^3$ , 600–1499  $\mu\text{m}^3$ , >1500  $\mu\text{m}^3$ ), substrate attachment with 3 categories (non-attached, pad and stalk), coloniality with two categories (solitary and colonial) and functional guild with four categories (High profile, low profile, motile and planktonic).

## 2.5. Benthic macroinvertebrates

Benthic macroinvertebrates were sampled using a Surber net sampler (0.05 m<sup>2</sup>, 0.5 mm mesh size) in October 2014, April and October 2015 and April 2016. Twelve samples per station and date were gathered in the field, sampling in a stratified manner every representative habitat occurring at the station following the standardize protocol NF T 90-333 for sampling benthic invertebrates in wadable streams to assess river quality according to Water Framework Directive (2000/60/EC). We adapted the protocol to deeper stations (S2, S3 and S4) by sampling always at wadable depth (~1m) nearby the shore. Samples were fixed in the field with 96° ethanol and stored until they were sorted under a binocular microscope and identified to species or genus level (most crustaceans and Insect larvae), except for Nematoda, Hydracarina (not identified further), and most Diptera (identified to the Family/tribe levels). We gathered 240 samples but only 202 were sorted because 38 samples were lost. Between 12 and 9 samples were analyzed for any sampling stations at any given date, except for S3 in September 2015 where only 8 samples were analyzed.

Once the taxonomic list was established, we assigned traits values to each invertebrate taxa according to Tachet et al. (2000). Whenever the taxonomic resolution between our list and the Tachet et al.'s data base did not match, we used the immediately upper taxonomic resolution level that matched with Tachet et al.'s work. Only the following traits were retained according to their potential sensitivity to transitions between lotic and lentic conditions: longitudinal distribution along the river course, substrate preference, water current preference, maximal body size and feeding habits (further information on traits categories is available in Usseglio-Polatera et al., 2000a; Usseglio-Polatera et al., 2000b).

## 2.6. Phytoplankton

Phytoplankton was collected monthly simultaneously to water for physico-chemistry assessment and preserved in acid Lugol. Identification to species level in most cases and counting were conducted under an optical microscope (400 ×) using a Nageotte chamber (Booth, 1993). At least 400 individuals per sample were counted (ind/mL). In the stream stations, S1 and S5, only one sample per month was gathered. In the lakes sampling stations, namely S2, S3 and S4, two samples were gathered (1 m from the surface and one from euphotic depth) and combined into one single sample for statistical analysis. Once the taxonomic list was established, taxa were assigned to morpho-functional groups according to Padisák et al. (2009) and Reynolds et al. (2002) classifications.

## 2.7. Data analysis

In order to quantify  $\alpha$  diversity changes among stations, we used rarefaction/extrapolation curves based on Hill's numbers, namely species richness, and the inverse of Simpson concentration. These diversity estimators allow for an unbiased comparison of effective number of taxa (Chao et al., 2014).

We also explored variation in community composition and structure among stations paying particular attention to transitions in flow regime between subsequent stations. Firstly, the relevance of environmental conditions shaping communities was tested for the three groups. Due to the different nature of data, replicated sampling for macroinvertebrate for any given date vs. single sample by date and station for phytoplankton and phytobenthos, two different analytical procedures were applied. In the case of phytoplankton and phytobenthos data, a db-RDA was performed on Bray-Curtis dissimilarities (Legendre and Anderson, 1999) with a forward variables selection by permutation procedure (Blanchet et al., 2008). A subsequent variance partitioning analysis was also performed on selected variables. Prior to db-RDA, abundances of phytoplankton and phytobenthos were  $\ln(x + 1)$  transformed to reduce the weight of superabundant taxa upon the analysis. The environmental matrix in the analysis included the aforementioned physicochemical measured variables plus Date, Year, Station and Season factors. In the case of phytobenthos analysis, because glass tiles were in the water for one month, we integrated the physicochemical conditions during the phytobenthos development averaging the physicochemical variables from the month where sampling took place and the month before.

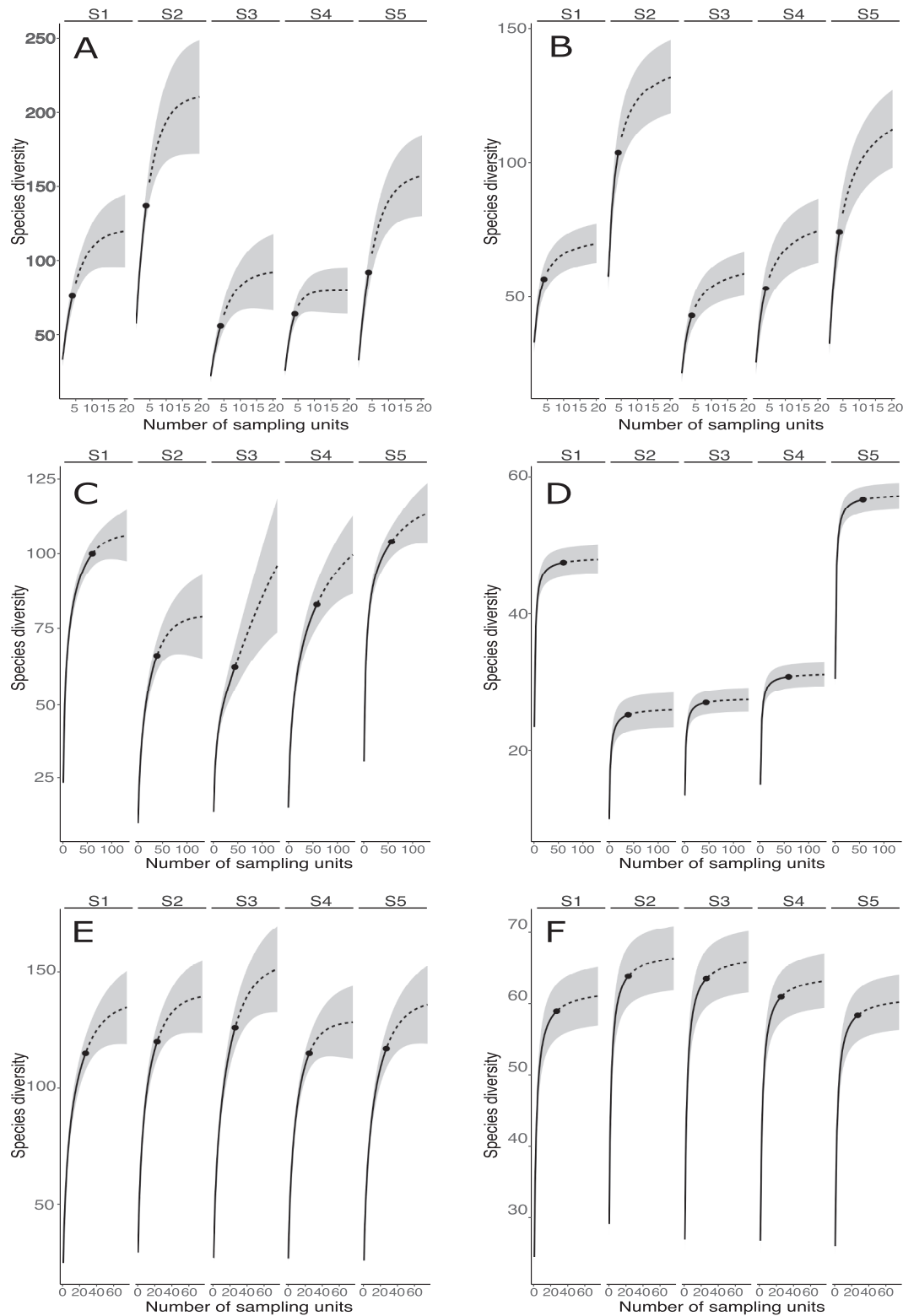
In the case of macroinvertebrates, much less sensible to slight variations in chemical water conditions than algae, and according to small differences in physicochemical variables between stations (Fig. 2), data were analyzed by means of a PERMANOVA (Anderson, 2001) with 999 permutations, on Bray-Curtis dissimilarities. The following factors were included in the analysis: Station (5 levels: S1, S2, S3, S4 and S5), Substrate (9 levels: Block, cobble, gravel, leaf-litter, silt, macrophyte, root, sand and mud) and their interaction. Prior to Bray-Curtis calculations, macroinvertebrate abundance matrix was  $\ln(x + 1)$  transformed to reduce the weight of superabundant taxa upon the analysis. Additionally, a NMDS on Bray-Curtis dissimilarities was performed to graphically show differences between the communities considering the analyzed factors.

Dealing with variation in community composition among station, we estimated total  $\beta$  diversity as the Sørensen dissimilarity ( $\beta_{\text{sor}}$ ), and its partition between turnover, measured as Simpson dissimilarity ( $\beta_{\text{sim}}$ ), and nestedness ( $\beta_{\text{sne}}$ ) components, measured as the difference between  $\beta_{\text{sor}}$  and  $\beta_{\text{sim}}$  on occurrence data (Baselga, 2010). Therefore, the aim was to assess whether the community composition in a given station resulted mostly from a subsampling of the community occurring in the upstream station, or otherwise the contribution of taxa replacement due to hydrological conditions shift was more important. We also estimated Whittaker  $\beta$  diversity as an absolute score for each station. It considers the proportional relationship between  $\gamma$  and  $\alpha$  diversities.



For each trait, abundances of all categories within the given trait were analyzed by a nonparametric factorial data analysis using aligned rank transformation (Wobbrock et al., 2011). For representation purposes we used relative proportion of each category within the given trait.

We used R software (R Core Team, 2019) for statistical analysis and plotting data. The following packages were used: vegan (Oksanen et al., 2019), iNEXT (Hsieh et al., 2019), betapart (Baselga et al., 2018), ARTool (Kay and Wobbrock, 2014) and ggplot2 (Wickham, 2016).



**Fig. 3.** Hill's numbers estimate of  $\alpha$  diversity, including assessed scores on actual values (solid line), projections (dotted lines) and 95% confidence interval (shaded area). A-B phyto-benthos, C-D benthic invertebrates and E-F phytoplankton. S1, S2, S3, S4 and S5 denote sampling stations from the most upstream station towards the most downstream station. A, C and E show species richness, and B, D and F show inverse Simpson concentration.

### 3. Results

#### 3.1. Community patterns in flow regime transitions

##### 3.1.1. $\alpha$ diversity patterns

In the lot-len transition macroinvertebrate's  $\alpha$  diversity significantly dropped, but there was not significant changes for phytobenthos and phytoplankton  $\alpha$  diversity (Fig. 3). In the len-len transition no significant change was observed (Fig. 3). In the len-lot transition phytobenthos and macroinvertebrate  $\alpha$  diversity significantly increased after the impoundment but phytoplankton's  $\alpha$  diversity did not change significantly (Fig. 3). Phytobenthos diversity peaked in the transitional station (S2), but did not differ significantly from S5 station, downstream the last dam (Fig. 3A-B). For macroinvertebrates, lentic stations (S2, S3 and S4) harboured the lowest diversity scores (Fig. 3D). For phytoplankton, all the stations exhibited a comparable diversity, the two stations located in the Vezins Reservoir, S2 and S3, being the most diverse (Fig. 3E-F).

##### 3.1.2. $\beta$ diversity patterns

Phytobenthos  $\beta$  diversity was the highest in the lot-len transition (Tables 2 and 3), reaching to 79% of non-shared species among S1 and S3 station, and followed by benthic invertebrates with 38% of non-

**Table 3**

Whittaker's  $\beta$ diversity scores for each station, showing how many times  $\gamma$  diversity is higher than  $\alpha$  diversity.

	S1	S2	S3	S4	S5
<b>Phytobenthos</b>	2.92	1.62	3.96	3.47	2.41
<b>Invertebrates</b>	1.24	1.88	2.07	1.53	1.19
<b>Phytoplankton</b>	1.36	1.30	1.23	1.36	1.33

shared species and only 19% for phytoplankton (Table 2).  $\beta$  diversity decreased in the len-len transition (S3-S4) for phytobenthos and benthic invertebrate, 45 and 28 % respectively, and remains low for phytoplankton (12%). Phytobenthos exhibited the highest non-shared species rate in the len-lot transition (51%), while  $\beta$  diversity slightly decreased for macroinvertebrate and phytoplankton (Table 3). For phytoplankton, co-occurring species accounted for >80% of the total recorded species

**Table 2**

Sorensen  $\beta$  diversity scores for all pair wise comparisons among sampling stations and  $\beta$  diversity partition between turnover and nestedness components.

	$\beta$ Sorensen				Turnover				Nestedness						
	S2	S3	S4	S5	S2	S3	S4	S5	S2	S3	S4	S5			
<b>Phytobenthos</b>	S	0.5	0.7	0.7	0.6	S	0.3	0.7	0.7	0.5	S	0.1	0.0	0.0	0.0
	1	2	9	9	2	1	3	5	7	8	1	9	4	2	4
	S		0.7	0.6	0.5	S		0.5	0.4	0.4	S		0.1	0.1	0.1
	2		3	7	3	2		4	8	2	2		9	9	1
	S			0.4	0.5	S			0.4	0.4	S			0.0	0.1
3			5	8	3			1	5	3			4	3	
S				0.5	S				0.4	S				0.1	
4				1	4				0	4				1	
<b>Invertebrates</b>	S	0.2	0.3	0.2	0.1	S	0.1	0.1	0.1	0.1	S	0.1	0.2	0.0	0.0
	1	8	8	6	4	1	1	5	8	5	1	9	1	9	2
	S		0.3	0.2	0.2	S		0.1	0.1	0.1	S		0.0	0.0	0.2
	2		5	9	6	2		1	3	4	2		3	8	1
	S			0.2	0.3	S			0.0	0.0	S			0.1	0.2
3			8	5	3			8	9	3			3	3	
S				0.2	S				0.1	S				0.1	
4				2	4				5	4				1	
<b>Phytoplankton</b>	S	0.1	0.1	0.1	0.1	S	0.0	0.1	0.1	0.1	S	0.0	0.0	0.0	0.0
	1	3	9	8	6	1	9	7	7	2	1	2	4	0	1
	S		0.1	0.1	0.1	S		0.3	0.2	0.0	S		0.0	0.0	0.0
	2		3	5	5	2		2	1	5	2		2	2	1
	S			0.1	0.1	S			0.1	0.1	S			0.0	0.0
3			2	2	3			5	2	3			4	3	
S				0.1	S				0.1	S				0.0	
4				6	4				1	4				1	



across all the transitions.

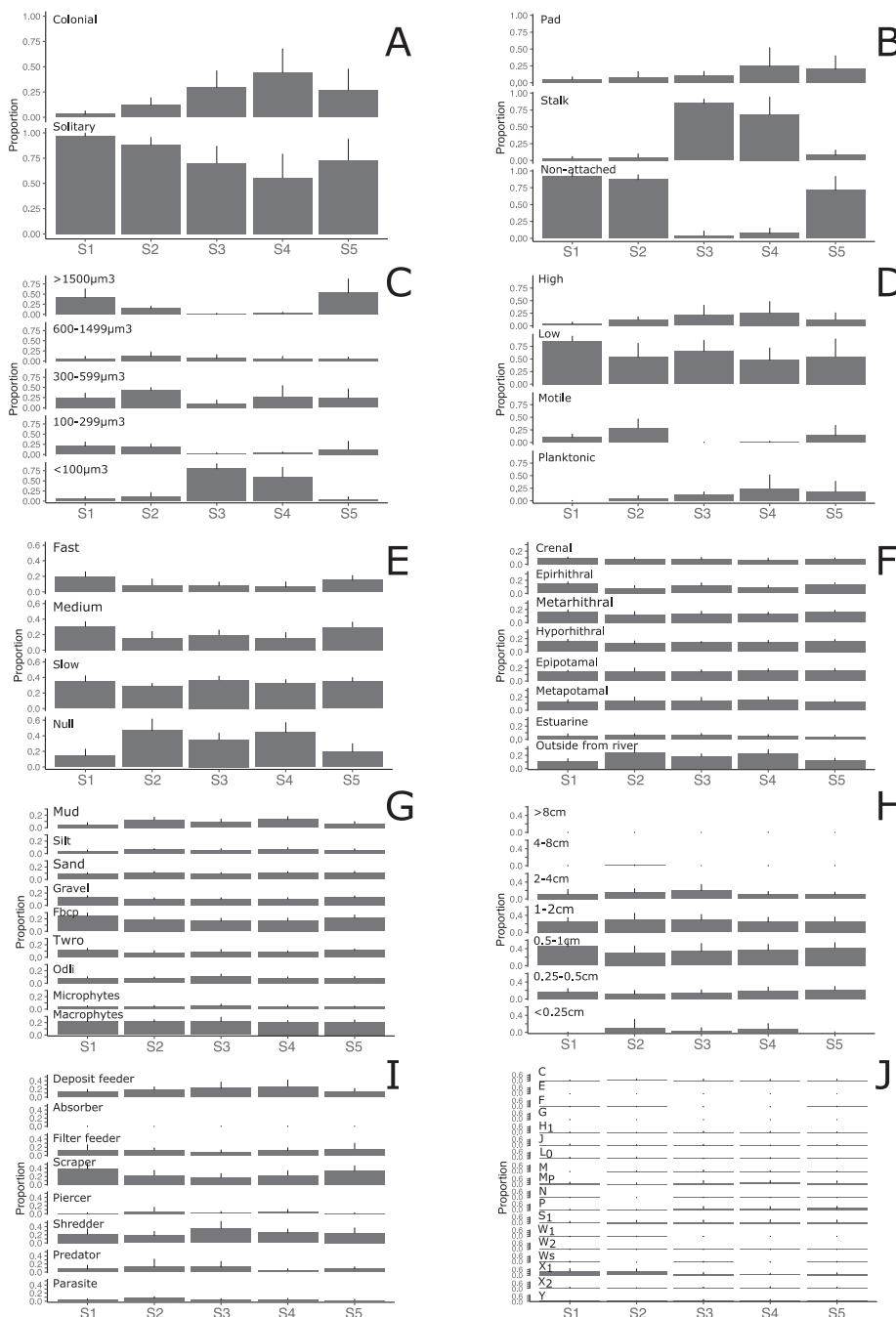
Nestedness  $\beta$  diversity component contributed the most to  $\beta$  diversity in the lot-len transition for benthic invertebrate (Table 2). On the contrary, turnover was the dominant component for phyto-benthos and phytoplankton for the same transition (Table 2). In len-len, species replacement dominated  $\beta$  diversity partition, but it is noteworthy that nestedness contributed with up nearly 50% and to 25–30% to  $\beta$  diversity partition for invertebrate and phyto-benthos respectively (Table 2). In the len-lot transition, both  $\beta$  diversity components contributed equally for invertebrates, but turnover overruled nestedness for phyto-benthos and phytoplankton (Table 2).

### 3.1.3. Community structure

For phyto-benthos, the best model explaining community structure (taxonomic composition and relative abundances) retained Station, Date

and Total Phosphorus variables ( $df = 8, F = 3.0, p = 0.001$ ). It expressed nearly 47% of the total squared distance among samples. Station factor explained 22% of the total variation and shared and additional 10% of the variation with Total Phosphorus content. Another 11% of the variation was explained by Date factor (Supplementary document 1).

For benthic invertebrate, PERMANOVA analysis showed that Station, Substrate type factors and their interaction significantly explained 42% of the macroinvertebrate community differences (Station  $df = 4F = 21.68p = 0.001$ ; Substrate  $df = 8F = 2.61p = 0.001$ ; Station  $\times$  Substrate  $df = 16F = 1.49p = 0.001$ ). And more precisely, more than half of this variability was explained solely by Station factor (27%). Pair-wise comparisons showed significant differences in  $\beta$  diversity among every comparison considered, namely lot-len: S1 vs S2 and S3, len-len: S2 vs S3 and S3 vs S4 and len-lot: S4 vs S5. Such a difference is graphically shown in Supplementary doc 2.



**Fig. 4.** The figure shows mean + se values of species' traits expressed as proportions for graphical purpose. Trait's modalities are shown in each graph. A-D figures show phyto-benthos' traits according to Rimet and Bouchez's (2012): coloniality (A), substrate attachment type (B), size classes expressed as volume (C) and functional groups (D). E-I figures show benthic invertebrates' trait according to Tachet et al. (2000): current velocity preference (E), longitudinal distribution along river course (F), substrate preferences (G; where Fbcp means Flags/boulders/cobbles and pebbles, Twro means twigs and roots, and Odlim means organic detritus and litter), maximal size classes expressed in length (H) and feeding guild (I). J figure shows phytoplankton's functional groups (Reynolds et al., 2002; Padisák et al., 2009). S1, S2, S3, S4, and S5 denote sampling stations.

The best model explaining phytoplankton's community structure retained Date, Station, Temperature, Total phosphorus and PO<sub>4</sub> variables and significantly explained differences among phytoplankton samples ( $df = 33$ ,  $F = 4.65$ ,  $p = 0.001$ ). It expressed nearly 42% of the total squared distance among samples. Date factor explained 33% of the total variation and shared and additional 4% of the variation with Temperature. In second place, Station factor explained 3% and shared with each of the variables Temperature and Phosphorus an additional 1%. According to centroids, ordination procedure assigned stations to two distinct groups, S1 and S2 in one group before the impoundment and S3, S4 and S5 in another group. Temperature and Phosphorus content marginally contributed to explain Bray-Curtis distances among samples (Supplementary doc 3).

### 3.2. Community traits selection in flow regime transitions

#### 3.2.1. Benthic diatoms

The lot-len transition selected for coloniality, therefore reducing significantly non-attached forms and favored more fragile attachments like stalks and, like species belonging to motile functional group (Fig. 4A–D, supplementary doc 4). It was also observed a significant increase of taxa included in planktonic functional group. Species belonging to the largest size class ( $>1500 \mu\text{m}^3$ ) significantly reduced their abundance, and on the contrary the tiniest size class species greatly increased their abundance (Fig. 4C, supplementary doc 4). No changes were observed in the selected traits in the len-len transition. In the len-lot transition non-attached forms increased and stalk-attached forms dropped in abundance significantly. A similar pattern was observed in the len-lot transition for size classes with a recovery of largest-sized species, and a significant reduction of tiniest forms (Fig. 4C, supplementary doc 4).

#### 3.2.2. Benthic invertebrate

In the first transition, namely lot-len, running waters features disappeared, and species holding traits associated to fast waters significantly reduced their abundance. For instance, upper and medium reaches associated species, showing medium and fast current preferences dropped, and species with null current preference significantly increased their abundance (Fig. 4E–F, supplementary doc 4). This transition also selected for taxa with preferences for the finest sediment classes, like mud, silt, sand, microphytes and organic detritus, and consequently dropping in their abundance species with preferences for coarse inert substrate, like gravel and blocks, and plant substrate (Fig. 4G, supplementary doc 4). Subsequently deposit feeders increased their abundance, while filterers and scrapers trophic guilds reduced their abundances (Fig. 4I, supplementary doc 4). A significant reduction in size occurred, with an increase of species belonging to the tiniest size class, and a reduction in species with sizes comprised in the size classes between 0.25 and 4 cm (Fig. 4H, supplementary doc 4).

In the len-len transition a slight, but significant, increase in the proportion of invertebrates with null-current and a reduction for slow current preferences happened (Fig. 4E). Such selection was also translated in an increase of species preferring the finest inorganic substrates and a decrease for those preferring fine organic substrates (Fig. 4G, supplementary doc 4).

The recovery of running waters condition in the len-lot transition, was reflected in the recovery of species with preferences for the condition lost in the first transition and the reduction of species associated to lentic conditions found in the reservoir lake. Including current velocity and substrate preferences, and size classes distribution (Fig. 4E–H, supplementary doc 4). It is noteworthy that species holding features of shredder and predator trophic guilds significantly increased their abundance (Fig. 4I, supplementary doc 4).

#### 3.2.3. Phytoplankton

Regarding phytoplankton morpho-functional groups, only H<sub>1</sub>, J, and

X<sub>1</sub> groups changed significantly. Changes occurred in the lot-len transition. J and X<sub>1</sub> groups significantly decreased in from the running water station S1 to the standing water station S3 (Fig. 4J, supplementary doc 4). On the other hand, H<sub>1</sub> group abundance raised from S1 to S3. Proportions did not significantly change in the following downstream transitions.

## 4. Discussion

The most interesting results of our study showed a markedly different response of phyto-benthos, benthic invertebrate and phytoplankton communities to the regulation of the Selune River by two consecutive dams. Riverine organisms' diversity showed significant differences among stations fitting differently to geographical distances and habitat conditions, while phytoplankton diversity did not differ too much between stations. Surprisingly, phytoplankton was already present in the river's waters upstream the first dam in an unexpected high diversity. Regarding species' traits, differences in traits composition between lotic and lentic communities occurred, but these traits compositions did not match perfectly our predictions.

### 4.1. Diversity patterns

Riverine organisms followed significant  $\alpha$  diversity modifications in the most contrasted transitions, namely lot-len and len-lot, confirming partially our first hypothesis. On the other hand,  $\alpha$  diversity remained unexpectedly unchanged between both reservoir lakes. Phytoplankton  $\alpha$  diversity pattern only agreed our prediction of no change in the len-len. This lack of significant change of  $\alpha$  diversity in len-len suggested that neither significant environmental condition changed, or dispersal limitations happened for none of the three biological groups in the transition between both reservoir lakes.

Concerning  $\beta$  diversity, as predicted in H<sub>2</sub>, higher values were observed in the most hydrological contrasted transitions (i.e. lot-len and len-lot), and lower at the len-len, with the exception of benthic invertebrate at len-lot that surprisingly exhibited low values of  $\beta$  diversity.

Phyto-benthos  $\alpha$  diversity and abundance peaked at S2, the transitional station in the first reservoir, where phyto-benthos benefited from less turbidity conditions (Fig. 2E), and high nutrient content, especially phosphorus (Fig. 2G), and at the same time enough flow velocity. On the other hand, at lentic stations (S3 and S4) flow velocity reduction, and phosphorus availability drop, likely consumed by phytoplankton, limited phyto-benthos diversity, in spite of water transparency enhancement (Fig. 2E). The observed increase in the  $\alpha$  diversity of phyto-benthos in the len-lot transition probably benefited from the recovery of running water conditions, appropriate coarse substrate availability and a better light penetration conditions due to the sediment sink in the reservoirs (Fig. 2E). Neif et al. (2017) highlighted also an increase in the diversity of phyto-benthos in tailwaters and showed experimentally that low flow velocity and fine sediments siltation reduced phyto-benthos abundance, but suggested that at intermediate flow velocities, other drivers, like nutrient availability, might override flow velocity control. On the other hand, Waffenhoff et al. (2013) did not find significant changes in phyto-benthos diversity under experimental manipulations of nutrient and fine sediments.

Phyto-benthos community structure exhibited a certain spatial ordination pattern confounded with habitat control in a least extent and a significant contribution of nestedness  $\beta$  diversity component. In a meta-analysis, Soinen et al. (2018) showed a five-fold contribution of turnover over nestedness for passive dispersal organisms. Soinen et al. (2018) analysis showed a significant negative contribution of turnover component for the same group of organisms. We identify three clusters of community similarity from upstream to downstream: S1-S2, S3-S4 and S5 (Supplementary doc 1). Much of the observed differences among communities were explained by Station factor, that increased the proportion of variability explained confounded with phosphorus availability (Supplementary

doc 1). Pure habitat control variables, like season variability and phosphorus concentration explained less amount of variability. Notwithstanding, nutrient load, flow intensity and seasonality have been repeatedly identified as important drivers shaping phyto-benthos communities (Krajenbrink et al., 2019; Neif et al., 2017; Wu et al., 2019).

Benthic invertebrate was the group that most straightforwardly responded to habitat control, although spatial control also contributed to community structure shaping. We found two clusters of similarity, lotic vs. reservoir's stations (Supplementary doc 2). For instance,  $\beta$  diversity score among lotic stations was low, but communities do not overlap completely, pointing out the contribution of species turnover to communities differentiation. In fact, diversity level in the station downstream both dams (S5) was even higher than in the most upstream station (S1). In line with our results, higher diversity values downstream than upstream the dam have been reported in a large geographical scale study in the UK (Passy, 2007), but the opposite diversity pattern have been also reported (Benítez-Mora and Camargo, 2014; Ladrera et al., 2015). White et al. (2017) showed that differences among communities upstream and downstream a set of dams in UK were related to thermal and flow regime variability. S1 and S5 also exhibited such a difference in environmental variables (Fig. 2B–I). Nestedness  $\beta$  diversity component prevailed in the lotic to lentic shift due to restrictions to riverine taxa. Contrastingly, a similar contribution of turnover and nestedness was observed in the len-lot transition, suggesting that invertebrate probably drifted through the dam.

Phytoplankton withstood the sharp environmental changes occurring in lot-len, len-len and len-lot transitions, and  $\alpha$  diversity remained unchanged. Accordingly to  $\beta$  diversity scores, community dissimilarity in transitions was low, suggesting that phytoplankton was neither limited by habitat conditions nor by dispersion. Likely, the short retention time observed in our study site, homogenized synchronously environmental conditions explaining the similarities among stations (Supplementary doc 3). Short generation time enable also algae to cope rapidly with environmental changes (Thomas et al., 2018), supporting so synchrony of phytoplankton communities in regulated rivers and lakes (e.g. Kent et al., 2007; Lansac-Tóha et al., 2019). But river regulation can also strongly alter phytoplankton temporal pattern, compelling spatially phytoplankton community differences upstream and downstream of dams (Sabater et al., 2008; Istvánovics et al., 2010; Qu et al., 2018).

According to the postulate that dams abruptly modify habitat conditions and may limit dispersal, altering so metacommunity structuring forces, and in view of our results, we suggest three theoretical models of organisms' responses to dams, that would influence metacommunity structure and bioindication usability: i) organisms indifferent or tolerant to dams effect, well represented upstream the reservoir, in the reservoir and downstream the reservoir. In our study phytoplankton community matched with this type; ii) organisms sensitive to habitat conditions shift but not limited in their dispersal capacity, that are absent or reduced greatly their diversity in the lentic habitat, but occurring upstream and downstream the dam. In our study this type in represented both by phyto-benthos and benthic invertebrates; iii) organisms limited in their dispersal by the dam, and occurring only upstream (and maybe in the reservoir) or downstream depending on the source population position. Diadromous fishes and some benthic invertebrates match this type (Katano et al., 2006; Sousa et al., 2020). Our results supported the expected dispersal limitation imposed by dams, but it is noteworthy that bigger organisms are more easily filtered out by a dam, while benthic invertebrates and algae readily disperse actively (insects) or passively (Shurin et al., 2009; De Bie et al., 2012). For tracking ecological consequences of multi-dam systems, only groups included in the above-mentioned second or third categories would be useful.

#### 4.2. Communities' traits composition

Organisms' traits did not fulfil completely our third hypothesis of two community types, lotic- and lentic- (H3). We found the strongest

support in the case of the macroinvertebrates' traits. Nevertheless, we should keep in mind that finding straightforward causality among community traits and habitat conditions may be blurred by the interaction among driving forces, geographical differences and different strategies deployed by the biota to withstand with habitat conditions. Such complex interactions might act on the observed results for benthic diatoms and phytoplankton communities trait composition (Lamouroux et al., 2004; Statzner and Bêche, 2010).

For diatoms, current velocity conditions in lotic stations favored concomitant traits like non-attached taxa, solitary species, as well as motile species, occurring more frequently in S1 and S2 (Fig. 4A–B–D). Likely, high turbidity conditions at S1 favored motile solitary species, capable of getting benefit from high nutrient load and tolerant to fine sediments (Neif et al., 2017; Wu et al., 2019). Low profile and pad-attached diatoms would be expected to occur preferentially in higher current velocities (Passy, 2007; Rimet and Bouchez, 2012), as it has been reported in large extent geographical studies in Denmark and UK (Krajenbrink et al., 2019; Wu et al., 2019), but no significant differences were observed between lotic and lentic stations. This observation might be an artefact of the artificial substrate that we provided for phyto-benthos sampling. Also unexpectedly according to literature (Wu et al., 2017), largest size class was significantly more frequent in lotic stations, and smallest size class in lentic ones (Fig. 4C, supplementary doc 4). However Sun et al. (2018) found in a German river that smallest diatoms' size class better correlated to low water conditions occurring in summer, whilst the largest size class occurred more frequently in high flow conditions occurring in winter and spring. Grazers, more frequently found in lotic stations (Fig. 4I, supplementary doc 4), might also contribute to diatoms' size selection by a selective size consumption (De Troch et al., 2006; Koetsier, 2005). Lentic stations conditions favored traits (Fig. 4A–B, supplementary doc 4) identified with the capability of coping with high sedimentation but with low tolerance to high current flow (Neif et al., 2017; Wu et al., 2019). Planktonic functional worked well as an indicator of lentic stations, as expected (Fig. 4D, supplementary doc 4).

Habitat conditions in the unregulated reaches of the Selune River determined a lotic-type community for benthic invertebrates. Such community type associated traits' modalities showing preference for upper river's sections (Fig. 4E–G, supplementary doc 4). Scrapers was the most characteristic trophic guild in lotic-type community, typically corresponding to a middle reach community. Unexpectedly, shredders were proportionally more abundant in lentic stations, as it would be expected from an upper reach section (Fig. 4I, supplementary doc 4). Lamouroux et al. (2004) found positive correlation among scrapers and an estimator of current force (Froude number), and negative correlation for shredders and deposit feeders. Dolédec et al. (2015) showed in restored reaches of Rhône river, a shredder decrease and filter feeders increase related to current velocity increase, suggesting a shift from CPOM- towards FPOM-based ecosystem functioning. We observed significantly increases of filter feeders and scrapers in the len-lot transition, suggesting a readily availability of FPOM and phyto-benthos resources in the tailwaters. In opposition to the most likely size range predicted in the literature for running waters (Statzner and Bêche, 2010; Townsend and Hildrew, 1994), we found significantly higher frequencies of intermediate sized macroinvertebrates (>0.25–4 cm; Fig. 4H, supplementary doc 4) in lotic stations. In line with our findings, Lamouroux et al. (2004) found a positive correlation among intermediate sizes (5–20 mm) and increasing current force, and Gallardo et al. (2014) reported from temperate rivers the prevalence of intermediate size invertebrate (about 1 cm and smaller). Slow current and high sedimentation rate observed in lentic stations portrayed a lentic-type community, with taxa holding null and slow current preferences (Fig. 4I), fine substrate affinity (Fig. 4G, supplementary doc 4) and deposit feeding diet, owing to the expected decrease in the CPOM/FPOM ratio in reservoirs (Fig. 4I, supplementary doc 4). Lentic conditions also favored the smallest body-sizes (Fig. 4H, supplementary doc 4). Descloux et al. (2014) suggested that clogged sediments would favor

small sized-invertebrate.

Lotic-type and lentic-type phytoplankton communities could not be readily distinguished using trait-based analyses (Fig. 4J). Only three functional groups, namely H1, J and X1, showed significant differences between lotic station (S1) and lentic station (S3). These functional groups are associated to enriched shallow aquatic systems reflecting the observed decrease in turbidity and in nutrient content in lentic stations. Most of functional classifications for phytoplankton have been proposed for lentic ecosystems (Borics et al., 2016; Kruk et al., 2010; Reynolds et al., 2002; Salmaso and Padisák, 2007). Even if they can be used successfully in large rivers (Abonyi et al., 2012), they are less adapted to small rivers like Seulne at S1 and S5. For instance in small rivers, Fraisse et al. (2013) observed some of the genera included in group D in contrasted situations: elongated cell forms (*Melosira*, *Closterium*, *Nitzschia*) in unregulated rivers and spherical diatoms (*Stephanodiscus*, *Cyclotella*) in regulated rivers in spring.

## 5. Conclusions

We conclude that from a community point of view both reservoirs acted as one single reservoir. Phytoplankton communities were neither hampered by changes in water flow velocity, and did not display dispersal limitation neither. Benthic invertebrate community was mainly shaped by habitat conditions, while phyto-benthos communities were influenced by both habitat conditions and spatial control. Such differences between these benthic groups likely reflects differences in dispersal capabilities and niche breadth.

Among the three studied groups, riverine organisms, namely phyto-benthos and benthic invertebrates, were the most useful indicators of transitions in this double dam system.  $\beta$  diversity assessment revealed as the most useful metric to understand the relative importance of dispersal limitation or habitat modification provoked by multiple dams. On the other hand, community's trait composition described well ecological transitions for benthic invertebrate communities, to a certain extent for benthic diatoms communities and poorly for phytoplankton communities.

## CRedit authorship contribution statement

**Héctor Rodríguez-Pérez:** Conceptualization, Formal analysis, Writing – original draft, Visualization. **Alexandrine Pannard:** Investigation, Supervision, Writing - review & editing. **Caroline Gorzerino:** Investigation, Supervision, Writing - review & editing. **Laura Pellan:** Investigation. **Stéphanie Massé:** Investigation. **Guillaume Bouger:** Investigation. **Marion Chorin:** Investigation. **Jean-Marc Roussel:** Writing - review & editing. **Christophe Piscart:** Conceptualization, Investigation, Supervision, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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