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## EDITED BY

Diana Hamilton,  
Mount Allison University, Canada

## REVIEWED BY

Rachelle Johnson,  
U.S. Geological Survey, United States  
Gabriel Singer,  
University of Innsbruck, Austria

## \*CORRESPONDENCE

Jean-Marc Roussel  
✉ jean-marc.roussel@inrae.fr

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# Effects of large dams on the aquatic food web along a coastal stream with high sediment loads

Jean-Marc Roussel <sup>1\*</sup>, St ephane Fraisse<sup>1</sup>, Olivier D ezerald <sup>1</sup>,  
Oph elie Fovet<sup>2</sup>, Alexandrine Pannard <sup>2,3</sup>,  
Hector Rodriguez-Perez<sup>3,4</sup>, Alain Crave<sup>5</sup>, Caroline Gorzerino<sup>1</sup>,  
Maxime Poupelin<sup>1</sup>, Guillaume Forget<sup>1</sup>, Dominique Huteau<sup>6</sup>,  
Alban Thomas<sup>1</sup>, Manuel Chev e<sup>1</sup>, Laura Soissons <sup>1</sup>  
and Christophe Piscart <sup>3</sup>

<sup>1</sup>DECOD, INRAE, IFREMER, L'Institut Agro, Rennes, France, <sup>2</sup>SAS, INRAE, L'Institut Agro, Rennes, France, <sup>3</sup>ECOBIO, CNRS, University of Rennes, UMR 6553, Rennes, France, <sup>4</sup>OFB, ECOAQUA, DRAS, Aix-en-Provence, France, <sup>5</sup>GEOSCIENCES Rennes, University of Rennes, CNRS, Rennes, France, <sup>6</sup>INRAE, Unite Experimentale d'Ecologie et Ecotoxicologie Aquatique, Rennes, France

The contribution of two basal energy sources – detrital organic matter and primary producers – as part of aquatic food webs varies typically along river continua. A host of barriers to river flow increase the water residence time and sediment and nutrient retention in reservoirs worldwide, and potentially alter the balance between detritus-based and algae-based energy pathways in the downstream food webs. We explored this issue on the S elune River (Normandy, France), a small coastal stream that drains an agricultural catchment with high sediment runoff. Seasonal measurements of the following parameters were compared upstream and downstream of the reservoirs of two large dams (16 m and 36 m high): sediment fluxes, nutrient and chlorophyll *a* concentrations, algal communities in the epilithic biofilm (taxonomic composition, biomass and growth), and benthic invertebrate communities (abundance and trophic guild structure). As anticipated, annual sediment fluxes were much lower downstream of the reservoirs, where significant decreases in water turbidity, phosphate and silicate concentrations were recorded. A higher chlorophyll *a* concentration in water and a higher contribution of pelagic algae taxa to the photosynthetic biofilm suggested drifting and deposition of reservoir-borne phytoplankton downriver. Photosynthetic biofilm growth was higher downstream of the reservoirs in spring and fall, and so was the abundance of herbivores in the invertebrate community, notably scrapers and algae eaters. Energy pathways within riverine food webs were traced using stable isotope analyses of carbon (C) and nitrogen in the tissues of aquatic consumers (invertebrates and fish). Mixing models revealed a discontinuity in the origin of the C entering the food webs along the river continuum, confirming a greater contribution of algal C to aquatic consumers downstream of the reservoirs. These results

illustrate mechanisms whereby large reservoirs can modulate C flow in food webs along a small coastal river with high sediment loads, and make it possible to anticipate the effects of dam removal on the future river ecosystem.

#### KEYWORDS

nutrient concentrations, sediment fluxes, photosynthetic biofilm, benthic invertebrates, fish, stable isotope analysis, mixing models, carbon flow

## 1 Introduction

Two major energy pathways exist in river food webs. On the one hand, dissolved nutrients and inorganic carbon (C) fuel primary producers, namely phytoplankton, benthic algae and aquatic plants (Elser et al., 2007; Bumpers et al., 2017). The organic C resulting from photosynthesis is called autochthonous C. It is available to herbivores and other consumers at higher trophic levels, and fuels the algae-based pathway. The dissolved inorganic carbon (DIC) that enters this energy pathway is a mix of terrestrial ( $\text{HCO}_3^-$  and dissolved  $\text{CO}_2$  from chemical weathering, soils and groundwater), aquatic (ecosystem respiration) and atmospheric (diffusion of  $\text{CO}_2$  at the air–water interface) sources (Mook and Tan, 1991; Finlay, 2003; Liu et al., 2011). Algae provide high-quality food resources to primary consumers (Guo et al., 2016a; Guo et al., 2016b), and the prevalence of algae-derived C in aquatic consumers has been reported in many river food webs (Mayer and Likens, 1987; Thorp and Delong, 2002; Lau et al., 2009; Brett et al., 2017). On the other hand, the detritus-based pathway involves primary consumers (fungi, bacteria and invertebrates) relying on dissolved or particulate organic C, notably fragments of dead plants, animals and feces. The available pool of detrital C is a combination of autochthonous C from aquatic organisms and allochthonous C from terrestrial ecosystem inputs, notably leaf litter from riparian trees (review by Marks, 2019). The influence of the detritus-based pathway on aquatic food web functioning is expected to vary along the river continuum. In theory, detrital C should prevail in headwater reaches receiving high allochthonous inputs from riparian trees (“river continuum concept” (RCC), Vannote et al., 1980). For instance, in small tributaries where a dense tree canopy strongly limits solar radiation, aquatic consumers mostly rely on C derived from riparian inputs (Roussel et al., 2021). According to the RCC, aquatic primary producers mostly support river food webs further downstream in intermediate reaches, while detrital and terrestrial C become dominant again in large rivers where primary production is hampered by water depth and turbidity. This pattern has been debated for large river ecosystems subjected to seasonal flooding, where macrophytes and/or floodplain plants can be a major C source in food webs (“flood pulse concept”, Junk et al., 1989). Various case studies in the literature support different predictions on the predominant C sources and energy pathways in

large river food webs (Hoeinghaus et al., 2007; Roach, 2013; Soto et al., 2019; Wang et al., 2021).

In addition to natural variations along the river continuum, human activities can modify the expected balance between the algae-based and detritus-based pathways in river food webs. By stimulating primary production, anthropogenic nutrient inputs – notably N and P – have major effects on freshwater ecosystems, including algal blooms (Galloway et al., 2004; Diaz and Rosenberg, 2008; Paerl et al., 2011; Penuelas et al., 2013). Such an increase of the primary producer biomass can reduce the DIC concentration, promote the diffusion of atmospheric  $\text{CO}_2$  into the water (Portielje and Lijklema, 1995; Schindler et al., 1997), and ultimately change the origin of C cycling in aquatic environments (Brenner et al., 1999; Roussel et al., 2014). Anthropogenic nutrients from non-point-source pollution also change microbial activity on detrital C and its assimilation by primary consumers (Rosemond et al., 2015; Guo et al., 2016b) and modulate the detritus-based pathway. Another obvious impact of human activity on river food webs is observed when a large amount of organic waste offers alternative resources of high nutritional value to primary consumers in benthic invertebrate communities (Camargo, 1992; Guilpart et al., 2012) and enhances the detritus-based pathway downstream of the inputs (Roussel et al., 2018; de Carvalho et al., 2020). The algae-based and detritus-based pathways within river food webs are under the influence of a complex balance that depends on the position along the river continuum and anthropogenic pressures. Therefore, the origin of the C inputs at the base of river food webs and C flow to higher trophic levels can significantly change when the availability of detrital C and/or nutrients to aquatic organisms is altered.

A host of barriers constrain natural river flows worldwide (Grill et al., 2019). In a recent review, Belletti et al. (2020) concluded to a mean density of 0.74 barrier per kilometer of river in Europe. By creating impoundments, barriers to river flow increase the water residence time and have major consequences on the natural process of sediment transfer. Using satellite imagery analyses on major rivers, Dethier et al. (2022) estimated that dams have halved the global sediment flux from lands to seas in the northern hemisphere. Large dams and reservoirs can trap and store huge quantities of suspended materials, including detrital C that is no longer available to downstream river ecosystems, estuaries and marine coastal areas

(Syvitski et al., 2005; Zarfl and Dun, 2022). Moreover, large reservoirs affect nutrient biogeochemistry and strongly modulate the downriver transfer of dissolved nutrients (review by Maavara et al., 2020). Phosphorus (P) is essential to freshwater primary producers in its dissolved inorganic form, but uptake by phytoplankton in reservoirs alter its availability to downstream food webs (Lu et al., 2016; Bao et al., 2018). After decades of impoundment, sediments trapped in reservoirs contain large quantities of legacy P, which can be released through various physical and biogeochemical processes (Orihel et al., 2017). Similarly, the blooming and sinking of silica diatoms in reservoirs deplete the dissolved silicon (DSi) available downriver and in marine areas (Tréguer and de la Rocha, 2013) during specific periods of the year (Chen et al., 2014). The intensity of depletion is correlated with the water residence time in reservoirs (Ma et al., 2018). In some cases, large dams and reservoirs massively reduce all dissolved nutrients (P, N, DSi) down to the ocean (Gupta et al., 2021). The diversity of patterns reported in the literature outlines that the complex biochemical processes occurring in large reservoirs alter both particulate and solute fluxes, and in turn (theoretically) the balance between the algae-based and detritus-based pathways and C flow in downriver aquatic food webs. However, literature on this issue mostly relies on the study of dams and reservoirs on large rivers, but the ecological processes at play in small river catchments have retained less attention to date.

We explored the effect of two large dams and their reservoirs on aquatic communities and the energy flow in the food web of a small coastal stream – the Sélune River, an 85-km stream discharging into

the Bay of Mont Saint-Michel (Normandy, France). In the early 20<sup>th</sup> century, two large hydropower dams (16 and 36 m high) were constructed in the lower third of the catchment, resulting in two consecutive reservoirs that covered 19 km of the initial river course. Agriculture is a dominant activity in the catchment; annual rainfall and erosion result in high quantities of suspended sediment and dissolved nutrients reaching the river (Fovet et al., 2020). In this context, we expected that high inputs of terrestrial organic matter and water turbidity would drive the aquatic ecosystem toward detritus-based functioning. We predicted that by hindering the transfer of suspended sediment, the dams and reservoirs could enhance the algae-grazer pathway and the contribution of algal C to aquatic biota downriver. Seasonal measurements of sediment fluxes, nutrient concentrations, photosynthetic activity, benthic algae and invertebrate communities together with stable isotope analyses of aquatic fauna were performed upstream and downstream of the reservoirs to test these assumptions. The broader goal of this work was to establish a baseline pattern of the food web of the Sélune River with its two reservoirs in order to evaluate river recovery after the scheduled removal of the two dams.

## 2 Materials and methods

### 2.1 Study site and context

The Sélune is a 85 km long river that drains a 1,083 km<sup>2</sup> watershed and flows into the Mont Saint-Michel Bay in Normandy

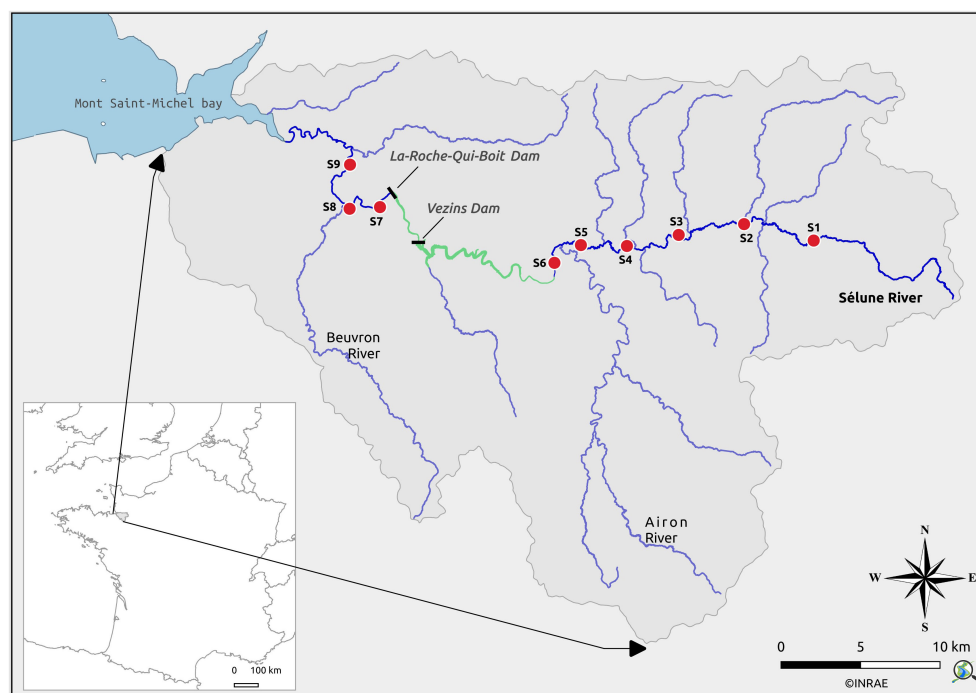


FIGURE 1

The Sélune River watershed, with two dams (black rectangles), two reservoirs (in green) and the study sites (red dots, S1 to S9). Distances, from source (0 km) to bay (85 km): S1 (15 km), S2 (23 km), S3 (29 km), S4 (34 km), S5 (39 km), S6 (42 km), Vezins dam (57 km), La-Roche-qui-Boit dam (61 km), S7 (62 km), S8 (65 km), S9 (70 km).

(France) (Figure 1). Climate is oceanic, with mean annual rainfall of ca. 800 mm, and high and low flow periods occurring in winter and early fall, respectively. The median daily flow is  $5 \text{ m}^3 \cdot \text{s}^{-1}$ , the total monthly flow varies from  $10^6 \text{ m}^3 \cdot \text{month}^{-1}$  during severe summer drought up to  $120 \cdot 10^6 \text{ m}^3 \cdot \text{month}^{-1}$  during high flood in winter (Fovet et al., 2020). The bedrock is composed of granite and Brioverian schist. Mixed crop–livestock farming covers 85% of the watershed area, with arable land covering 46% of this surface and grassland 39% (<https://www.theia-land.fr/en/product/land-cover-map/>). The watershed is vulnerable to soil erosion, hence high water turbidity and sediment loads are recorded (Vongvixay et al., 2018). In the early 20<sup>th</sup> century, two large hydropower dams (Figure 1) were built on the river: La-Roche-qui-Boit (16 m high and 125 m long, reservoir volume  $90 \cdot 10^3 \text{ m}^3$ ) and Vezins (36 m high and 278 m long,  $18 \cdot 10^6 \text{ m}^3$ ). Depending on the season, the mean water residence time varied from 1 to 4 days in La-Roche-qui-Boit, and from 14 to 47 days in Vezins (Fovet et al., 2020). The two reservoirs covered a total distance of 19 km, which is more than 20% of the initial river course (Figure 1). Owing their volume, spatial coverage and high water residence time, they were considered as large reservoirs on such a watershed. Water in the reservoirs was nutrient-rich; the mean summer nutrient concentrations varied between 7.4 and  $16.5 \mu\text{g} \cdot \text{L}^{-1}$  P-PO<sub>4</sub> and between 4.0 and  $5.3 \text{ mg} \cdot \text{L}^{-1}$  N-NO<sub>3</sub> along the water column (Fovet et al., 2020).

Considering the low hydropower capacity (27 GWh) of the two dams, potential safety issues because of the condition of their structure, periodic toxicity events in summer associated with cyanobacterial blooms in the reservoirs, and law on diadromous fish species, dismantling was decided by the French government in 2009. Operations started in spring 2017 by emptying Vezins reservoir, while dismantling of Vezins dam was completed by summer 2020. The same procedure for La-Roche-qui-Boit started in 2021 and ended in early 2023. A long-term multidisciplinary scientific program (2012–2027) aims at evaluating the Sélune River restoration processes after dam removal (<https://programme-selune.com>). The present study is part of this program, and focuses on the pre-removal period, *i.e.* before spring 2017. The overall work took place at nine flowing sites located along the river continuum (Figure 1). For financial reasons it was not possible to record all variables (*i.e.* water discharge, sediment and nutrient concentrations, algal communities in epilithic biofilm and benthic invertebrate communities; see below for description) at each site. However, for each variable, the sampling design allowed comparisons between sites located upstream and downstream of the reservoirs. The choice of a site was constrained by specific criteria. For sediment and water chemistry, auto-samplers needed power supply and support made of concrete on bankside, whereas biofilm was studied with fragile glass slides installed mid-channel in sunny, shallow but not too fast-flowing habitats to avoid damage. For benthic invertebrate collection, we favored easily wadable sites with a great variety of substrates. An overall criterion was that the habitat conditions at upstream and downstream sites were as similar as possible for each variable. This explains why S5 or S6 (upstream), and S7 or S8 (downstream) sites were chosen depending on the variable to record (Figure 1). These sites (S5

and S6; S7 and S8) were very close (about 2 km) one from another, and we did not expect any bias coming out of this. The Airon tributary increases the Sélune River discharge between S5 and S6, but it does not cause major differences in dissolved nutrients as it drains an area with similar soils and land use pattern on the Sélune River catchment. Finally, we extended our sampling to eight sites for stable isotope analysis on animal tissues to get a clearer picture of food web shifts along the river gradient (see Section 2.5).

## 2.2 Sediment and solutes

Water, sediment and solutes were monitored at S6 (upstream the reservoirs) and S8 (downstream the reservoirs) from January 2015 to March 2017 (Figure 1). The water level, temperature and turbidity were recorded at a (sub-)hourly time step (1h at S6; 6 min at S8) using dedicated sensors (Hach Lange SOLITAX sc). Water discharge was computed from the measured water level using a rating curve established and kindly provided by DREAL 50 (State office in charge of hydrometric monitoring) and EDF (Electricité de France, the hydropower company). At both sites, grab samples were collected weekly, and ISCO autosamplers collected 10–20 samples (800 mL each) during storm events (see Fovet et al., 2020 for details). In the laboratory, a subsample from each sample was filtered at  $0.45 \mu\text{m}$  on nitrate cellulose filters, dried at  $105^\circ\text{C}$  and weighed. The filtered volume (at least 350 mL) was measured to determine the suspended solids (SS) concentrations (EN 872:2005, 2005). A 30-mL aliquot of filtered water was used to measure NO<sub>3</sub> concentrations by ionic chromatography (Dionex ICS3000, EN 10304-1:1995, 1995), and dissolved silica (DSi) and orthophosphate (PO<sub>4</sub>) concentrations by colorimetry (Seal Analytical AQ2, NF T 90-007:2001, 2001; EN 6878:2004, 2004). Another subsample was filtered at  $0.45 \mu\text{m}$  on glass fiber filters and used for analyzing the carbon (C) and nitrogen (N) contents in SS particles using an Elemental Analyzer (Thermo Finnigan FLASH EA 1112).

Data were pooled by site (S6 and S8) and season: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Specific discharge was calculated by dividing the discharge values ( $\text{m}^3 \cdot \text{s}^{-1}$ ) by the drained surface ( $629 \text{ km}^2$  at S6 and  $777 \text{ km}^2$  at S8) to compare discharge between sites. The molar C:N ratio of SS was used as a proxy of the origin of particulate organic matter, considering that values above or below eight suggest terrigenous or phytoplanktonic origin, respectively (Hedges et al., 1997; Kendall et al., 2001; Balakrishna and Probst, 2005). We fitted a regression between the SS concentrations and the turbidity values at S6 and S8 to estimate the SS fluxes from turbidity time series. Regression coefficients and their 95% confidence intervals were used to compute instantaneous loads of SS and uncertainty associated with the regression coefficients, and then cumulated over the water years. “Site” (upstream or downstream the reservoirs) and “season” (winter, spring, summer and fall) effects were tested with two-way ANOVAs followed by Tukey’s *post-hoc* test ( $p < 0.05$ ) on the following response variables: water discharge, turbidity, SS concentrations, the C:N ratio, phosphate, nitrate and dissolved silicon.

## 2.3 Phytoplankton and photosynthetic biofilm

Phytoplankton biomass was measured monthly at S5 (upstream the reservoirs) and S8 (downstream the reservoirs) by fluorescence using a multiparametric probe (Idronaut Ocean Seven 316Plus CTD, Milan, Italy) from January 2015 to October 2016. Water samples were collected monthly at the sub-surface and in mid-channel to measure chlorophyll *a* concentrations after filtration on Whatman GF/F glass-fiber filters and extraction overnight at 4°C in 90% acetone (Lorenzen, 1967). Absorbance was measured at 665 nm and 750 nm with a spectrophotometer, before and after acidification, following Lorenzen's method (Lorenzen, 1967).

The photosynthetic biofilm was studied from January 2015 to October 2016 on a monthly basis. Four glass slides (30 × 10 × 3 mm) were installed vertically in opened plastic boxes with perforated sides to allow water flow. The boxes were covered with a plastic mesh (2 cm mesh size) to prevent large debris from entering. They were anchored in the middle of the riverbed at S5 and S8, and the glass slides were changed every month, *i.e.* after one month of incubation (Biggs, 1988; Morin et al., 2008). The boxes were occasionally inaccessible due to high water flow, or damaged. However, we successfully retrieved glass slides in winter (once at S8), spring (six times at S5 and six times at S8), summer (six times at S5 and six times at S8), and fall (one and two times at S5 and S8, respectively). Chlorophyll *a*, ash-free dry mass (AFDM), taxa and photosynthetic activity were evaluated on separate glass slides.

For chlorophyll *a*, the glass slide was scraped on both sides using a razor blade to retrieve the biofilm, which was immediately stored in a plastic tube, kept in the dark in a cooling box in the field, and then freeze-dried in the laboratory. Overnight extraction with acetone was performed before spectrophotometric measurements following Lorenzen's method (Lorenzen, 1967). The chlorophyll *a* concentration ( $\mu\text{g}\cdot\text{L}^{-1}$ ), the incubation duration and the glass slide surface were used to calculate the biofilm biomass increase in time, expressed in  $\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ . For AFDM, the biofilm was scraped in the same way as for chlorophyll *a*, oven-dried at 105°C for 48 h to get total dry mass (algae, bacteria, fungi, and detritus, in  $\text{g}\cdot\text{m}^{-2}$ ), and then burnt for 1 h at 500°C to obtain AFDM. The percentage of organic matter was expressed as the AFDM:dry mass ratio. The photosynthetic biomass:total biomass ratio corresponding to the autotrophic index (Weber, 1973) was calculated to describe the trophic nature of the biofilm (autotrophic *versus* heterotrophic). For taxonomic identification, the biofilm was scraped off from the slide, immediately fixed in Lugol solution and kept in the dark at 4°C. Microalgae were identified and counted using a light microscope (Leica DM4000B) and a Nageotte counting chamber. Taxa were classified as benthic, benthopelagic, planktonic, or unknown according to the literature (Germain, 1981; Bourrelly, 1990; John et al., 2002; Rimet and Bouchez, 2012) and the Diatoms of North America online database (<https://diatoms.org/>).

Finally, we measured the photosynthetic activity of the biofilm on the fourth glass slide right after its removal from the river. Repeated measurements of fluorescence signals were performed using a four-wavelength-excitation pulse amplitude modulation fluorometer (Phyto-PAM, Heinz Walz® GmbH, Effeltrich,

Germany) equipped with an emitter-detector fiberoptics unit. The fiber device was placed at 2 mm from the glass slide surface with a 4-cm diameter adapter to control irradiance. The PAM calculates photosynthesis as the relative electron transport rate (rETR) through photosystem II ( $\mu\text{mol e}^{-}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) at different levels of light (Kromkamp and Forster, 2003). After 15 min of dark adaptation, rapid photosynthesis-light curves (RLC) were performed in triplicate with increasing light intensities (16 to 265  $\text{mmol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ), with a 20 s time interval (Jakob et al., 2005). The light-saturated maximum rETR was calculated by applying the nonlinear least squares regression model of Eilers and Peeters (1988) to fit the rETR-irradiance curves. "Site" and "season" effects were tested separately with two-way ANOVAs followed by Tukey's *post-hoc* test ( $p < 0.05$ ) for chlorophyll *a*, AFDM, taxonomic identification and photosynthetic activity.

## 2.4 Benthic invertebrates

A Surber net sampler (0.05 m<sup>2</sup>, 0.5 mm mesh size) was used to collect benthic invertebrates at S5 (upstream the reservoir) and S7 (downstream the reservoir) in fall (October 2014 and 2015) and spring (April 2015 and 2016), following the NFT 90-333 protocol and the Water Framework Directive (2000/60/EC). Twelve samples were collected *per* date and site to encompass the diversity of aquatic habitats in the river channel (96 samples in total, all dates and sites included). The samples were fixed with 96% ethanol and stored. In the laboratory, each sample was sorted under a binocular microscope, and taxa were identified down to the genus or species level (crustaceans, molluscs, insect larvae) or family/tribe levels (Diptera); Nematoda and Hydracarina were not identified further.

Following Tachet et al. (2010), two traits associated to invertebrate diet were considered: food items (9 modalities) and feeding behavior (8 modalities). For a given taxon and diet trait, an affinity score was assigned to each modality, ranging from "no affinity" (zero) to "high affinity" (3 for feeding behavior, 5 for food items). These values provide information on the intensity of the link between the taxa and each modality (*i.e.* low or high affinity) and the amplitude of the preference or tolerance of the taxon (*i.e.* the number of modalities used). We retained 8 modalities connected to the diet of primary consumer taxa for further analysis: deposit feeder, shredder, filter feeder, scraper (feeding behavior traits), small (<1 mm) and large (>1 mm) organic debris, and algae and macrophytes (food item traits). For each site and season, the diet trait modality affinities of the taxa (expressed as frequencies) weighted by their abundances were summed to determine the number of individuals in each modality at the community level (see Usseglio-Polatera et al., 2000 for further details). We run PERMANOVA on  $\log(x + 1)$  transformed data to test differences in community structure according to the diet traits (feeding behavior and food items). Then we tested for differences in the number of individuals in each modality to identify which modalities drove the difference observed for each diet trait, using non-parametric analysis of variance of aligned rank transformed data (Wobbrock et al., 2011) since the data did not meet the assumptions of parametric ANOVA. "Site" (2 levels), "season" (2 levels) and

their interactions were considered in both PERMANOVA and non-parametric analysis of variance. The *vegan* 2.5-7 (Oksanen et al., 2020) and *ARTool* 0.11.1 (Kay et al., 2021) R packages were used for PERMANOVA and variance of aligned rank transformed data, respectively.

## 2.5 Stable isotope analysis

Primary and secondary consumers were sampled in summer (July 2014 and July 2015) at sites upstream (S1, S2, S3, S4, S5) and downstream (S7, S8, S9) of the reservoirs (Figure 1). A Surber sampler was used to collect benthic invertebrates, which were identified at the family level and sorted into three feeding behavior categories: herbivores, detritivores, and omnivores (see Table S1 for list of taxa) following Tachet et al. (2010) and Usseglio-Polatera et al. (2000). Each invertebrate was cleaned and stored individually in a microtube. For the smallest taxa, up to 10 specimens were pooled to reach the minimum weight for stable isotope analyses (see below). Six to 18 samples *per* feeding group were collected at each site and date, depending on availability. Small invertivorous fish were caught by electrofishing in shallow, coarse substratum habitats (see Table S1 for list of taxa). Depending on their availability, 10–30 individuals were collected at each site, their total body length ranging between 50 and 129 mm. Lamprey larvae were caught by electrofishing in the soft substrate habitats where they had buried; catch success and body length varied greatly among sites (1–10 individuals, 60–160 mm, respectively). Crayfish were caught by electrofishing at sites S1 and S5 only (60 and 54 samples, respectively, body length 15–41 mm from rostrum to telson). Fish and lamprey were anaesthetized using a benzocaine bath, and all animals (fish, lamprey, crayfish) were euthanized and kept in a cooler in the field. The experiment complies with the French regulations on animal care and ethics (license number R-2012-JLB-02 and 201602051204637 delivered to INRAE) and electrofishing survey (permit number 2014-DDTM-SE-0036 and 2015-DDTM-SE-0019 delivered to INRAE).

Dorsal muscle (fish) or abdominal muscle (crayfish) samples were dissected in the laboratory, with special attention to avoid skin, scales and bones. Invertebrate and muscle samples were freeze-dried, ground to a homogenous powder using a mixer mill, weighed (*ca.* 0.9–1.1 mg) and encapsulated in tin foil.  $^{13}\text{C}$ : $^{12}\text{C}$ ,  $^{15}\text{N}$ : $^{14}\text{N}$  and C:N ratios were measured by continuous-flow isotope-ratio mass spectrometry, using mass spectrometers (Delta Plus XP and Delta V Plus, Thermo Finnigan) interfaced with elemental analyzers (Carlo Erba NC2500 and Costech 4010, Thermo Finnigan). Isotopic ratios were expressed using the conventional  $\delta$  notation as parts *per* thousand (‰). Five hundred and five samples were run in four separate batches. Repeat analyses of 12–15 certified standards showed maximum standard deviations (SD) of 0.29 ( $\delta^{13}\text{C}$ ) and 0.38 ( $\delta^{15}\text{N}$ ). Thirty-two samples were analyzed twice (*i.e.* 32 duplicates); the SD values of the duplicates were constantly lower than the SD values of the standards. All stable isotope analyses were performed at the Stable Isotopes in Nature Laboratory, University of New Brunswick (Canada).

C:N ratios were checked to identify possible lipid bias in  $\delta^{13}\text{C}$  values (Post et al., 2007). When C:N  $\geq$  3.5, the  $\delta^{13}\text{C}$  value was corrected using the equations of Post et al. (2007) for aquatic organisms.  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot and the standard ellipse areas (SEAc, sample size-corrected for  $n < 30$ ) that integrated 75% of the sample variance (also called isotopic niche breadths) were drawn to visualize the isotopic niches of aquatic consumers upstream (S1 to S5) and downstream (S7 to S9) of the reservoirs, using SIBER (Jackson et al., 2011). The *tRophicPosition* package (Quezada-Romegialli et al., 2018) was used to estimate the trophic position of consumers and the discrimination factor between C of algal and detrital origins ( $\alpha$ ), *i.e.* the contribution of each C source to the feed of consumers. Calculations were based on Bayesian models using stable C and N isotopes and combined with Markov chain Monte Carlo simulations (60,000 iterations). A two-baseline model with trophic enrichment factors on C and N was run for each site separately, using isotopic values of herbivores (primary consumers of algal C) and detritivores (primary consumers of detrital organic C) as end-members. The diet-tissue fractionation values of +3.7 ‰  $\delta^{15}\text{N}$  between mixed invertebrate diet and fish proposed by Bunn et al. (2013) for streams and rivers, and of +0.4 ‰  $\delta^{13}\text{C}$  *per* trophic level (Post, 2002) were used. Because mixing models are highly sensitive to variations in discrimination factors (Bond and Diamond, 2011), we kept the high SDs ( $\pm 2.4$  for  $\delta^{15}\text{N}$  and  $\pm 1.3$  for  $\delta^{13}\text{C}$ ) proposed as priors in Bayesian models in the literature to better reflect uncertainties in posterior estimates.

## 3 Results

### 3.1 Sediment and solutes

The median seasonal values of specific discharge were similar downstream (S8) and upstream (S6) of the reservoirs (Figure 2A), in line with the dam management rules whereby the water flow downstream of the dams should mimic the natural flow variations recorded upstream. Median seasonal turbidity varied between 0 and 1098 NTU and was lower downstream (Figure 2B). Similarly, the seasonal suspended solid (SS) concentrations were 85–88% lower downstream (Figure 2C). R-square values for the fitted regressions between turbidity and SS were 0.96 and 0.84 at S6 and S8, respectively. Using regressions, the estimated sediment fluxes were  $19.2 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$  ( $\pm 11\%$ ) upstream and  $11.6 \text{ t}\cdot\text{km}^{-2}\cdot\text{yr}^{-1}$  ( $\pm 14\%$ ) downstream for the September 2015–August 2016 water year (Table 1). The average ( $\pm$  SD) C:N molar ratios of SS were higher upstream, notably in spring ( $11.1 \pm 0.97$  vs.  $7.54 \pm 0.83$ ) and summer ( $9.43 \pm 0.94$  vs.  $7.82 \pm 1.47$ ), indicating a greater contribution of phytoplankton-derived particles to organic matter in the SS downstream of the reservoirs (Figure 2D). The mean  $\text{NO}_3$ ,  $\text{PO}_4$  and DSi concentrations (Figures 2E–G) varied seasonally. P concentrations were significantly and systematically lower downstream ( $p < 0.001$ ) except in winter, whereas between-site variations in N concentrations were not consistent. Similarly, DSi was lower downstream in all seasons except winter ( $p < 0.001$ ).

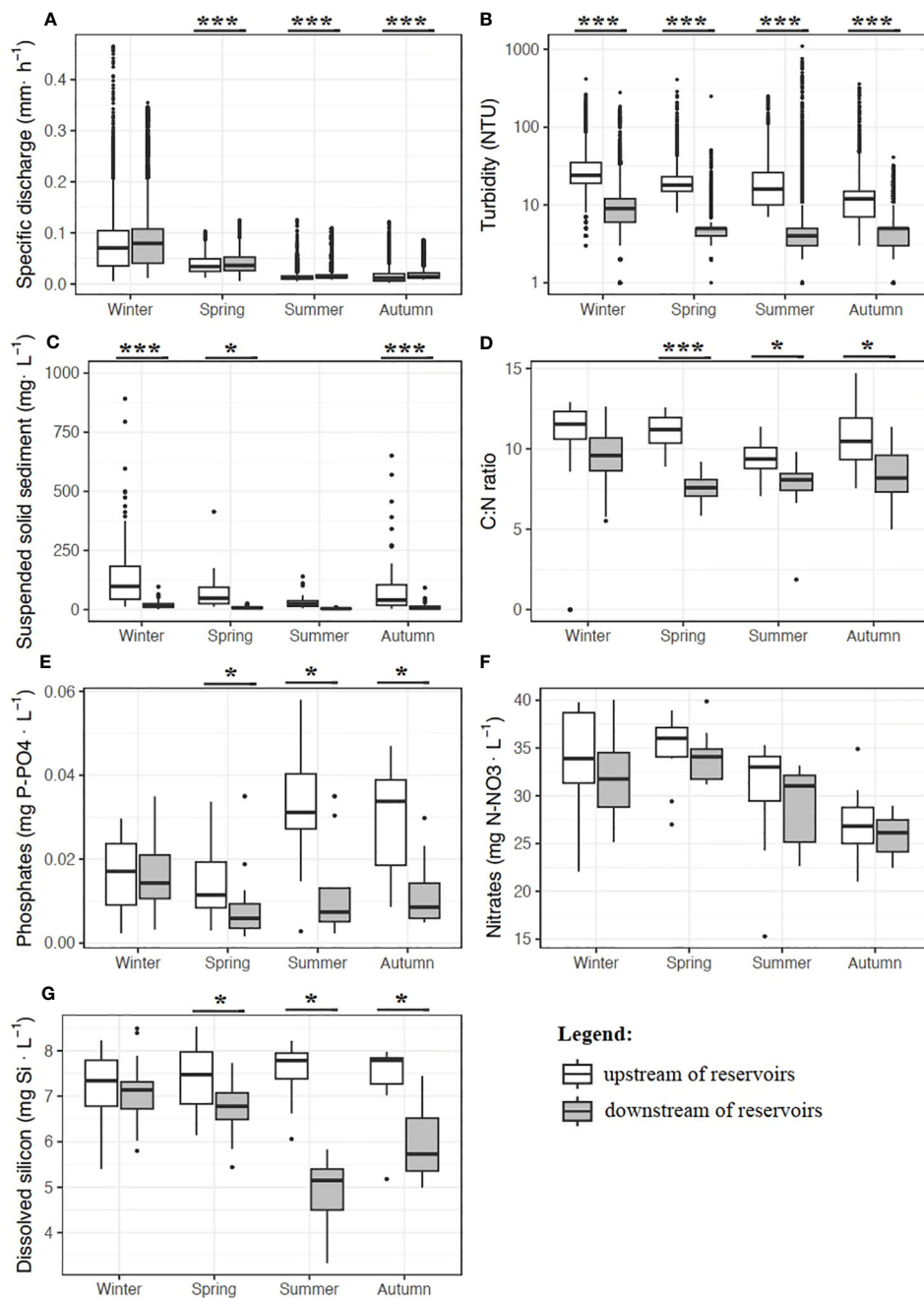


FIGURE 2

Seasonal variations of specific discharge (A), water turbidity (B), the suspended solid concentration (C), the molar ratio of particulate C:N (D), phosphates (E), nitrates (F) and dissolved silicon (G) concentrations in the Sêlune River, upstream (white) and downstream (gray) of the reservoirs. Each box plot shows the 25<sup>th</sup> and 75<sup>th</sup> percentiles around the median; vertical lines represent 1.5 times the interquartile range and dots are outliers. Stars indicate significant differences between upstream and downstream sites (\*\*\* $p < 0.001$ ; \* $p < 0.05$ ).

### 3.2 Photosynthetic biofilm

The chlorophyll *a* concentration in the water was higher downstream of the reservoirs irrespective of season, and the difference was significant in summer (Figure 3A;  $p < 0.01$ ). The N:P molar ratio based on N-NO<sub>3</sub> and P-PO<sub>4</sub> concentrations ranged from 180 to 10,300 between sites and seasons (Figure 3B) and were

significantly higher downstream of the reservoirs in summer and fall ( $p < 0.001$ ), indicating potential P limitation for primary producers downstream. The percentage of organic matter in the biofilm samples was significantly lower upstream in spring ( $p < 0.001$ ), indicating more inorganic sediment embedded in the biofilm matrix (Figure 3C). The biofilm algal community upstream of the dams mostly contained benthic species ( $85.6 \pm$



TABLE 1 Total rainfall and estimated runoff and sediment flux upstream and downstream of the Sélune River dams from January 2015 to March 2017.

|                   | Total rainfall (mm) | Upstream dams (S6) |   | Downstream dams (S8) |   |
|-------------------|---------------------|--------------------|---|----------------------|---|
|                   |                     | Total runoff (mm)  | Total sediment flux (t·km <sup>-2</sup> ) | Total runoff (mm)    | Total sediment flux (t·km <sup>-2</sup> ) |
| Jan.2015–Aug.2015 | 522                 | 248                | 12.8 (±11%)                               | 311                  | 5.2 (±18%)                                |
| Sep.2015–Aug.2016 | 758                 | 355                | 19.2 (±11%)                               | 443                  | 11.6 (±14%)                               |
| Sep.2016–Mar.2017 | 324                 | 61                 | 1.5 (±17%)                                | 76                   | 0.5 (±29%)                                |

Percentage values in parentheses represent the deviation between the mean and the 95% CI values estimated from linear regressions.

10.9%) and a few planktonic ( $2.9 \pm 1.2\%$ ) and benthopelagic ( $6.1 \pm 5.8\%$ ) species (Figure S2). Conversely, the contribution of planktonic and benthopelagic species increased downstream to average  $8.2 \pm 6.6\%$  and  $17.6 \pm 19.4\%$ , respectively (Figure S2). Algal biomass growth (chlorophyll *a*,  $\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ ) and photosynthetic activity (maximum rETR,  $\mu\text{mol e}^{-}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) in the biofilm decreased in fall and winter to reach values close to zero (Figures 3D, E). Biomass growth was higher in spring and fall downstream of the reservoirs, yet not significantly so. The maximum rETR values were very similar upstream and downstream of the reservoirs. Median values of the autotrophic index ranged between 1.9 and 2.3 in spring and summer upstream and downstream the reservoirs, indicating a biofilm where autotrophy and heterotrophy were balanced (Figure 3F), while values tended to increase toward heterotrophy in fall and winter upstream of the reservoirs ( $p < 0.02$ ).

### 3.3 Benthic invertebrates

Irrespective of season, the abundance of benthic invertebrates caught in Surber net samples was higher downstream (12,273 individuals in spring; 17,267 in fall) than upstream (8,927 in spring; 6,613 in fall). A total of 45,080 individuals were sorted and identified. Among them, 39,653 (88.0%) and 36,332 (80.6%) were identified as primary consumers according to their feeding behavior trait (deposit feeder, shredder, filter feeder, scraper) or food item trait (small or large organic debris, algae, macrophytes), respectively. The most influential taxa are listed in Table S3.

The community structure of invertebrate primary consumers significantly differed between sites for the food item trait (PERMANOVA, Site pseudo- $F = 15.26$  and  $p = 0.001$ ; Season pseudo- $F = 1.41$  and  $p = 0.2$ ; Station  $\times$  Season pseudo- $F = 0.69$  and  $p = 0.5$ ) and for the feeding behavior trait (Site pseudo- $F = 16.59$  and  $p = 0.001$ ; Season pseudo- $F = 1.28$  and  $p = 0.2$ ; Station  $\times$  Season pseudo- $F = 1.0$  and  $p = 0.3$ ) but not between seasons (Figure 4). Primary consumer taxa were significantly more abundant downstream than upstream of the reservoirs, regardless of the modalities and traits (analysis of variance on aligned rank transformed data, see Table 2). No significant seasonal variation was detected except for filter feeders that were more abundant downstream the reservoirs in fall only. Scrapers and algae eaters were the two most abundant modalities found among primary consumers irrespective of season.

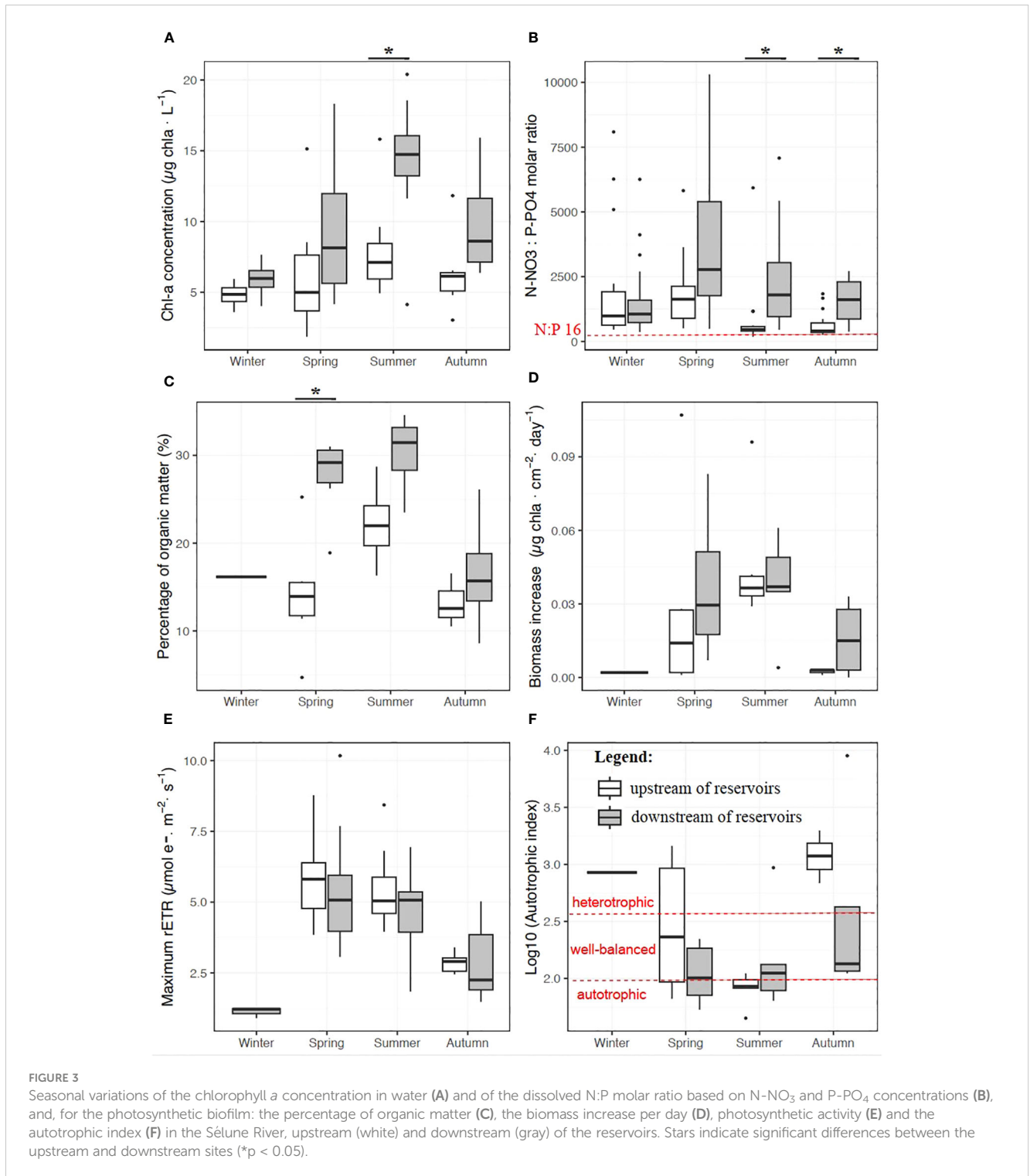
### 3.4 Stable isotopes and food web analyses

The isotopic values of the samples collected along the Sélune River ranged from  $-21.3\text{‰}$  to  $-32.6\text{‰}$  and from  $0.8\text{‰}$  to  $16.9\text{‰}$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively (Figure 5A). Invertebrate herbivores (grazers and scrapers pooled) were consistently  $^{13}\text{C}$ -depleted compared to detritivores (shredders), while omnivores and crayfish displayed intermediate values. As expected, invertivorous fish were  $^{15}\text{N}$ -enriched compared with invertebrates. The isotopic niche breadths (ellipses including 75% of the variance) upstream of the dams (sites S1 to S5 pooled) and downstream of the dams (sites S7 to S9 pooled) mostly overlapped for invertebrates but not for fish and lamprey (Figure 5A).

Using invertebrate herbivores and detritivores as end-members for Bayesian mixing models, invertebrate omnivores showed trophic positions of 2.5, and C of algal and detrital origin equally contributed to their tissues (Figure 5B). Crayfish followed a similar pattern, with a slightly higher trophic position (2.7). Simulations confirmed that fish had the highest trophic position ( $>3$ ), and revealed that fish and juvenile lamprey shifted toward a higher algal-C contribution downstream of the dams. Posterior distributions of coefficient  $\alpha$  at each site showed that detrital C dominated in aquatic fauna only at the most upstream site S1, whereas algal C prevailed downstream of the dams at S7 and S8, and equal contributions of detrital and algal C were observed at S2, S3, S4, S5 and S9 (Figure 5C).

## 4 Discussion

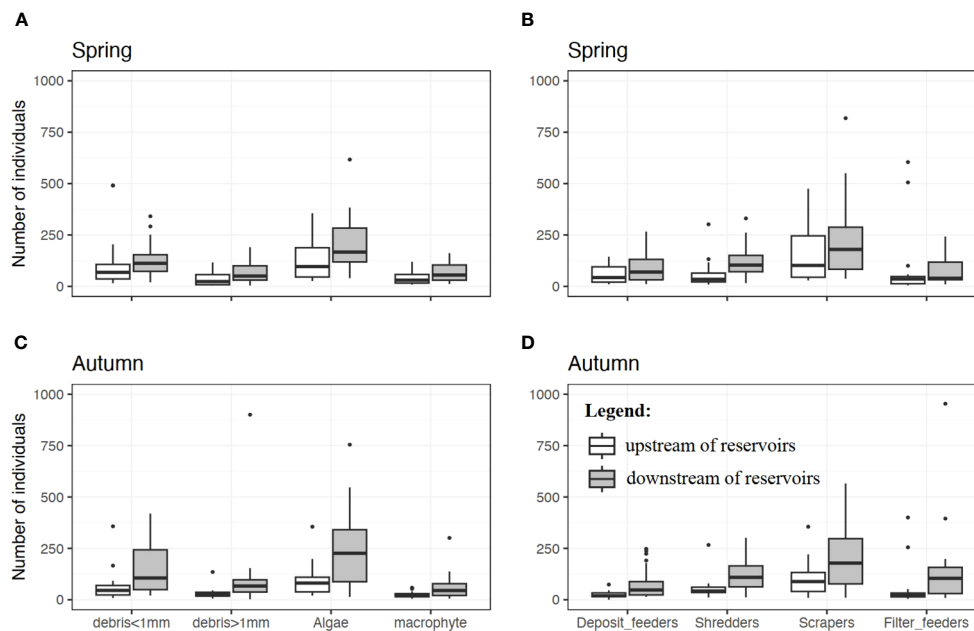
In the study, we explored the mechanisms whereby two sequential large dams and their reservoirs can control the balance between detritus-based and algae-based energy pathways in aquatic food webs along a river continuum. Investigations were made on the Sélune River (Normandy, France), a small-coastal stream draining an agricultural catchment with high sediment runoff and discharging into the Mont Saint-Michel Bay (France). The river has been impounded by two dams (16 and 36 m high) in its lower part for a century. As anticipated, the two reservoirs significantly retained sediments, phosphates and silicates for which concentrations were much lower downstream of the reservoirs. There were no large tributaries flowing into the reservoirs, nor was there a specific land use pattern in the vicinity of the reservoirs, that could have influenced water discharge and dissolved nutrient



concentrations. Measures of the photosynthetic activity in epilithic biofilm showed no clear differences, but their biomass growth tended to be higher downstream of the reservoirs in spring and fall, and so was the abundance of herbivores in the benthic invertebrate community. A greater contribution of algae-based energy to aquatic invertebrates and fish downstream of the reservoirs was corroborated by stable isotopes analysis, clearly suggesting that the dams caused a major discontinuity in the

origin of C entering and flowing in aquatic food webs along the river continuum.

Identifying the relative importance of different energy sources is a basic prerequisite for understanding river food web dynamics and ecosystem restoration. Aquatic primary consumers rely on two major basal sources defined by the origin of their C component – aquatic (autochthonous) or terrestrial (allochthonous) primary producers. The contribution of these two C sources to higher



**FIGURE 4** Abundance of invertebrate primary consumers in the Sélune River upstream (white) and downstream (gray) of the reservoirs. Box-plots display the spring (A, B) and fall (C, D) values according to the food items they ingest (A, C) and their feeding behavior (B, D). Each box-plot shows the 25<sup>th</sup> and 75<sup>th</sup> percentiles around the median; the vertical line represents 1.5 times the interquartile range, and dots are outliers.

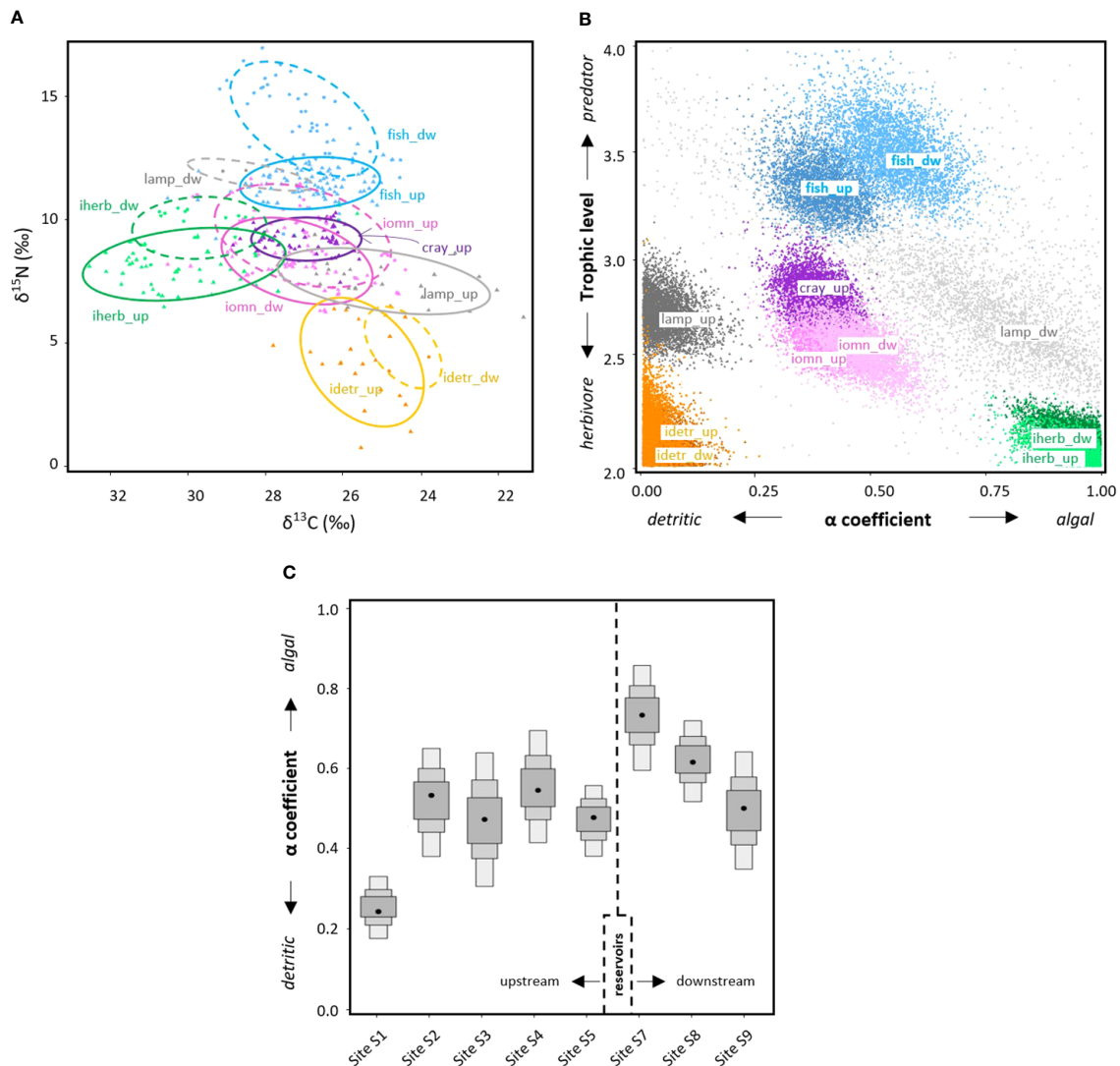
trophic levels, notably fish, depends on the position along the upstream–downstream gradient (Vannote et al., 1980; Finlay, 2001; Hoeninghaus et al., 2007). Several studies have illustrated significant contributions of terrestrial C to small headwater streams and large rivers, where terrestrial organic matter inputs from riparian trees (headwater streams) and floodplains (large rivers) supply the aquatic food webs (Reid et al., 2008; Wang et al., 2014; Soto et al., 2019; Roussel et al., 2021; Wang et al., 2021). Seasonal variations in discharge, local stream geomorphology and riparian communities also drive the food web reliance on C sources (Ou and Winemiller, 2016; Venarsky et al., 2020), outlining the complex balance of allochthonous and autochthonous C supply to the biomass of primary consumers and transfer to higher trophic

levels. In this context, artificial barriers to river flow and related impoundments have major effects on the downstream ecosystem metabolism. Chowanski et al. (2020) observed that the gross primary production in a large, temperate, oligotrophic river increased downstream of a large reservoir, and postulated that sediment retention and lower water turbidity downriver increased light availability to aquatic producers. Such a pattern seems to be commonplace in literature on dams. In Mediterranean rivers, artificially stable flow regimes below dams promoted a shift from detritus-based to algae-based food webs (Mor et al., 2018). In large tropical rivers as in the Mekong basin, a seasonal combination of algae and terrestrial energy sources supports fish production, but the contribution of algal C appears greater below dams (Ou and

**TABLE 2** Analysis of variance (aligned rank transformed data) of the food items and feeding behavior of benthic invertebrates showing the effect of “site” (upstream or downstream of the dams), “season” (spring or fall) and their interaction.

| Food items       | Organic debris, large (>1 mm) |               | Organic debris, small (<1 mm) |                   | Algae             |                   | Macrophytes       |               |
|------------------|-------------------------------|---------------|-------------------------------|-------------------|-------------------|-------------------|-------------------|---------------|
|                  | F <sub>1,90</sub>             | p             | F <sub>1,90</sub>             | p                 | F <sub>1,90</sub> | p                 | F <sub>1,90</sub> | p             |
| Site             | 12.80                         | <b>0.0006</b> | 23.51                         | <b>&lt;0.0001</b> | 15.94             | <b>0.0001</b>     | 12.52             | <b>0.0006</b> |
| Season           | 0.10                          | 0.7           | 0.51                          | 0.5               | 0.003             | 1                 | 1.56              | 0.2           |
| Site x Season    | 1.11                          | 0.3           | 0.77                          | 0.4               | 1.19              | 0.3               | 0.06              | 0.8           |
| Feeding behavior | Deposit feeder                |               | Shredder                      |                   | Filter feeder     |                   | Scraper           |               |
|                  | F <sub>1,90</sub>             | p             | F <sub>1,90</sub>             | p                 | F <sub>1,90</sub> | p                 | F <sub>1,90</sub> | p             |
| Site             | 10.19                         | <b>0.002</b>  | 32.30                         | <b>&lt;0.0001</b> | 18.0              | <b>&lt;0.0001</b> | 7.68              | <b>0.007</b>  |
| Season           | 2.88                          | 0.09          | 2.29                          | 0.1               | 3.95              | <b>0.05</b>       | 0.47              | 0.5           |
| Site x Season    | 0.01                          | 0.9           | 2.33                          | 0.1               | 4.27              | <b>0.04</b>       | 0.15              | 0.7           |

Significant p-values are in bold.



**FIGURE 5**  
 $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of samples collected in the Sélune River (A). Isotopic niche breadths (SEAc) of each invertebrate consumer group (iherb, herbivores; idetr, detritivores; iomn, omnivores), crayfish (cray), lamprey (lamp) and fish are depicted for sites located upstream (up, solid ellipses) and downstream (dw, dashed ellipses) of the dams. Simulated values of the trophic position and carbon-origin discrimination coefficient ( $\alpha$ ) obtained from end-members Bayesian mixing models for consumers upstream and downstream of the dams (B). The dual contributions of algal vs. detrital C origin to aquatic fauna is displayed along the Sélune River profile (C), each box indicating 50%, 75% and 95% Bayesian credibility intervals around the median (dot); the dashed line shows the position of the reservoirs.

Winemiller, 2016). Similarly, algae contribute more to the diet of macroinvertebrates in the Colorado River below Glen Canyon dam, while terrestrial-based food increases further downstream with increasing water turbidity and organic matter inputs from tributaries (Wellard Kelly et al., 2013). Various case studies in both temperate and tropical ecosystems highlight a shift toward greater assimilation of algal C by aquatic consumers downstream of reservoirs in large rivers. However, little attention has been given to the pattern of C flow in small stream food webs below such large reservoirs.

Carbon and N stable isotope ratios of invertebrate and fish tissue samples were used to estimate the contribution of basal sources supporting aquatic food webs along the course of the Sélune River. Using long-lived (>6 months) primary consumers

in mixing models to limit stochastic isotopic signatures of basal sources (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999), we found a 3-fold variation in the contribution of the algal energy pathway within a 70-km-long stretch of river. At 15 km from the source, 75% of the food web C was derived from terrestrial detritus assimilated by invertebrate shredder species, notably Limnephilidae (*Halesus* sp., *Chaetopteryx* sp., *Limnephilus* sp., *Potamophylax* sp.) and Sericostomatidae (*Sericostoma* sp.). Consistent with theory (Vannote et al., 1980; Junk et al., 1989; Finley 2001; Hoeinghaus et al., 2007), this result confirms the dominant role of terrestrial supplies in the upstream reaches of the Sélune River (Site S1, Figures 1, 5C). However, the contribution of algal C equalled the detrital contribution at most sites, indicating that autochthonous and allochthonous sources of energy together

sustained aquatic food webs in most of the river course. This result was somehow unexpected owing to the high sediment load and water turbidity in the river supposed to hamper primary production. Our simulations may have exaggerated the contribution of algae-derived C in the river food webs because we collected our samples in shallow, fast-flowing habitats where primary production is known to be at its maximum in rivers (Finlay, 2004). However, many studies have shown that agriculture in industrialized countries is a major source of nutrients in rivers and coastal waters, involving a number of effects including the increase in biomass of primary producers (e.g. Paerl et al., 2011; Grizzetti et al., 2012; Dupas et al., 2015; Boardman et al., 2019). Accordingly, the high concentration in nutrients is a favorable background to aquatic primary producers in the Sélune River, and this likely promotes the influence of the algae-based pathway in aquatic food webs despite high water turbidity and sediment loads.

The annual flux of sediment estimated in the Sélune River upstream of the reservoirs ( $19.2 \text{ t.km}^{-2}.\text{yr}^{-1}$ ) is consistent with the observed pattern of European Atlantic rivers with a similar catchment size (Vanmaercke et al., 2011). Despite greater uncertainty about the sediment load estimates downstream of the dam where suspended sediment quantities were sometimes very low and more difficult to measure accurately, the annual flux of sediment dropped ( $11.6 \text{ t.km}^{-2}.\text{yr}^{-1}$ ) downstream of the reservoirs. This corresponds to an amount of  $12,077 \text{ t.yr}^{-1}$  and  $9,013 \text{ t.yr}^{-1}$  upstream and downstream of the dams, respectively, meaning that the reservoirs trapped and stored about  $3 \cdot 10^3$  tons of sediment from September 2015 to August 2016. With 758 mm rainfall, this water year was consistent with the inter-annual variability observed on the river. One immediate consequence was a drastic drop in water turbidity downstream of the reservoirs irrespective of season (Figure 2B) that set off a chain reaction in the entire river food web, from epilithic biofilm to invertivorous fish. The percentage of inorganic sediment in the epilithic biofilm samples was lower downstream of the reservoirs. Seasonal biofilm dynamics were substantial everywhere, with higher biomass and productivity in spring and summer. Biofilm growth on a virgin glass support measured as the increase in chlorophyll *a* per day was slightly, but not significantly, higher downstream than upstream of the reservoirs in spring and fall. Moreover, the trophic nature of the biofilm estimated using the autotrophic index (Weber, 1973) remained similar to the autotrophic threshold downstream irrespective of season, whereas heterotrophy prevailed upstream of the reservoirs in fall. This result was corroborated by measurements of the C:N molar ratio of suspended sediment. The ratio of organic matter exported from soils was close to the expected values (Kendall et al., 2001) upstream of the reservoirs, but it strongly decreased downstream in spring and summer when solar radiation, water turbidity and water temperature were most favorable to primary producers. It indicates that the reservoirs produced a fraction of organic matter – algae-derived C drifting downstream – as also supported by continuous monitoring of the chlorophyll *a* concentration in the water column downstream of the reservoirs (Fovet et al., 2020), hence the presence of pelagic forms (notably diatoms) in the epilithic biofilm matrix downriver.

Therefore, the composition of the epilithic biofilm differed remarkably downstream of the reservoirs as a response to lower water turbidity, siltation, and the input of pelagic microalgae drifting from the reservoirs.

In the Sélune River, the higher abundance of herbivores (algae eaters, scrapers) within invertebrate communities downstream of the reservoirs suggests an enhancement of the algal pathway. The shift from detritivores to herbivores in invertebrate communities has been reported in river food webs downstream of large reservoirs (Mor et al., 2018). Stable isotope analysis of aquatic consumers, invertebrates and fish, gives support to this assumption. We estimated that an average 75% of the C flowing into the river food web 1 km downstream of the reservoirs was derived from aquatic primary producers, *i.e.* + 25% compared to the river food web just upstream of the reservoirs. This effect was still perceived 4 km downstream of the reservoirs (60% of algae-derived C in the food web) and stopped further downstream where equal contributions of autochthonous and allochthonous C were found. Phytoplankton that drifted from the reservoirs and deposited on the epilithic biofilm likely contributed to higher algal C contribution in the downstream food web, as reported in other studies (Angradi, 1993; Hoeinghaus et al., 2007; Doi et al., 2008; Ru et al., 2020). According to methodological recommendations (Cabana and Rasmussen, 1996; Vander Zanden and Rasmussen, 1999), invertebrate primary consumers (herbivores and shredders) were used in our mixing models, and it was not possible to estimate the contribution of a specific basal food sources (*i.e.* phytoplankton *vs.* phytobenthos). However, nine kilometers downstream of La-Roche-Qui-Boit reservoir (Site S9, Figure 1), equal contributions of algal C and detrital C to aquatic consumers were reported, meaning that the effect of the dams on C flow in the aquatic food webs had disappeared. This suggests that terrestrial-based food sources increased in the lower reaches of the Sélune River, outlining the possible influence of organic matter inputs from downstream tributaries, notably the Beuvron River (Figure 1).

In our analysis, values of nutrient concentrations, benthic algal and invertebrate communities and stable isotope ratios on aquatic organisms were considered jointly, revealing subtle interactions between C and nutrient biogeochemical cycles in the Sélune River. It also outlines mechanisms whereby large dams and reservoirs can affect these cycles and food web functioning in a small agricultural stream. Primary producers rely upon dissolved inorganic C (DIC) that originates from the terrestrial ecosystem (e.g.  $\text{HCO}_3^-$  and dissolved  $\text{CO}_2$  from chemical weathering and soils), respiration of the aquatic ecosystem, and diffusion of atmospheric  $\text{CO}_2$  into water (Mook & Tan, 1991; Finlay, 2003; Liu et al., 2011). During photosynthesis, algae preferentially assimilate  $^{12}\text{C}$  (Hecky and Hesslein, 1995), but when productivity is high and DIC concentration is depleted, less discrimination against  $^{13}\text{C}$  can lead to higher  $\delta^{13}\text{C}$  values in primary producers. Moreover, a lower DIC concentration can promote the diffusion of atmospheric  $\text{CO}_2$  into water. Since the  $\delta^{13}\text{C}$  value of atmospheric  $\text{CO}_2$  is high (about  $-8\%$ , Keeling et al., 2010), primary producers are expected to be  $^{13}\text{C}$ -enriched in more productive rivers (Roussel et al., 2014). In the Sélune River, the contribution of algal C to aquatic food webs was higher downstream of the reservoirs, but we did not find higher

$\delta^{13}\text{C}$  values in herbivorous invertebrates (Figure 5A). Fluorescence measurements on the epilithic biofilm did not reveal higher photosynthetic activity downstream of the reservoirs, and it is likely that the observed higher algal-C contribution to the aquatic food web downstream of the reservoirs was a consequence of a lower detrital-C contribution rather than higher primary production. Indeed, both  $\text{PO}_4$  measurements and the N:P molar ratios in water samples showed that phosphorus availability decreased downstream of the reservoirs. Phosphorus is essential to freshwater primary producers, but the blooming and sinking of phytoplankton in reservoirs can massively reduce its availability to downstream food webs during specific periods of the year (Chen et al., 2014; Lu et al., 2016; Bao et al., 2018), notably in large reservoirs where water residence time is high (Ma et al., 2018). Therefore, we argue that low phosphorus availability restricted primary production in reaches downstream of the reservoirs in the Sélune River, despite less water turbidity and better light availability. Taken together, those results illustrate how large reservoirs on a small, agricultural stream with high nutrient concentrations and sediment loads could affect the balance between the algae-based and the detritus-based energy pathways, and modulate C flow in the riverine food webs from primary producers to predators.

Finally, our study outlines some of the drivers of the reliance on different C sources in the food web of a small, coastal stream with high sediment loads. We notably highlighted mechanisms whereby large dams and reservoirs can induce a major discontinuity in the natural process of C flow in aquatic food webs and along the river continuum. By changing the downstream transfer of suspended particulate matter and dissolved nutrients, the two dams on the Sélune River artificially maintained environmental conditions that promoted the contribution of the algae-based pathway the riverine food webs. This conclusion comes from data and samples collected between 2015 and 2017, before the removal of the two dams. The dismantling operations were completed by early 2023, and the downstream transfer of sediment and solutes are being restored after a century of disruption (Fovet et al., 2023). Profound impacts on the river ecosystem are expected from now, and our results will help understand how nutrients and C flow in food webs will change during the river restoration process. We anticipate that the prevalence of algal C in aquatic consumers should fade out rapidly downstream of the reservoirs. Except in the upstream reaches and headwater tributaries where detrital C may prevail, equal contributions of algal and detrital C to the aquatic food web should be observed along the Sélune River continuum. Moreover, the expected return of diadromous species, e.g. Atlantic salmon and sea lamprey (*Salmo salar*, *Petromyzon marinus*), will disseminate marine-derived nutrients throughout the watershed, as observed in the Elwha River and the Penopscot River (Duda et al., 2011; Tonra et al., 2015; Zydlewski et al., 2023). European eel (*Anguilla anguilla*) will also colonize the headwaters, and this species is known to have a large impact on other fishes in the Sélune River (Lizé et al., 2023). These new driving forces will require attention in order to understand how the river ecosystem and the aquatic food webs will be restored along the Sélune River over the next decade.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The animal study was approved by “Comité Rennais en matière d'éthique et d'expérimentation animale”. The study was conducted in accordance with the French legislation and institutional requirements on animal care and ethics.

## Author contributions

J-MR conceived the idea, supervised the project and wrote the manuscript. OF and AC (sediment and solutes), AP and CG (photosynthetic biofilm), HR-P and CP (macroinvertebrates) and J-MR (stable isotopes and food web) designed the project, collected the samples, co-supervised the work and wrote the corresponding text sections of early drafts. MP, CG, GF, DH contributed to data and sample collection in the field, processed the samples in the laboratory and prepared the data. OF, CG, AP, HR-P, OD and J-MR analyzed the data, prepared the illustrations, and revised the manuscript. AT and MC developed and managed the geographic information system SISélune; SF and LS managed the project. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1250892/full#supplementary-material>

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