

## RESEARCH ARTICLE

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# Long-term reconstruction of energy fluxes in an alpine river: Effects of flow regulation and restoration

Gabriele Consoli<sup>1,2</sup>  | Andre R. Siebers<sup>3</sup> | Andreas Bruder<sup>4</sup>  | Christopher T. Robinson<sup>1,2</sup>

<sup>1</sup>Department of Aquatic Ecology, Eawag, Duebendorf, Switzerland

<sup>2</sup>Institute of Integrative Biology, ETH-Zürich, Zürich, Switzerland

<sup>3</sup>Centre for Freshwater Ecosystems, La Trobe University, Wodonga, Victoria, Australia

<sup>4</sup>Institute of Microbiology, University of Applied Sciences and Arts of Southern Switzerland (SUPSI), Mendrisio, Switzerland

## Correspondence

Gabriele Consoli, Department of Aquatic Ecology, Eawag, Duebendorf 8600, Switzerland.  
Email: [gabriele.consoli@unil.ch](mailto:gabriele.consoli@unil.ch)

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## Abstract

Flow regulation of montane and alpine headwater streams can fundamentally alter food web structure and energy flows through changes in productivity, resource availability, and community assembly. Dam flow-release schemes can be used to mitigate the environmental impacts of flow regulation via environmental flows, which can increase discharge variability and other ecologically important hydrological properties. In particular, managed floods can reintroduce disturbance to the system and stimulate the reactivation of physical habitat dynamics. However, how managed floods might restore ecosystem processes is virtually unknown. In this study, we examined patterns in potential energy fluxes before, during and after a long-term experimental flood program on the river Spöl, a regulated alpine River in southeast Switzerland. We used benthic samples collected during long-term monitoring and stable isotope analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of macroinvertebrates and their potential food sources to reconstruct secondary production, and potential energy fluxes, over a 20-year study period. The experimental floods did not alter the relative importance of basal resources but resulted in a considerable decline in secondary production, which remained low after the discontinuation of the floods. Our data suggest that a lack of recolonization by mosses following the discontinuation of the experimental flood program on the river Spöl may have driven patterns in energy fluxes by limiting macroinvertebrates using mosses for habitat. The effects of environmental flows on energy flows in this system thus depend on flood disturbance and the environmental context following the discontinuation of floods.

## KEYWORDS

environmental flows, experimental floods, food web, macroinvertebrates, secondary production, stable isotopes

## 1 | INTRODUCTION

Flow regulation from damming is a primary source of river alteration worldwide (Bunn & Arthington, 2002; Lehner et al., 2011; Nilsson

et al., 2005), with substantial global effects on nutrient cycling (Maavara et al., 2020), sediment regimes (Vörösmarty et al., 2003), and freshwater biodiversity (Dudgeon et al., 2006; Reid et al., 2019). Below a dam, the alteration of flow, sediment, organic matter, and

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wood regimes causes major in-stream environmental changes, and limits connectivity between aquatic and terrestrial ecosystems (Petts & Gurnell, 2005; Ward & Stanford, 1983). These effects are particularly pronounced in rivers where seasonal flood disturbance controls geomorphological dynamics and ecological processes, such as for alpine rivers (Bundi, 2010). Alpine rivers have been extensively regulated to generate hydroelectricity (Truffer et al., 2001; Wehren et al., 2010), altering the natural, seasonal cycles of disturbance that shape community structure and fluvial functional properties (Milner et al., 2001). These alterations ultimately modify the river's natural habitat template, and relationships between abiotic conditions, biota, and processes (Bunn & Arthington, 2002; Poff & Zimmerman, 2010).

In unregulated alpine rivers, specific life history and functional adaptations of biota confer resilience to the elevated bedload scouring, high suspended sediment transport, and seasonal variation in resource availability caused by intense rainfall or snow and ice-melt-driven floods (Milner et al., 2001). In contrast, stable flow regimes under regulation can result in the build-up of periphyton and benthic organic matter, favoring taxa with more cosmopolitan life history traits and ecological requirements (Poff et al., 2007), and increasing the density of generalists (Robinson et al., 2018; Robinson & Uehlinger, 2008). In other regulated rivers, stable flows and increased primary productivity have been shown to alter the relative importance of organic resources, shifting the ecosystem's trophic base towards autotrophy (as in the Colorado River, Cross et al., 2011). Associated increases in the secondary production of invasive, generalist taxa can result in the local extinction of species (Bunn & Arthington, 2002; Poff & Zimmerman, 2010), generation of trophic dead-ends (Cross et al., 2010; Vinson & Baker, 2008), constraints on food-web attributes and interactions (McHugh et al., 2010; Sabo et al., 2009; Wootton et al., 1996), and changes in energy pathways and trophic linkages (Power et al., 1996). Reductions in the number of floods caused by damming can also drive complex, unpredictable changes in the structure of stream food webs (e.g., Mor et al., 2018). Despite the strong dependence of alpine rivers on seasonal floods, little is known of how flow regulation affects their functional as opposed to structural properties.

In recent times, river authorities have begun developing methods to modify water release schemes from dams (environmental flows) to mitigate the eco-morphological degradation of rivers (Acreman & Ferguson, 2010; Owusu et al., 2021) and the deterioration of ecosystem services caused by flow regulation (Auerbach et al., 2014). Environmental flows are commonly designed to reintroduce selected components of the original flow regime to achieve specific eco-morphological targets (Gillespie et al., 2015; Konrad et al., 2011; Tonkin et al., 2021; Yarnell et al., 2015), such as the simulation of seasonal floods by implementing periodic experimental floods (Konrad et al., 2011). Although high implementation costs can limit the application of experimental floods (see Andrews & Pizzi, 2000; Scheurer & Molinari, 2003), several studies on systems such as the Colorado (Melis, 2011) and Spöl (Robinson et al., 2018) have demonstrated the utility of experimental flood programs to restore ecological dynamics from flow disturbance (Cross et al., 2011, 2013; Korman et al., 2011;

Robinson et al., 2018). In particular, the application of a functional perspective involving, for example, trophic interactions, can explain observed counterintuitive patterns, such as the rainbow trout-chironomid-simuliid trophic nexus on the Colorado River (Cross et al., 2011). However, few studies have looked at flow restoration from a functional/trophic point of view (e.g., Cross et al., 2011; Korman et al., 2011; Sabo et al., 2018; Weisberg & Burton, 1993).

In this study, we used macroinvertebrate data collected before, during, and after the course of a long-term experimental flood program on the Spöl, Switzerland (Robinson et al., 2018) to investigate the effects of artificial floods on the trophic structure and energy fluxes in the river. Specifically, we (i) estimated the secondary production of macroinvertebrates using biomass data from pre, during, and post-flood program periods, (ii) reconstructed dietary requirements using stable isotope (C and N) analysis of macroinvertebrates and potential food sources, and (iii) integrated trait information on food preferences (Tachet et al., 2010) to estimate energy fluxes within the community. We expected to see an inverse relationship between secondary production and disturbance, and hypothesized that community re-assembly from the floods would be linked to changes in trophic state (Dodds, 2007; Marcarelli et al., 2011).

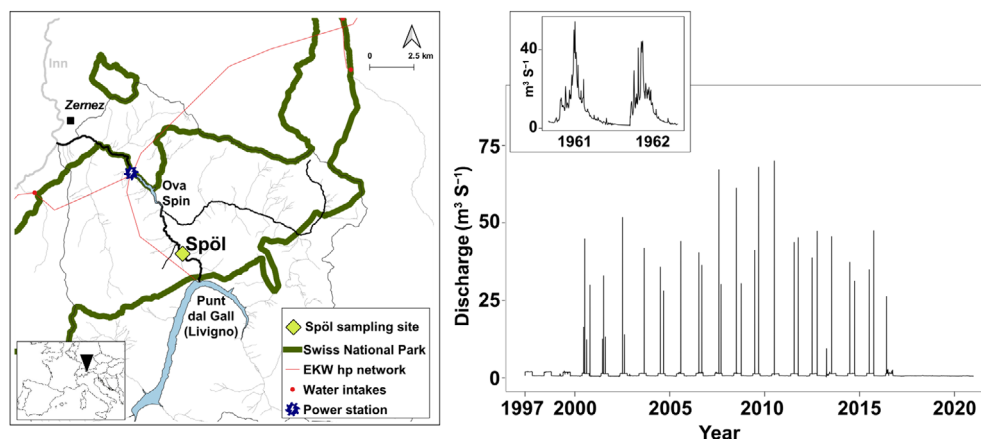
## 2 | METHODS

### 2.1 | Study site and the experimental flood program

The Spöl is a fifth-order regulated river located in the central Alps. The regulated reach begins at the Italian/Swiss border where the Punt dal Gall dam (built in the 1960s) creates the Livigno reservoir. The study site is located inside the Swiss National Park in a residual flow reach ~2.5 km below Punt dal Gall (Figure 1) and ~3.5 km above a second reservoir (Ova Spin). It is a riffle-run section (Figure S1) characterized by boulder-cobble substrate, flowing in a forested area mostly composed of *Pinus* sp., while riparian vegetation is mostly grass and sporadic willow shrubs (see Robinson, Aebischer, and Uehlinger (2004) for details on the study site).

The experimental flood program (Scheurer & Molinari, 2003) started in 2000 to counteract the benthic habitat degradation imposed by prolonged stable discharge conditions under flow regulation. Up to three floods, simulating seasonal high flows, were released each year from Punt dal Gall (Figure 1). Simultaneously, a long-term survey program was initiated to monitor the ecological responses to the floods. Thirty-two floods were released until 2016 when the program was discontinued due to Polychlorinated biphenyls (PCBs) contamination after dam retrofitting (Klose, 2021). However, ecological monitoring was still carried out to assess ongoing ecosystem dynamics following the lack of flow disturbance. The periodic flood disturbance enhanced streambed conditions for biota by reducing substrate clogging and removing filamentous algae (Uehlinger et al., 2003). This result increased suitable spawning habitats for brown trout (*Salmo trutta*), and shifted macroinvertebrate assemblages towards an alpine-

**FIGURE 1** Left panel: Spöl catchment, showing sampling site location and the hydropower network (EKW). Right panel: Discharge data measured at Punt dal Gall gauging station. Daily mean discharge is shown, except for the experimental flood peaks that show maximum flood discharge. The inset shows a sample of two hydrological years before regulation (source of data: FOEN). [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



like structure (Robinson et al., 2018). Notably, densities of the crustacean, *Gammarus fossarum*, a species absent in the Spöl main stem before regulation, dropped from peaks of 15,000 ind/m<sup>2</sup> to <3000 after the flood program began.

## 2.2 | Biomass sample collection and treatment

Macroinvertebrate sampling for the long-term monitoring consisted of quantitative Hess samples ( $n = 3$ , mesh 250  $\mu\text{m}$ , 0.045 m<sup>2</sup>) collected from riffle-run habitats at around 1.5-month intervals, between spring (April/May) and autumn (October/November), from 12/05/1999 to 03/09/2020. Due to adverse conditions (snow/ice on trails), winter months usually were not sampled. Samples were stored in 70% ethanol, and macroinvertebrates were sorted and identified to the lowest practical taxonomic level (mostly genus, see Table 1) using Tachet et al. (2010). After identification, macroinvertebrate samples were dried (60°C), and then dry mass was measured. In this study, some years were discarded from analyses (2008–2013, and 2015) because they presented too coarse taxonomic resolution or lacked biomass data. At the sampling site, water temperature was measured hourly during the study period with data loggers (HOBO Tidbit v2) and used for the calculation of yearly means and standard deviations (SD).

## 2.3 | Stable isotope sample collection and treatment

Samples for C and N stable isotope (SI) analysis ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were collected in spring (11/07/2019) and autumn (17/10/2019) from a 20-m reach of the river where the long-term sampling took place. Sampling was carried out following Siebers et al. (2019). Three qualitative kick-sample sweeps were collected across ca 2 m<sup>2</sup> of riffle habitat. In some cases, additional samples were required to collect enough individuals to meet the minimum biomass requirement for SI analysis (~0.5 mg dry mass). Macroinvertebrates were hand-picked and placed in 50-ml PET falcon tubes filled with stream water, separating prey

and predator taxa. Tubes were stored in a cooler box, and macroinvertebrates were kept alive for ~8 h to allow for stomach clearance. Macroinvertebrates were then identified to the lowest practical level (mostly genus) after Tachet et al. (2010) and stored at -20°C.

Samples for potential food sources were collected on the same dates as macroinvertebrates. Particulate organic matter (POM) samples were collected from 3 to 5 depositional areas in the study reach and consolidated. Moss, periphyton, and filamentous algae were collected from representative rocks in the study reach. Periphyton was scrubbed with a metal brush from a rocks' upper surface, rinsed, and stored as suspension. Leaves were collected from the three dominant terrestrial plant species (two tree species: *Pinus mugo* Turra, *Pinus cembra* L.; and grasses belonging to the Poaceae family) present in the riparian area. Due to park restrictions regarding biological sample collection, we limited the food-web analysis to macroinvertebrates, as the brown trout population (sole fish present in the Spöl; Mürle et al., 2003) could not be sampled.

In the laboratory, POM was separated into coarse (CPOM) and fine (FPOM) organic fractions by sieving (CPOM >1 mm > FPOM >0.25 mm). Samples were elutriated to remove excess sediment and the CPOM was rinsed with distilled water. Moss was rinsed with distilled water, and large, non-moss particles entangled in moss (e.g., organic matter, sediment) were manually removed. Periphyton and filamentous algae samples were carefully inspected using a stereomicroscope to remove small invertebrates and other particles. Periphyton was further centrifuged to separate sediment, harvesting the upper layer of each sample. Lastly, CPOM, FPOM, moss, and periphyton samples were placed in crucibles in a desiccator for 24 hrs together with an open vial of 37% HCl for acid fumigation (Harris et al., 2001) to remove carbonates originating from calcareous rocks in the watershed (Dolomites).

Leaves from terrestrial plants, CPOM, and moss were oven-dried at 60°C for 72 h before grinding and homogenization. Macroinvertebrates were placed into Eppendorf tubes and freeze-dried for 48 h (Lyovac GT 2-E lyophilizer) and each homogenized after drying; this process was also followed for samples of FPOM, filamentous algae, and periphyton. Macroinvertebrate samples comprised a minimum of three individuals. We weighed 0.6–0.8 mg of macroinvertebrate

material, and 1–1.5 mg of organic resource material into tin cups and combusted them in a Vario PYRO Cube elemental analyzer (elemental Analysensysteme GmbH, Langensfeld, Germany) connected to an IsoPrime isotope ratio mass spectrometer (GV Instruments Ltd., Wythenshawe, UK) for measurement of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Reference materials for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were provided by Biogeochemical Laboratories, Indiana University (NBS 19, L-SVEC, IAEA-N-1, and IAEA-N-2). Analytical uncertainty was 0.1‰ for  $\delta^{13}\text{C}$  and 0.2‰ for  $\delta^{15}\text{N}$ .

## 2.4 | SI data analysis

Spring and autumn samples were aggregated to obtain a mean (+SD) of  $\delta^{13}\text{C}$ ‰ and  $\delta^{15}\text{N}$ ‰. Macroinvertebrates were further grouped into main feeding groups (grazers, detritivores, predators) after Tachet et al. (2010), while resources were represented individually. To estimate the relative contribution of basal resources to consumers, we used the Bayesian mixing model MixSIAR (Stock et al., 2018). Sample suitability was evaluated with the mixing polygon method (Smith et al., 2013). *Isoperla* sp. samples were excluded after falling outside the 95% confidence polygons bounds (Figure S7). Trophic enrichment factors were set as  $0.4 \pm 0.3$ ‰ (mean  $\pm$  standard deviation) for  $\delta^{13}\text{C}$  (Post, 2002), and  $2.2 \pm 0.3$ ‰ for  $\delta^{15}\text{N}$  (McCutchan Jr et al., 2003) for primary consumers, while for omnivores these values were multiplied by a factor of 1.5 and for predators by factor 2 (to account for sequential steps in trophic level from basal resources) (Siebers et al., 2019). Two trophic enrichment factors were used because the estimated TEF for  $\delta^{13}\text{C}$  has the same quoted mean value in Post (2002) and McCutchan Jr et al. (2003), but a greater SD for Post (2002), allowing a more conservative approach given the lack of TEFs specific to alpine fauna. In the case of  $\delta^{15}\text{N}$ , the algal-specific TEF (McCutchan Jr et al., 2003) was considered more appropriate than a generalist approach given the greater potential error involved. Leaves and CPOM were then aggregated as a single source, as were periphyton and filamentous algae (Phillips et al., 2005). Moss (*Fontinalis* spp.; Robinson, Uehlinger, & Monaghan, 2004) was used as the third source, where we assumed that a fraction of the material was epiphytic biofilm (Chantha et al., 2000; Glime & Clemons, 1972; Suren, 1991). Acid fumigation of algal samples might result in alterations of  $\delta^{15}\text{N}$  signature of +1‰ (Schlacher & Connolly, 2014), thus we estimated the influence of this potential alteration by comparing resource partitioning results with those of an identical model where +1‰ were added to the  $\delta^{15}\text{N}$  mean isotopic signature of algal resources.

## 2.5 | Biomass data analysis

Annual secondary production was calculated for taxa for which SI data were available (*Baetis* sp., Heptageniidae, Chironomidae, *Protonemura* sp., Limnephilidae, *Gammarus* sp., Limoniidae, and Rhyacophilidae). Of the total number of samples, ~9% of biomass belonged to taxa not

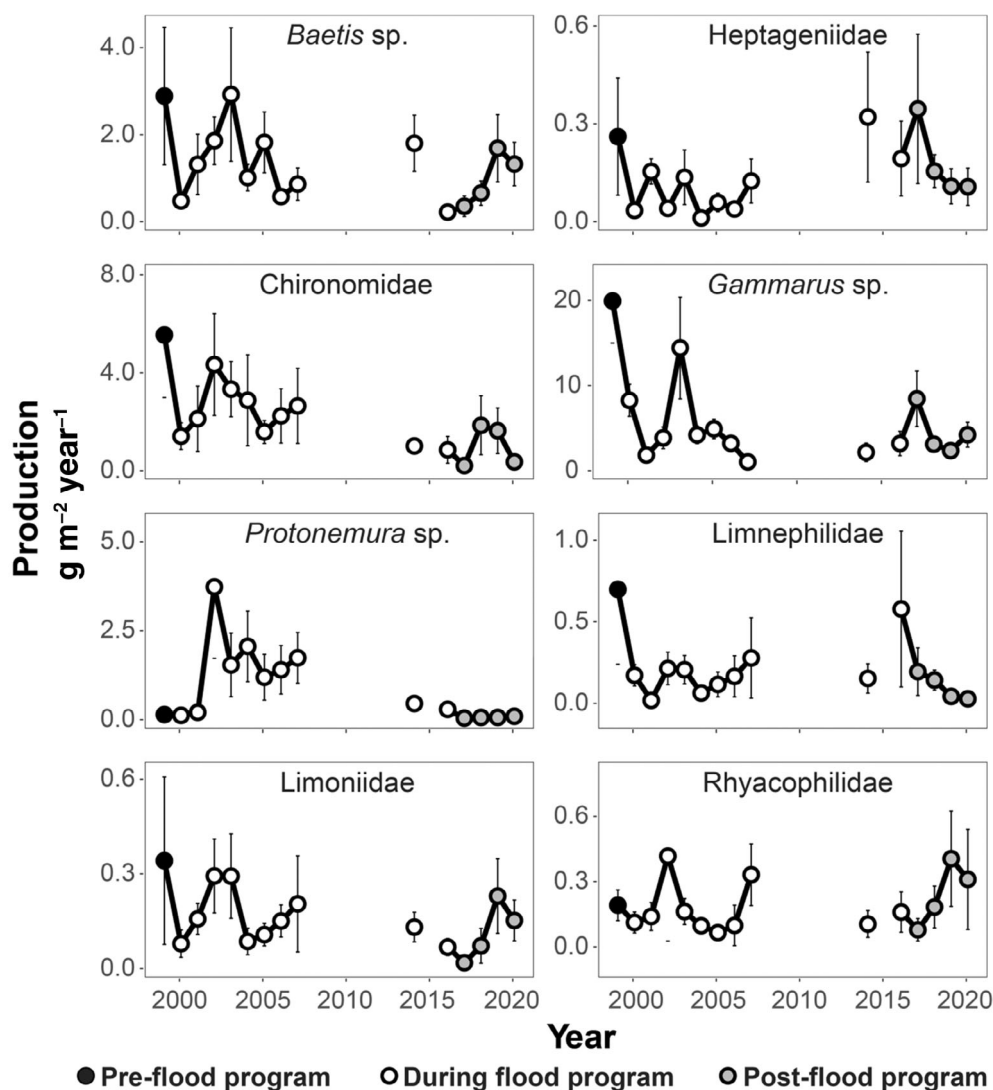
present in the SI analysis and was discarded from further analysis (Simuliidae 1%, *Leuctra* sp. 4%, *Nemoura* sp. 0.05%, Perloidea 0.4%; Turbellaria 3%, Oligochaeta 1%, Hydracarina 0.02%, Other taxa 0.1%). Biomass data (dry mass) were available for the years 1999–2007, 2014, and 2016–2020, for a total of 315 samples (105 sampling dates). Dry mass estimates of preserved samples are affected by biomass losses induced by ethanol fixation (e.g., Leuven et al., 1985; Wetzel et al., 2005), with non-uniform effects across taxa, posing additional challenges to secondary production estimates. While most studies focus on live mass alterations after preservation (e.g., Stanford, 1973), correction factors accounting for dry mass loss were available only for part of the taxonomic groups used in this study, however, they uniformly reported losses ranging between 20% and 30%, for hard and soft-bodied organisms (Chironomidae 20.4% (Mährlein et al., 2016); Limoniidae 22.9% (Dermott & Paterson, 1974); Gammaridae 27.3% (Wetzel et al., 2005) – 22.4% (Mährlein et al., 2016); Baetidae 30% (Mährlein et al., 2016)). These correction factors were applied to biomass estimates of the aforementioned taxa (as mean if more than one correction factor was available), while for the remaining taxa a global mean was calculated and applied (+24.6%). Annual mean areal biomass (B, g dry mass/m<sup>2</sup>) and SD were further determined after standardization to the size of the Hess sampler. Mean (and SD) individual biomass (M, g dry mass) was calculated by dividing taxa biomass by abundance for each sample.

We visually explored temporal patterns of mean individual biomass (Figure S3) to detect the existence of size distribution patterns. Furthermore, we fitted generalized additive models (GAMs; smoothing functions of the form  $y \sim s(x, k = 3)$ ) to test relationships between  $\ln + 1$  transformed sample biomass versus mean individual biomass, and sample biomass versus density. Model selection was done by visually comparing different smoothing curves (linear, quadratic, loess, GAM) and then by comparing the fit of the two best-fitting models (GAM and linear) to test the relationships (Figures S4 and S5). For each taxon, annual benthic production (BP, as g/m<sup>2</sup>/year) was then estimated using the empirical model developed by Morin and Bourassa (1992) using mean areal biomass (B), mean individual biomass (M) and mean water temperature (T):

$$BP = 0.18B^{1.01} \times M^{-0.34} \times 10^{0.037T}$$

Yearly production was further weighted by diet estimates (MixSIAR output; Stock et al., 2018) using uninformed priors (i.e., presumed probability distributions of resource usage for a given taxa based on previous knowledge on the system) to estimate the relative contribution of different carbon and nitrogen sources to the food web. To evaluate the sensitivity of MixSIAR resource partitioning results (posteriors) to the model priors, we calculated Hellinger distance and Kullback–Leibler divergence between prior and posterior distributions using the package BayeSens (Brown et al., 2018). We carried out Spearman correlation tests based on the relative production data of each taxa for each sampling date to identify relationships between taxa responses in production patterns (Figure S6).

**FIGURE 2** Temporal patterns in annual secondary production (mean ± standard error). Note the difference in scale of y-axis among plots.



### 2.6 | Assumptions of temporal reconstructions of dietary estimates

The temporal reconstruction of food-web composition and relative contribution of basal resources was based on stable isotope data from 2019. This approach comes with three major assumptions: (1) no major changes in diet (or feeding plasticity) of macroinvertebrates; (2) no limitation of resource availability caused by the experimental floods; and (3) no change in interspecific competition after community rearrangement, which could potentially alter resource/habitat availability for certain taxa.

### 2.7 | Trait analysis

We selected the “food preference” functional trait of Tachet et al. (2010), which describes a taxa's affinity for different food sources (microorganisms; detritus <1 mm, dead plant material ≥1 mm; living microphytes; living macrophytes; dead animal material ≥1 mm;

living microinvertebrates; living macroinvertebrates) as a descriptor of the trophic characteristics of the macroinvertebrate assemblage. Trait scores were extracted from Tachet et al. (2010) and standardized for each category to range between 0 (no affinity) to 1 (maximum affinity) (Table S2). In this analysis, we included some of the taxa excluded from SI analysis (*Simuliidae*, *Leuctra* sp., *Nemoura* sp., *Perlodes* sp., *Turbellaria*, *Oligochaeta*) because trait scores were available, thus 99.8% (in biomass) of the assemblage was represented. Trait scores were available mostly at the genus level. For some taxa identified at lower taxonomic resolution (*Chironomidae*, *Limoniidae*, *Heptageniidae*, *Simuliidae*, *Oligochaeta*), we calculated a weighted trait score based on the relative abundance of species belonging to each taxonomic group present in the stream (data provided by Hydra GmbH, Germany). Production associated with each trait category for each year was calculated as follows:

$$\sum_{i=1}^n p_i t_{ji}$$

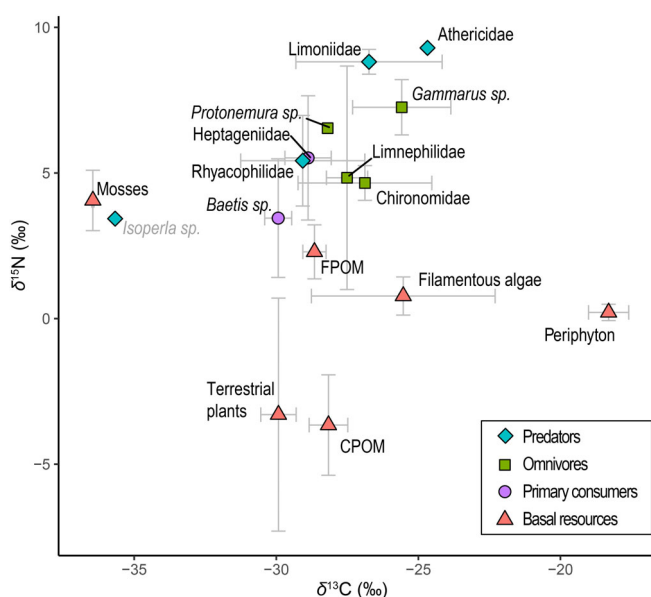


where  $n$  is the number of taxa in a community,  $p_i$  is the production of taxon  $i$ , and  $t_j$  is the trait score for each trait category  $j$  for each taxon  $i$ . We further compared the relative abundance of each trait modality for every year against the relative abundance observed in 1999 ( $\Delta\%$  99). All analyses and data visualizations were carried out using R version 4.1.1 (R Core Team, 2021).

### 3 | RESULTS

#### 3.1 | Secondary production

Before the flood program in 1999, secondary production was dominated by *Gammarus* sp. (66.6%) and Chironomidae (18.5%). During the



**FIGURE 3** Mean ( $\pm$  SD)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for basal resources and macroinvertebrates. Values not corrected for trophic enrichment as in the MixSIAR model (see methods). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

flood program, taxa responded differently to the increased disturbance caused by floods (Figure 2). Notably, *Gammarus* sp. production dropped from pre-flood values of  $19.8 \pm 5.0 \text{ g m}^{-2} \text{ year}^{-1}$  to values below  $\sim 8.5 \text{ g m}^{-2} \text{ year}^{-1}$ , reaching lowest levels in 2007, where it contributed to 12.9% of secondary production. *Protonemura* sp. was virtually absent from the system before the floods and increased its production to  $3.7 \pm 2.3 \text{ g m}^{-2} \text{ year}^{-1}$  in 2002. However, its production further declined over time, reaching pre-floods levels ( $< 0.1 \text{ g m}^{-2} \text{ year}^{-1}$ ) in 2020. Chironomidae and *Baetis* sp. production fluctuated greatly in the early flood years but showed an overall decline over time. Limnephilidae contributed marginally to pre-flood production ( $0.7 \pm 0.6 \text{ g m}^{-2} \text{ year}^{-1}$ ), and values declined to  $< 0.2 \text{ g m}^{-2} \text{ year}^{-1}$  following the floods, except for 2016 ( $0.6 \pm 0.5 \text{ g m}^{-2} \text{ year}^{-1}$ ). Other taxa with relatively low production ( $< 1 \text{ g m}^{-2} \text{ year}^{-1}$ ), such as Heptageniidae, Limoniidae, and Rhyacophilidae, showed production fluctuations throughout the years with no evident relation to the floods (Figure 2).

#### 3.2 | Trophic structure

Basal resources in the Spöl showed isotopic distinction in  $\delta^{13}\text{C}$  values (Figure 3). Resource  $\delta^{13}\text{C}$  values ranged from relatively high values in periphyton (mean  $\pm$  SD;  $-18.3\text{‰} \pm 0.7$ ) to low values in mosses ( $-36.5\text{‰} \pm 0.0$ ), and intermediate values in filamentous algae ( $-25.5\text{‰} \pm 3.2$ ), CPOM ( $-28.2\text{‰} \pm 0.7$ ), and terrestrial plants ( $-29.9\text{‰} \pm 0.6$ ). The multi-source origin of FPOM (a mixture of basal resources and excretion from macroinvertebrates and fish) likely determined its central placement between basal resources ( $\delta^{13}\text{C}$   $-28.7\text{‰} \pm 0.4$ ;  $\delta^{15}\text{N}$   $2.3\text{‰} \pm 0.9$ ). Moss had the highest  $\delta^{15}\text{N}$  values ( $4.1\text{‰} \pm 1.0$ ), and was the only resource with values comparable with those of some consumers (e.g., *Baetis* sp.  $3.5\text{‰} \pm 2.0$ ). Filamentous algae ( $0.8\text{‰} \pm 0.6$ ) and periphyton ( $0.2\text{‰} \pm 0.3$ ) had similar mean  $\delta^{15}\text{N}$  values, as did terrestrial plants ( $-3.3\text{‰} \pm 4.0$ ) and CPOM ( $-3.7\text{‰} \pm 1.7$ ) (Figure 3). The large variability of  $\delta^{15}\text{N}$  values in terrestrial plants reflected the difference found between leaves of riparian grasses ( $1.5\text{‰} \pm 1.1$ ) and trees ( $-5.7\text{‰} \pm 1.7$ ). Macroinvertebrate

**TABLE 1** MixSIAR results-Relative proportional contribution of different carbon and nitrogen sources to benthic macroinvertebrates (mean  $\pm$  standard deviation).

Taxon	Feeding category	Periphyton + fil. algae	CPOM + terrestrial plants	Moss + Ephemeroptera biofilm
<i>Baetis</i> sp.	PC	$0.29 \pm 0.1$	$0.29 \pm 0.2$	$0.42 \pm 0.1$
Heptageniidae	PC	$0.31 \pm 0.2$	$0.30 \pm 0.2$	$0.39 \pm 0.2$
<i>Gammarus</i> sp.	OMN	$0.54 \pm 0.2$	$0.20 \pm 0.2$	$0.26 \pm 0.1$
<i>Protonemura</i> sp.	OMN	$0.43 \pm 0.2$	$0.24 \pm 0.2$	$0.33 \pm 0.2$
Chironomidae	OMN	$0.56 \pm 0.2$	$0.16 \pm 0.2$	$0.28 \pm 0.1$
Limnephilidae	OMN	$0.46 \pm 0.1$	$0.23 \pm 0.2$	$0.31 \pm 0.1$
Athericidae	PRE	$0.43 \pm 0.2$	$0.24 \pm 0.2$	$0.33 \pm 0.2$
Limoniidae	PRE	$0.40 \pm 0.2$	$0.24 \pm 0.2$	$0.36 \pm 0.2$
Rhyacophilidae	PRE	$0.41 \pm 0.2$	$0.22 \pm 0.2$	$0.36 \pm 0.2$

Note: Feeding categories: OMN, omnivore; PC, primary consumer; PRE, predator.

taxa were distributed along a trophic enrichment gradient in  $\delta^{15}\text{N}$  values, where primary consumers (Heptageniidae and *Baetis* sp.) had lowest ( $4.5\text{‰} \pm 2.0$ ), predators (Athericidae, Limoniidae, and Rhyacophilidae) highest ( $7.6\text{‰} \pm 2.1$ ), and omnivores (Chironomidae, *Protoneura* sp. and Limnephilidae) intermediate values ( $5.1\text{‰} \pm 2.1$ ).

Reliance on basal resources varied among groups with autochthonous resources being overall more important than allochthonous resources (Table 1). Primary consumer diets were mostly composed of mosses + epiphytic biofilm ( $40.5\% \pm 11.2$ ), while periphyton + filamentous algae ( $30\% \pm 11.2$ ) and terrestrial + CPOM ( $29.5\% \pm 14.1$ ) contributed equally. The potential alterations of acidification on algal samples showed negligible effects on resource partitioning for all trophic groups (primary consumers, omnivores, predators), as on average it modifies resource partitioning  $\pm 1.6\%$  (1.2 SD).

### 3.3 | Energy fluxes

Total production estimates were highest for 1999 ( $29.8 \text{ g m}^{-2} \text{ year}^{-1}$ ) before the beginning of the flood program (Figure 4). Production declined in early flood years (2000–2003) to  $13.4 \pm 7.2 \text{ g m}^{-2} \text{ year}^{-1}$ , but with high variation (max  $22.8 \text{ g m}^{-2} \text{ year}^{-1}$  in 2003, min  $5.7 \text{ g m}^{-2} \text{ year}^{-1}$  in 2001). In later years (2004–2007, 2014, 2016), before the discontinuation of experimental floods, production was  $\sim 1/4$  of that in 1999, with small inter-annual fluctuations ( $7.6 \pm 1.9 \text{ g m}^{-2} \text{ year}^{-1}$ ). In 2016, the year of the last flood, production was the lowest in the study period ( $5.3 \text{ g m}^{-2} \text{ year}^{-1}$ ). Production remained relatively low and did not return to pre-flood levels after the floods were discontinued in 2016, averaging  $7.0 \pm 1.6 \text{ g m}^{-2} \text{ year}^{-1}$  (2107–2020). The relative contribution of basal resources to the stream food web suggested that  $\sim 80\%$  of production was from autochthonous resources (periphyton + filamentous algae  $\sim 50\%$ , moss + epiphytic biofilm  $30\%$ ),

with little variation over time (Figure 4). The sensitivity analysis (BayeSens) of mixing model outcomes (posteriors) to the uninformed priors used in the analysis showed generally a low to moderate informativeness of the data and the model used (Table S1). Results from primary consumers show that the combination of mosses and epiphytic biofilm showed the highest degree of informativeness (Hellinger distance = 0.4; Kullback–Leibler divergence = 1.2).

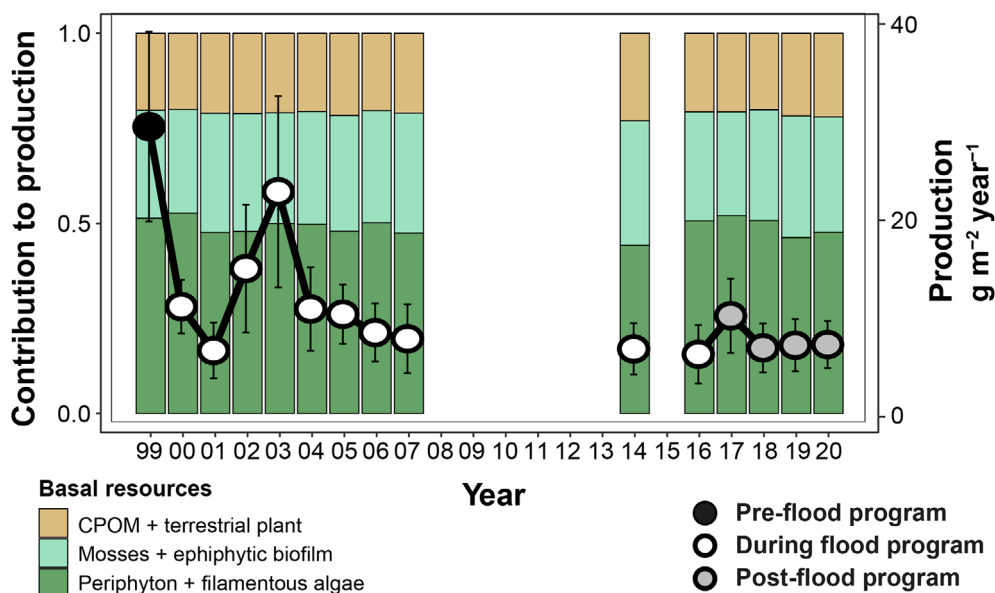
The analysis of food preference (Table 2) indicated that CPOM represented the main source of food before the floods (production  $8.6 \pm 2.6 \text{ g m}^{-2} \text{ year}^{-1}$ ), followed by living microphytes ( $5.7 \pm 2.3 \text{ g m}^{-2} \text{ year}^{-1}$ ) and FPOM ( $4.5 \pm 1.9 \text{ g m}^{-2} \text{ year}^{-1}$ ). Other food sources (microorganisms, living macrophytes, living macroinvertebrates, living microinvertebrates, and dead animals  $>1 \text{ mm}$ ) likely only contributed marginally to secondary production. Floods did not result in substantial directional changes in food preference, and relative changes were mostly within a  $\pm 10\%$  range when compared to the pre-flood community (1999). The exception was FPOM consumers with an increase of 10% in 2007.

## 4 | DISCUSSION

### 4.1 | Temporal patterns in macroinvertebrate production

Our results follow Robinson (2012), Robinson et al. (2003), Robinson, Aebischer, and Uehlinger (2004), Robinson, Uehlinger, and Monaghan (2004), Robinson et al. (2018), and support the hypothesis that restoration of flow variability enhanced the ecological condition of the regulated sections of the river Spöl, promoting gradual shifts towards an alpine-like ecosystem by introducing disturbance and enhancing streambed physical habitat conditions. Secondary production of macroinvertebrates in the river Spöl was highest before the first

**FIGURE 4** Relative basal resource contribution to annual secondary production (mean  $\pm$  standard error). Left y-axis refers to stacked bar plots and indicates the relative proportional contribution to production (range 0–1). Right y-axis refers to the line-and-dots plot and indicates total annual secondary production. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**TABLE 2** Food preference traits (FP) expressed as mean annual production (prod; g m<sup>-2</sup> year<sup>-1</sup>) and as % difference with 1999 pre-flood relative trait production (Δ%99).

Year	FP_1		FP_2		FP_3		FP_4		FP_5		FP_6		FP_7		FP_8	
	Prod	Δ% 99	Prod	Δ%99	Prod	Δ% 99	Prod	Δ% 99	Prod	Δ% 99	Prod	Δ% 99	Prod	Δ% 99	Prod	Δ% 99
1999	0.6	-	4.5	-	8.6	-	5.7	-	2.0	-	3.1	-	3.1	-	2.1	-
2000	0.1	-0.6	1.3	-2.3	3.3	+2.3	1.8	-2.5	0.7	-0.1	1.2	+0.9	1.2	+1.5	0.8	+0.7
2001	0.2	+1.3	1.4	+7.3	1.2	-4.9	1.4	+4.4	0.3	-1.1	0.4	-3.0	0.3	-3.4	0.4	-0.6
2002	0.4	+0.7	3.6	+8.1	4.2	+1.7	3.4	+3.5	0.6	-2.7	0.7	-5.2	0.7	-4.8	0.9	-1.1
2003	0.4	-0.7	3.5	+0.2	6.9	+2.0	4.6	+1.6	1.4	-0.5	2.3	-0.5	2.2	-1.1	1.4	-1.1
2004	0.3	+0.6	2.3	+7.8	3.0	+1.7	2.2	+2.4	0.5	-2.5	0.7	-4.1	0.7	-3.7	0.5	-2.2
2005	0.2	-0.5	1.7	+3.2	2.9	+1.2	2.2	+5.2	0.6	-1.0	0.9	-2.3	0.7	-3.5	0.5	-2.3
2006	0.2	+1.0	1.7	+7.6	2.2	+1.1	1.6	+1.8	0.4	-2.3	0.5	-4.5	0.5	-3.7	0.5	-1.0
2007	0.3	+1.5	1.9	<b>+10.0</b>	1.8	-0.9	1.7	+3.8	0.3	-2.7	0.2	-6.6	0.3	-5.6	0.5	+0.5
2014	0.1	+0.1	1.1	+3.1	1.6	-2.2	1.6	+8.9	0.4	-0.2	0.5	-2.9	0.3	-5.1	0.3	-1.7
2016	0.1	+1.8	0.7	+1.5	1.6	-1.6	1.0	+2.4	0.4	+0.4	0.5	-5.1	0.5	-4.0	0.5	+4.6
2017	0.1	-1.5	0.8	-8.3	3.2	+6.2	1.6	-2.6	0.7	+0.8	1.2	+2.5	1.2	+2.4	0.7	+0.6
2018	0.2	+1.7	1.2	+6.5	1.5	-4.9	1.2	+1.8	0.4	-1.0	0.5	-2.9	0.5	-2.2	0.5	+1.0
2019	0.2	+0.6	1.3	+4.9	1.5	-6.3	1.6	+6.0	0.4	-0.7	0.5	-3.0	0.4	-3.8	0.6	+2.3
2020	0.1	-1.7	0.8	-4.0	1.9	0.0	1.4	+4.2	0.4	+0.3	0.7	+0.2	0.6	-1.3	0.5	+2.3

Note: Trait categories (1–8): (1) microorganisms, (2) detritus <1 mm (FPOM), (3) dead plants ≥1 mm, (4) living microphytes, (5) living macrophytes, (6) dead animals ≥1 mm, (7) living microinvertebrates, (8) living macroinvertebrates. Boldface indicates differences ≥ +/- 10%.

environmental flood release (Figure 4). Production flourished under stable flows (mean 29.8 g m<sup>-2</sup> year<sup>-1</sup>), resulting in annual amounts largely exceeding (up to 10 times) those estimated for riffle habitats in montane streams of similar size (Benke, 1993; Lugthart & Wallace, 1992; Smock et al., 1985) or from a similar geographic area (Buffagni & Comin, 2000). However, comparisons with secondary production estimates from other studies must be interpreted with caution, as different methods (e.g., cohort or size-structure), or the use of preserved versus fresh specimens for biomass estimation might lead to different results (Dolbeth et al., 2012; Leuven et al., 1985). Secondary production before the floods was dominated (~70%) by the amphipod *G. fossarum*, which colonized the system after dam construction (Figure 3). However, production considerably declined four-fold after a few years of periodic flood disturbance. This confirms previous observations that flow regulation altered the ecosystem functioning of this alpine river, as *Gammarus* plays a central role in organic matter recycling and energy fluxes in rivers, representing an important source of food for higher trophic levels (MacNeil et al., 1997).

In pre-flood years, Robinson, Aebischer, and Uehlinger (2004) and Uehlinger et al. (2003) reported high density of macroinvertebrates, moss, and periphyton in the river. Experimental floods were implemented initially (2000, 2001) with higher frequency, with peak flows ranging between 12 and 45 m<sup>3</sup>/s, while later floods were mostly released twice a year (Figure 1, Kevic et al., 2018). After an initial fluctuation, total secondary production steadily declined to values <10 g m<sup>-2</sup> year<sup>-1</sup>. This response, however, was not homogeneous across taxa. In particular, during the first years, some taxa had a swift

decline followed by peaks in 2002 and 2003. Robinson and Uehlinger (2008) attributed these changes to a period of non-equilibrium during the early stages of the flood program, where all biotic parameters measured showed the largest increases in coefficient of variation, suggesting the passing of an ecological threshold towards the onset of an ecosystem shift. Due to a gap in biomass data, we could not make estimates between 2008 and 2013, the period when high-magnitude floods were released (Kevic et al., 2018). However, Robinson (2012), Robinson et al. (2018) reported that macroinvertebrate density was lowest in 2010, with a concomitant increase in taxa richness, a condition that persisted until 2015. The positive relationship observed between biomass and density (Figure S5) suggests that macroinvertebrate production in that period would likely have been low. Yet contrary to expectations, total secondary production did not substantially increase after the floods were discontinued in 2016; production values were comparable to those observed during the floods, even 4 years after the end of the program, mostly due to the slow recovery of *Gammarus*. However, some taxa such as Baetidae, Rhyacophilidae, and Limoniidae showed a gradual increase in production after flood discontinuation, suggesting that the experimental floods might have long-term effects on overall physical habitats conditions in riffles, which became less suitable for gammarids (Figure 2). This result suggests the existence of a flood legacy, particularly in the continued low abundance of *Gammarus*.

Field observations initially reported that the extensive moss beds, which covered even small cobbles before the floods, were effectively (and completely) removed (0/10 of cobbles) after the early floods



(Robinson & Uehlinger, 2008; Uehlinger et al., 2003). Yet in our last sampling of the river (October 2020), we did not observe a conspicuous moss re-growth in the study riffle, except for isolated patches (Figure S1). Mosses reduce flow velocity, trap sediment, and organic matter, offer substrate for epiphytes and biofilm growth (Stream Bryophyte Group, 1999; Suren, 1991; Wulf & Pearson, 2017), and can sustain significantly greater macroinvertebrate densities compared to other benthic substrates (Suren, 1991, and references therein). For macroinvertebrates, mosses are prime habitats for feeding and oviposition, and an important refugia from predation (e.g., see Parker et al., 2007; Suren, 1991).

Mosses are sensitive to flow disturbance, and recolonization occurs through dispersal of fragments supplied from upstream populations (Stream Bryophyte Group, 1999), which can potentially take up to 10 years (Englund, 1991; Rader et al., 2008; Slavik et al., 2004). The long-term sampling site is above the first tributaries that re-enter the river Spöl below Punt dal Gall (Figure 1). The lack of moss cover, even after the end of the experimental flood program, may thus reflect disconnection from upstream seed populations caused by the reservoir (Ellis & Jones, 2013). Conversely, moss was present in the main channel following construction of the dam, and there was ca. 30 years between construction and the start of the experimental floods program for moss to colonize from side channels, local streams or springs in the area (e.g., see Von Fumetti & Blattner, 2017). Slow recolonization by mosses, and a concomitant limitation on habitat availability and substrate for food production and accumulation, may thus explain the residual lag in secondary production following the end of the flood program.

## 4.2 | Temporal patterns in trophic dynamics

The combination of temporal patterns of production with taxon-specific estimates of basal resource consumption revealed no considerable effects of the floods on the relative importance of basal resources, and that changes in energy flux were instead correlated with overall macroinvertebrate biomass (Figure 4). Our results suggest that macroinvertebrates in the river relied mostly on autochthonous sources, which can enter the food web via direct consumption and as part of amorphous detritus (FPOM). Patterns of food preference traits supported the estimation that no major changes occurred in the Spöl during the flood period but highlighted the importance of FPOM at the base of the food web.

In the river Spöl, overall resource availability was initially reduced by the floods (Robinson et al., 2018). The decline of periphyton and benthic organic matter (FPOM + CPOM) biomass, however, did not correspond to a change in ratios between resources, with periphyton biomass density roughly double that of benthic organic matter (Figure S2). These observations suggest that the density of autotrophic sources consistently exceeded that of heterotrophic sources in the river, even when experimental floods were operating. In natural rivers, floods can increase the availability of allochthonous resources for aquatic organisms, via lateral inputs from tributaries and runoff,

and by temporarily allowing organisms to access inundated lateral habitats (Junk et al., 1989). However, in regulated systems, these inputs can be largely limited (e.g., Wellard Kelly et al., 2013). Similarly, Cross et al. (2011) found that algae were a dominant basal resource in the Colorado River below Hoover Dam, a condition that changed only after major tributary confluences further downstream (Sabo et al., 2018). A notable difference is that FPOM retained a terrestrial signature from the reservoir in Colorado, whereas FPOM appears to be a combination of terrestrial and aquatic sources in the Spöl. Alpine River systems are, in general, limited in terrestrial organic matter inputs and constrained by autochthonous resource availability (Siebers et al., 2022). Our results suggest that these limitations might also control energy fluxes in the food web.

Our observations on trophic relationships highlight the functional importance of moss, not only as substrate or refugium but also as a potential source of food. Mosses are mostly avoided by larger herbivores due to chemical defence compounds (Parker et al., 2007), and traditionally have been described as a secondary food source for macroinvertebrates (Dangles, 2002; Stream Bryophyte Group, 1999). Some taxa appear to avoid mosses as substrate due to the inability to feed on it, or an inability to move through the intricate weave created by their stems (Suren, 1991). However, evidence indicates that mosses can be actively selected as a food source (Parker et al., 2007), and that, for example, *Fontinalis* sp., is an important source of fatty acids for some macroinvertebrates (Torres-Ruiz et al., 2007). In the Spöl River, mosses can enter the food web directly or as FPOM, as indicated by its isotopic signature and the frequency of fine detritus feeding traits, which could help explain the apparent contradiction between trophic importance and density. Alpine rivers are typically low in productivity overall, and access to these essential dietary elements may thus be vital for growth and development of some consumers (Niedrist & Füreder, 2017).

Bayesian mixing models characteristically calculate relative contribution of all the sources included in the model, thus implying that all resources are consumed (Brown et al., 2018). The decision to include moss in the analysis was based on the C isotopic signature of consumers, comprising periphyton and moss. Further studies are required to assess the viability of this decision, and confirm that moss usage in the Spöl food web is not a model artifact (e.g., Field et al., 2014; Miller et al., 2013), as the sensitivity analysis of the informativeness of priors could not conclusively resolve this question. In effect, the feeding plasticity of stream macroinvertebrates determines substantial dietary differences of taxa along environmental gradients (e.g., Wellard Kelly et al., 2013). Gut content analysis with the application of sequencing techniques could better elucidate the trophic function of mosses in the Spöl River (Casey et al., 2019).

In this study, we showed that the experimental floods on the Spöl reduced the magnitude of energy fluxes between basal resources and consumers. The proportional contribution of different resources to energy fluxes was unchanged, however, and indicates that the system is likely limited by autochthonous resource availability. Further, a return to the stable, pre-flood flow regime was not followed by an increase in secondary production or change in trophic structure.

Based on these findings, we hypothesize that the lag in secondary production after a return to the pre-flood flow regime could be attributed in part to the slow recovery of moss, which represents an important habitat, food source, and trap for fine particulate matter. Our findings, by addressing collateral functional responses to experimental floods, therefore contribute to the understanding of the consequences of long-term flow restoration from a whole-ecosystem perspective (*sensu* Tonkin et al., 2021).

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## ORCID

Gabriele Consoli  <https://orcid.org/0000-0002-9336-9151>

Andreas Bruder  <https://orcid.org/0000-0002-4591-491X>

## REFERENCES

- Acreman, M. C., & Ferguson, A. J. D. (2010). Environmental flows and the European water framework directive. *Freshwater Biology*, 55(1), 32–48.
- Andrews, E. D., & Pizzi, L. A. (2000). Origin of the Colorado River experimental flood in grand canyon. *Hydrological Sciences Journal*, 45(4), 607–627.
- Auerbach, D. A., Deisenroth, D. B., McShane, R. R., McCluney, K. E., & Poff, N. L. (2014). Beyond the concrete: Accounting for ecosystem services from free-flowing rivers. *Ecosystem Services*, 10, 1–5.
- Benke, A. C. (1993). Concepts and patterns of invertebrate production in running waters. *SIL Proceedings, 1922–2010*, 25(1), 15–38.
- Brown, C. J., Brett, M. T., Adame, M. F., Stewart-Koster, B., & Bunn, S. E. (2018). Quantifying learning in biotracer studies. *Oecologia*, 187(3), 597–608.
- Buffagni, A., & Comin, E. (2000). Secondary production of benthic communities at the habitat scale as a tool to assess ecological integrity in mountain streams. *Hydrobiologia*, 422, 183–195.
- Bundi, U. (2010). *The handbook of environmental chemistry: Alpine waters*, Vol. 6, D. Barceló & A. G. Kostianoy, eds. Springer-Verlag.
- Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, 30(4), 492–507.
- Casey, J. M., Meyer, C. P., Morat, F., Brandl, S. J., Planes, S., & Parravicini, V. (2019). Reconstructing hyperdiverse food webs: Gut content metabarcoding as a tool to disentangle trophic interactions on coral reefs. *Methods in Ecology and Evolution*, 10(8), 1157–1170.
- Chantha, S. C., Cloutier, L., & Cattaneo, A. (2000). Epiphytic algae and invertebrates on aquatic mosses in a Quebec stream. *Archiv Für Hydrobiologie*, 147(2), 143–160.
- Cross, W. F., Baxter, C. V., Donner, K. C., Rosi-Marshall, E. J., Kennedy, T. A., Hall, R. O., Wellard Kelly, H. A., & Rogers, R. S. (2011). Ecosystem ecology meets adaptive management: Food web response to a controlled flood on the Colorado River, Glen canyon. *Ecological Applications*, 21(6), 2016–2033.
- Cross, W. F., Baxter, C. V., Rosi-Marshall, E. J., Hall, R. O., Kennedy, T. A., Donner, K. C., Wellard Kelly, H. A., Seegert, S. E. Z., Behn, B. E., & Yard, M. D. (2013). Food-web dynamics in a large river discontinuum. *Ecological Monographs*, 83(3), 311–337.
- Cross, W. F., Rosi-Marshall, E. J., Behn, K. E., Kennedy, T. A., Hall, R. O., Fuller, A. E., & Baxter, C. V. (2010). Invasion and production of New Zealand mud snails in the Colorado River, Glen canyon. *Biological Invasions*, 12(9), 3033–3043.
- Dangles, O. (2002). Functional plasticity of benthic macroinvertebrates: Implications for trophic dynamics in acid streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(9), 1563–1573.
- Dermott, R. M., & Paterson, C. G. (1974). Determining dry weight and percentage dry matter of chironomid larvae. *Canadian Journal of Zoology*, 52(10), 1243–1250.
- Dodds, W. K. (2007). Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology and Evolution*, 22(12), 669–676.
- Dolbeth, M., Cusson, M., Sousa, R., & Pardal, M. A. (2012). Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(7), 1230–1253.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. In *Biological Reviews of the Cambridge Philosophical Society*. Cambridge University Press.
- Ellis, L. E., & Jones, N. E. (2013). Longitudinal trends in regulated rivers: A review and synthesis within the context of the serial discontinuity concept. *Environmental Reviews*, 21(3), 136–148.
- Englund, G. (1991). Effects of disturbance on stream Moss and Invertebrate community structure. *Journal of the North American Benthological Society*, 10(2), 143–153.
- Field, J. C., Litvin, S. Y., Carlisle, A., Stewart, J. S., Gilly, W. F., & Ruiz-Cooley, R. I. (2014). Stable isotope analysis of Humboldt squid prey: Comment on Miller et al.(2013). *Marine Ecology Progress Series*, 500, 281–285.
- Gillespie, B. R., Desmet, S., Kay, P., Tillotson, M. R., & Brown, L. E. (2015). A critical analysis of regulated river ecosystem responses to managed environmental flows from reservoirs. *Freshwater Biology*, 60(2), 410–425.
- Glime, J. M., & Clemons, R. M. (1972). Species diversity of stream insects of Fontinalis SPP. compared to diversity on artificial substrates. *Ecology*, 53(3), 458–464.
- Harris, D., Horwath, W. R., & van Kessel, C. (2001). Acid fumigation of soils to remove carbonates prior to total organic carbon or CARBON-13 isotopic analysis. *Soil Science Society of America Journal*, 65(6), 1853–1856.
- Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106(1), 110–127.
- Kevic, M., Ortlepp, J., Mürle, U., & Robinson, C. T. (2018). Effects of experimental floods in two rivers with contrasting valley morphologies. *Fundamental and Applied Limnology/Archiv Für Hydrobiologie*, 2, 145–160.
- Klose, R. (2021). Poison source in the idyll. [www.empa.ch/web/s604/pcb-im-nationalpark](http://www.empa.ch/web/s604/pcb-im-nationalpark)
- Konrad, C. P., Olden, J. D., Lytle, D. A., Melis, T. S., Schmidt, J. C., Bray, E. N., Freeman, M., Gido, K. B., Hemphill, N. P., Kennard, M. J., McMullen, L. E., Mims, M. C., Pyron, M., Robinson, C. T., & Williams, J. G. (2011). Large-scale flow experiments for Managing River systems. *Bioscience*, 61(12), 948–959.

- Korman, J., Kaplinski, M., & Melis, T. S. (2011). Effects of fluctuating flows and a controlled flood on incubation success and early survival rates and growth of age-0 rainbow trout in a large regulated river. *Transactions of the American Fisheries Society*, 140(2), 487–505.
- Lehner, B., Liermann, C. R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., ... Wisser, D. (2011). High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Frontiers in Ecology and the Environment*, 9(9), 494–502.
- Leuven, R. S. E. W., Brock, T. C. M., & van Druten, H. A. M. (1985). Effects of preservation on dry- and ash-free dry weight of some common aquatic macro-invertebrates. *Hydrobiologia*, 127, 151–159.
- Lugthart, G. J., & Wallace, J. B. (1992). Effects of disturbance on benthic functional structure and production in mountain streams. *Journal of the North American Benthological Society*, 11(2), 138–164.
- Maavara, T., Chen, Q., Van Meter, K., Brown, L. E., Zhang, J., Ni, J., & Zarfl, C. (2020). River dam impacts on biogeochemical cycling. *Nature Reviews Earth & Environment*, 1(2), 103–116.
- MacNeil, C., Dick, J. T., & Elwood, R. W. (1997). The trophic ecology of freshwater Gammarus spp. (Crustacea: Amphipoda): Problems and perspectives concerning the functional feeding group concept. *Biological Reviews*, 72(3), 349–364.
- Mährlein, M., Pätzig, M., Brauns, M., & Dolman, A. M. (2016). Length-mass relationships for lake macroinvertebrates corrected for back-transformation and preservation effects. *Hydrobiologia*, 768(1), 37–50.
- Marcarelli, A. M., Baxter, C. V., Mineau, M. M., & Hall, R. O. (2011). Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, 92(6), 1215–1225.
- McCutchan, J. H., Jr., Lewis, W. M., Jr., Kendall, C., & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, 102(2), 378–390.
- McHugh, P. A., McIntosh, A. R., & Jellyman, P. G. (2010). Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters*, 13(7), 881–890.
- Melis, T. S. E. (2011). Effects of three high-flow experiments on the Colorado River ecosystem downstream from Glen canyon dam, Arizona. *U. S. Geological Survey Circular*, 1366(February), 147 pp.
- Miller, T. W., Bosley, K. L., Shibata, J., Brodeur, R. D., Omori, K., & Emmett, R. (2013). Contribution of prey to Humboldt squid *Dosidicus gigas* in the northern California current, revealed by stable isotope analyses. *Marine Ecology Progress Series*, 477, 123–134.
- Milner, A. M., Brittain, J. E., Castella, E., & Petts, G. E. (2001). Trends of macroinvertebrate community structure in glacier-fed rivers in relation to environmental conditions: A synthesis. *Freshwater Biology*, 46(12), 1833–1847.
- Mor, J. R., Ruhí, A., Tornés, E., Valcárcel, H., Muñoz, I., & Sabater, S. (2018). Dam regulation and riverine food-web structure in a Mediterranean river. *Science of the Total Environment*, 625, 301–310.
- Morin, A., & Bourassa, N. (1992). Empirical models of annual production and P/B ratio in benthic invertebrates of running water. *Canadian Journal of Fisheries and Aquatic Sciences*, 49(3), 532–539.
- Mürle, U., Ortlepp, J., & Zahner, M. (2003). Effects of experimental flooding on riverine morphology, structure and riparian vegetation: The river Spöl, Swiss National Park. *Aquatic Sciences*, 65(3), 191–198.
- Niedrist, G. H., & Füreder, L. (2017). Trophic ecology of alpine stream invertebrates: Current status and future research needs. *Freshwater Science*, 36(3), 466–478.
- Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, 308(5720), 405–408.
- Owusu, A. G., Mul, M., van der Zaag, P., & Slinger, J. (2021). Re-operating dams for environmental flows: From recommendation to practice. *River Research and Applications*, 37(2), 176–186.
- Parker, J. D., Burkepile, D. E., Collins, D. O., Kubanek, J., & Hay, M. E. (2007). Stream mosses as chemically-defended refugia for freshwater macroinvertebrates. *Oikos*, 116(2), 302–312.
- Petts, G. E., & Gurnell, A. M. (2005). Dams and geomorphology: Research progress and future directions. *Geomorphology*, 71(1–2), 27–47.
- Phillips, D. L., Newsome, S. D., & Gregg, J. W. (2005). Combining sources in stable isotope mixing models: Alternative methods. *Oecologia*, 144(4), 520–527.
- Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, 104(14), 5732–5737.
- Poff, N. L., & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, 55, 194–205.
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83(3), 703–718.
- Power, M. E., Dietrich, W. E., & Finlay, J. C. (1996). Dams and downstream aquatic biodiversity: Potential food web consequences of hydrologic and geomorphic change. *Environmental Management*, 20, 887–895.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rader, R. B., Voelz, N. J., & Ward, J. V. (2008). Post-flood recovery of a macroinvertebrate community in a regulated river: Resilience of an anthropogenically altered ecosystem. *Restoration Ecology*, 16(1), 24–33.
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermarie, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873.
- Robinson, C. T. (2012). Long-term changes in community assembly, resistance, and resilience following experimental floods. *Ecological Applications: A Publication of the Ecological Society of America*, 22(7), 1949–1961.
- Robinson, C. T., Aebischer, S., & Uehlinger, U. (2004). Immediate and habitat-specific responses of macroinvertebrates to sequential experimental floods. *Journal of the North American Benthological Society*, 23(4), 853–867.
- Robinson, C. T., Siebers, A. R., & Ortlepp, J. (2018). Long-term ecological responses of the river Spöl to experimental floods. *Freshwater Science*, 37(3), 433–447.
- Robinson, C. T., & Uehlinger, U. (2008). Experimental floods cause ecosystem regime shift in a regulated river. *Ecological Applications*, 18(2), 511–526.
- Robinson, C. T., Uehlinger, U., & Monaghan, M. T. (2003). Effects of a multi-year experimental flood regime on macroinvertebrates downstream of a reservoir. *Aquatic Sciences*, 65, 210–222.
- Robinson, C. T., Uehlinger, U., & Monaghan, M. T. (2004). Stream ecosystem response to multiple experimental floods from a reservoir. *River Research and Applications*, 20(4), 359–377.
- Sabo, J. L., Caron, M., Doucett, R., Dibble, K. L., Ruhí, A., Marks, J. C., Hungate, B. A., & Kennedy, T. A. (2018). Pulsed flows, tributary inputs and food-web structure in a highly regulated river. *Journal of Applied Ecology*, 55(4), 1884–1895.
- Sabo, J. L., Finlay, J. C., & Post, D. M. (2009). Food chains in freshwaters. *Annals of the New York Academy of Sciences*, 1162, 187–220.
- Scheurer, T., & Molinari, P. (2003). Experimental floods in the river Spöl, Swiss National Park: Framework, objectives and design. *Aquatic Sciences*, 65(3), 183–190.
- Schlacher, T. A., & Connolly, R. M. (2014). Effects of acid treatment on carbon and nitrogen stable isotope ratios in ecological samples: A review and synthesis. *Methods in Ecology and Evolution*, 5(6), 541–550.
- Siebers, A. R., Paillex, A., & Robinson, C. T. (2019). Flow intermittency influences the trophic base, but not the overall diversity of alpine stream food webs. *Ecography*, 42(9), 1523–1535.
- Siebers, A. R., Paillex, A., & Robinson, C. T. (2022). Seasonal and functional variation in the trophic base of intermittent alpine streams. *Limnology and Oceanography*, 67(5), 1098–1110.

- Slavik, K., Peterson, B. J., Deegan, L. A., Bowden, W. B., Hershey, A. E., & Hobbie, J. E. (2004). Long-term responses of the Kuparuk river ecosystem to phosphorus fertilization. *Ecology*, *85*(4), 939–954.
- Smith, J. A., Mazumder, D., Suthers, I. M., & Taylor, M. D. (2013). To fit or not to fit: Evaluating stable isotope mixing models using simulated mixing polygons. *Methods in Ecology and Evolution*, *4*(7), 612–618.
- Smock, L. A., Gilinsky, E., & Stoneburner, D. L. (1985). Macroinvertebrate production in a southeastern United States Blackwater stream. *Ecology*, *66*(5), 1491–1503.
- Stanford, J. A. (1973). A centrifuge method for determining live weights of aquatic insect larvae, with a note on weight loss in preservative. *Ecology*, *54*(2), 449–451.
- Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, *2018*(6), e5096.
- Stream Bryophyte Group. (1999). Roles of bryophytes in stream ecosystems. *Journal of the North American Benthological Society*, *18*(2), 151–184.
- Suren, A. M. (1991). Bryophytes as invertebrate habitat in two New Zealand alpine streams. *Freshwater Biology*, *26*(3), 399–418.
- Tachet, H., Richoux, P., Bournaud, M., & Usseglio-Polatera, P. (2010). *Invertébrés d'eau douce: systématique, biologie, écologie* (2nd ed.). CNRS Editions.
- Tonkin, J. D., Olden, J. D., Merritt, D. M., Reynolds, L. V., Rogosch, J. S., & Lytle, D. A. (2021). Designing flow regimes to support entire river ecosystems. *Frontiers in Ecology and the Environment*, *19*(6), 326–333.
- Torres-Ruiz, M., Wehr, J. D., & Perrone, A. A. (2007). Trophic relations in a stream food web: Importance of fatty acids for macroinvertebrate consumers. *Journal of the North American Benthological Society*, *26*(3), 509–522.
- Truffer, B., Markard, J., Bratrich, C., & Wehrli, B. (2001). Green electricity from alpine hydropower plants. *Mountain Research and Development*, *21*(1), 19–24.
- Uehlinger, U., Kawecka, B., & Robinson, C. T. (2003). Effects of experimental floods on periphyton and stream metabolism below a high dam in the Swiss Alps (river Spöl). *Aquatic Sciences*, *65*(3), 199–209.
- Vinson, M. R., & Baker, M. A. (2008). Poor growth of rainbow trout fed New Zealand mud snails *Potamopyrgus antipodarum*. *North American Journal of Fisheries Management*, *28*(3), 701–709.
- Von Fumetti, S., & Blattner, L. (2017). Faunistic assemblages of natural springs in different areas in the Swiss National Park: A small-scale comparison. *Hydrobiologia*, *793*(1), 175–184.
- Vörösmarty, C. J., Meybeck, M., Fekete, B., Sharma, K., Green, P., & Syvitski, J. P. M. (2003). Anthropogenic sediment retention: Major global impact from registered river impoundments. *Global and Planetary Change*, *39*(1–2), 169–190.
- Ward, J. V., & Stanford, J. A. (1983). Serial discontinuity concept of lotic ecosystems. In T. D. Fontaine Illand & S. M. Bartell (Eds.), *Dynamics of lotic systems* (pp. 29–42). Ann Arbor Science Publishers.
- Wehren, B., Schädler, B., & Weingartner, R. (2010). Human interventions. In U. BUNDI (Ed.), *Alpine waters* (pp. 71–92). Springer.
- Weisberg, S. B., & Burton, W. H. (1993). Enhancement of fish feeding and growth after an increase in minimum flow below the Conowingo dam. *North American Journal of Fisheries Management*, *13*(1), 103–109.
- Wellard Kelly, H. A., Rosi-Marshall, E. J., Kennedy, T. A., Hall, R. O., Cross, W. F., & Baxter, C. V. (2013). Macroinvertebrate diets reflect tributary inputs and turbidity-driven changes in food availability in the Colorado River downstream of Glen canyon dam. *Freshwater Science*, *32*(2), 397–410.
- Wetzel, M. A., Leuchs, H., & Koop, J. H. E. (2005). Preservation effects on wet weight, dry weight, and ash-free dry weight biomass estimates of four common estuarine macro-invertebrates: No difference between ethanol and formalin. *Helgolander Marine Research*, *59*(3), 206–213.
- Wootton, J. T., Parker, M. S., & Power, M. E. (1996). Effects of disturbance on river food webs. *Science*, *273*(5281), 1558–1561.
- Wulf, P., & Pearson, R. G. (2017). Mossy stones gather more bugs: Moss as habitat, nurseries and refugia for tropical stream invertebrates. *Hydrobiologia*, *790*(1), 167–182.
- Yarnell, S. M., Petts, G. E., Schmidt, J. C., Whipple, A. A., Beller, E. E., Dahm, C. N., Goodwin, P., & Viers, J. H. (2015). Functional flows in modified riverscapes: Hydrographs, habitats and opportunities. *Bioscience*, *65*(10), 963–972.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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