Importance of artificial high flows in maintaining the ecological integrity of a regulated river

Christopher T. Robinson [a,b,*], Gabriele Consoli [a,b], Johannes Ortlepp [c]

[a] Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology (Eawag), 8600 Duebendorf, Switzerland
[b] Institute of Integrative Biology, ETH-Zurich, 8092 Zürich, Switzerland
[c] Hydra, Büro für Gewässerökologie Mürle & Ortlepp, Mühlweg 17, 75223 Niefern-Öschelbronn, Germany

HIGHLIGHTS

- Artificial floods mobilized bed sediments, reducing biofilms and benthic organic matter.
- Floods reduced macroinvertebrate densities with quick recovery between floods.
- Floods shifted community assembly to be more alpine in character.
- Floods increased spawning habitat for brown trout, increasing abundances.
- Flood discontinuation shifted assemblages to pre-flood conditions.
- Flood discontinuation resulted in degradation of the system.

GRAPHICAL ABSTRACT
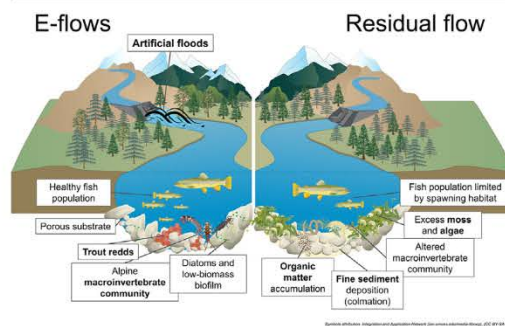
ABSTRACT

Artificial high flows attempt to simulate natural flood pulses in flow-regulated rivers with the intent to improve their ecological integrity. The long-term use of such high flow events have shown beneficial ecological effects on various rivers globally. However, such responses are often non-linear and characterized by underlying feedback mechanisms among ecosystem components. The question arises as to what happens when such high flow releases are disrupted or even discontinued. Here, we used the long-term (22 years) monitoring dataset from the river Spöl to examine whether discontinuation (2016–2021) of the flood program (annual artificial high flows from 2000 to 2016) resulted in the ecological degradation of the river. We used monitoring data of physico-chemistry, periphyton, benthic organic matter, macroinvertebrates and fish (brown trout, *Salmo trutta fario* L.) in the analysis. The flood program had no long-term effect on water physico-chemistry with most parameters showing typical variations associated with season and inter-annual weather patterns. The floods were effective at mobilizing bed sediments that reduced periphyton biomass and benthic organic matter following each flood. Increases in periphyton biomass and benthic organic matter occurred between floods, but both parameters showed no significant increase with discontinuation of the flood program. Floods reduced macroinvertebrate densities, but with density increases occurring between floods. The pulsed disturbances, and the progressive change in the habitat template, resulted in shifts in community assembly by reducing densities of *Gammarus fossarum*, a dominant crustacean, which allowed other taxa to colonize the system. Macroinvertebrate densities remained low after discontinuation of the floods, although *G. fossarum* densities have increased substantially while other taxa, especially some stoneflies, remained low in abundance. Notably, community assembly returned to a pre-flood composition with discontinuation of the floods. The abundance of brown trout increased substantially during the flood program but returned to low pre-flood numbers with discontinuation of the floods. We conclude that the flood program was beneficial to the ecology of the river Spöl and discontinuation of the floods resulted in degradation

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* Corresponding author at: Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology (Eawag), 8600 Duebendorf, Switzerland.
  E-mail address: robinson@eawag.ch (C.T. Robinson).

of the system after a relatively short lag period. However, the system showed high resilience to an earlier perturbation, a sediment spill in 2013, suggesting a rapid positive response by biota with resumption of the flood program.

1. Introduction

The integration of flow, sediment, and temperature regimes drive the habitat template of natural rivers (Poff et al., 1997; Caissie, 2006; Wohl et al., 2015), underlain by the physical-chemistry of local catchments and basins (Allan, 2004). This fluvial habitat template, in turn, dictates the eco-evolutionary dynamics of riverine flora and fauna (sensu Southwood, 1977, 1988) across space and time (Ward, 1989). Indeed, natural rivers and associated floodplains harbor a diverse assemblage of plants and animals adapted to local environmental drivers (Robinson et al., 2003). The alteration of rivers via large dams, channelization, and urbanization decouples these natural drivers with consequent effects on biota (Ward and Stanford, 1979; Polunin, 2008), resulting in the need of innovative restoration and mitigation measures (Poff et al., 1997). One measure in flow-regulated rivers is the implementation of experimental (artificial) floods to simulate the physical properties of the natural flow regime towards improving their ecological integrity (Konrad et al., 2011; Gillespie et al., 2015), although mitigation goals are often system specific (Olden et al., 2014). Unfortunately, the use of experimental high flows have been limited to single or infrequent events, with only a few examples of long-term and multiple flow releases such as on the Colorado River, USA (Melis, 2011), Ebro River, Spain (Madaleno, 2017) and Spöl River, Switzerland (Robinson, 2012). These long-term experimental flow programs have demonstrated the general positive effects of such mitigation measures and the use of artificial floods to meet various management goals. However, long-term flow management requires adaptation to novel environmental conditions; e.g., flow release limits due to ongoing drought (Colorado system; Korman et al., 2023) or human-caused perturbations (Spöl River; Robinson et al., 2018). In this context, a major question arises as to what happens to a system upon discontinuation of artificial floods at both short and long time intervals.

Long-term monitoring is not novel, what is novel is the scientific understanding gained by analyzing long-term datasets. Globally, there are numerous long-term research programs, e.g., (e)LTER, GLEON and NEON, used to understand and forecast ecosystem state changes over time. Restoration activities also typically include monitoring programs to assess outcomes, document success and failure, and adapt management activities based on results and future objectives (Palmer et al., 2010; Thompson et al., 2018). Often, ecological surprises and novel insights emerge from the analysis of long-term datasets (Dodds et al., 2012). Unfortunately, the majority of monitoring programs implemented following habitat restoration are short-lived, usually due to time and finance constraints. Long-term monitoring requires dedicated personnel and resources, and even serendipity can play a role in future efforts.

The Swiss National Park, in cooperation with the local hydropower company, initiated the Spöl long-term flood program in 2000 to improve habitat conditions for the fishery, integrating monitoring as a means to assess results (Scheurer and Molinari, 2003). The program involves a scientific steering committee that meets in late winter to discuss options regarding the flood (s) for the coming year. Floods each year are based on past results as well as water availability for the coming year. For example, low water years (dry conditions) typically result in single small floods compared to the usual multiple (2–3) floods implemented most years. Further, management actions can be required at short notice, such as from the sediment spill in the Spöl in 2013 that required a flushing flow in early summer or the discontinuation of floods following the 2016 PCB spill during dam renovation. Fortunately, a long-term database was available (and is ongoing) to document ecological responses to both perturbations and forecast future dynamics (post 2016 spill) when flow releases are again resumed.

Artificial high flows are experimental due to the lessons learned from monitoring and data synthesis. Expected ecological responses to high flows come from theoretical foundations, e.g., disturbance ecology (Resh et al., 1988; Lake, 2000), as well as previous experiences from individual and multiple high flow events (e.g., Olden et al., 2014). Dams alter fluvial habitats both upstream and downstream, acting as habitat filters that influence colonization and population dynamics (Poff, 1997), as well as shifting community assembly (Cross et al., 2013). Flow regulation below dams also alter other ecosystem properties such as primary production (Deemer et al., 2022) and metabolism (Uehlinger, 2000) via changes in environmental regimes (after Scheffer et al., 2001). Dams fragment rivers and especially the flora and fauna that disperse along rivers (Dudgeon, 2019). Importantly, the results from high flow experiments can provide knowledge regarding dam removals (Bellmore et al., 2019), which have increased substantially in recent years (see e.g., www.damremoval.eu), or to improving the ecological commissioning of new dams being built around the globe (Zarfl et al., 2015). For example, flow experiments can be used to provide more optimal and functional flows below dams (Poff et al., 1997; Olden and Naiman, 2010; Owusu et al., 2020), whereas dam regulation can, in turn, provide information regarding the temporal response patterns of discontinuing an experimental flood program, such as what occurred on the Spöl River in this study.

The aim of this study was to examine the long-term monitoring data from the Spöl River in relation to an artificial flood program initiated in 2000 and discontinued in 2016. The flood program was stopped in 2016 when high PCB levels associated with renovating the dam were found in sediments below the dam. The power company stopped the flood program in order to minimize the displacement of sediments downriver and facilitate the intended removal of contaminated sediments near the dam. This study compares abiotic and biotic responses during the flood program with the 5 years post 2016 in which no floods occurred. We expected abiotic and biotic properties of the river would develop degraded conditions post 2016 similar to those observed before the flood program. In particular, we predicted physico-chemical properties of river to remain as they were because no program was in place to alter the chemical milieu of surface waters in the river. We predicted macroinvertebrate assemblages to return to the composition and densities observed before the flood program in response to the new habitat template lacking a flow disturbance. Lastly, we predicted the abundance of the local brown trout (*Salmo trutta fario* L.) to return to pre-flood levels as spawning areas progressively become covered/clogged (colmation) with fine sediments and periphyton, thereby reducing the potential for population recruitment.

2. Study site description

The flow-regulated stretch of the Spöl begins below Livigno reservoir on the Swiss-Italian border within the central Alps (E10°11′22″, N46°36′38″), flowing from Punt dal Gall dam at the reservoir through a canyon-confined valley within the Swiss National Park for ca. 5.7 km before entering Ova Spin reservoir (Fig. 1). Both reservoirs are used for hydropower production (see Scheurer and Molinari, 2003). The Spöl flows into the Inn River, a major tributary of the Danube, at Zernez, Switzerland. The study reach is located about 2.3 km downstream of Punt dal Gall at 1660 m a.s.l. Before regulation in 1970, the Spöl had a typical snow-melt/glacial-melt flow regime with high flows in summer and low flows in winter (Fig. 1). At that time, periodic floods ranging between 20 and 60 m^3/s usually occurred during summer/autumn due to heavy precipitation. Regional climate is continental with high seasonal variation in temperature but relatively low precipitation (Barry, 1992). Terrestrial vegetation is mostly coniferous forest (*Picea excelsa*, *Pinus mugo*) with alder (*Alnus incana*) being a common riparian tree.

The Spöl below Livigno reservoir is part of a complex hydroelectric scheme that became operational in 1970 (Scheurer and Molinari, 2003). Dam regulation decreased the mean annual discharge of 8.6 to 1.0 m^3/s, averaging 0.55 m^3/s in winter and 2.5 m^3/s in summer using hypolimnetic water from the reservoir (Fig. 1). Two post-regulation floods occurred in 1979 at 42 m^3/s and in 1990 at 33 m^3/s prior to the flood program initiated in 2000 (Scheurer and Molinari, 2003). Residual flows were reduced (0.55 m^3/s winter, 1.45 m^3/s summer) beginning in 1999 to compensate for water used for the floods (Uehlinger et al., 2003). The residual flows lacked the power to entrain and transport coarse sediments, thus allowing the riverbed to be clogged with fine sediments (Ortlepp and Mürle, 2003) and pools to form upstream of lateral debris fans (Mürle et al., 2003). The stable flows resulted in dense algal mats, extensive moss beds, and an invertebrate assemblage dominated by the crustacean *Gammarus fossarum* (Robinson et al., 2003). Gammarid densities before the flood program ranged from 8000 to 15,000 individuals/m^2 at the study reach (Robinson et al., 2018; Robinson, 2012), and was an important food resource for the trout (Ortlepp and Mürle, 2003). The native brown trout was low in abundance due to a lack of suitable spawning habitat from colmation of the streambed (Ortlepp and Mürle, 2003). Consequently, the Engadine power company, the National Park, and state authorities began using experimental floods in 2000 to improve habitat conditions for the brown trout (Scheurer and Molinari, 2003).

Thirty-two separate floods were released between 2000 and end of 2016 with timing and magnitude dependent on research needs and water availability (Fig. 1). Controlled floods lasted between 6 and 8 h with step-like rising and falling limbs being constrained by release valve mechanics. Peak flood flows usually lasted 2–3 h with the falling limb designed to be relatively gradual to minimize fish stranding. Although shorter than most natural floods, the high flows were effective in mobilizing bed sediments and reducing algal levels without causing high fish mortality (Ortlepp and Mürle, 2003; Uehlinger et al., 2003).

The flood program started with three floods each in 2000 and 2001, and alternated between one and two floods/year from 2002 to 2016. The floods in 2000 and 2001 consisted of two smaller flows between 12 and 16 m^3/s in June and August that bounded a higher flow (42 and 55 m^3/s, respectively) in July. An unplanned flood in October 2000 due to heavy rainfall caused a 3-day release of surplus water that peaked at 28 m^3/s. After 2002, the June flood was discontinued. In years with two floods, a high flow usually occurred in July (>30 m^3/s) with a smaller 'flushing' flow released in late August/early September (15–25 m^3/s) (see Fig. 1). Single floods were implemented in 2003 (41.5 m^3/s), 2005 (11.2 m^3/s), 2010 (37 m^3/s) and 2012 (26 m^3/s) to meet research needs or from low water availability that year. A single flood in 2013 (50 m^3/s) was used as a flushing flow to remove fine sediments accidently released from the reservoir earlier that spring (Task Force Spöl, 2015). The sediment spill impacted the fishery and macroinvertebrate assemblages in the river as discussed below (see Robinson et al., 2018). A 4-day flushing flow also was released from 19 to 22 June 2009 that peaked at 41 m^3/s. Lastly, the flood program was discontinued in late 2016 due to a PCB spill at Punt dal Gall dam during renovation, resulting in 5 years of post-flood monitoring data in the current study.

3. Methods

3.1. Long-term monitoring

A 50-m long reach ca. 2.3 km downstream of Punt dal Gall dam was monitored during the 22 years of study (coordinates: N10°11′, E46°38′). The site was accessed by foot via a National Park trail. The Federal Office of Hydrology and Geology records discharge at a gauging station just downstream of the dam (https://www.hydrodaten.admin.ch/en/2239.html). A temperature logger (Minilog, Vemco Inc., Nova Scotia, Canada) was installed at the study site and recorded temperature at 1-h intervals. The study reach was sampled over 150 times during the monitoring period (1999–2022). Samples were collected every 3–5 weeks when accessible for the long-term study, along with samples collected 1–3 days before and 1–2 days after specific floods for examining short-term dynamics. The sampling frequency varied among study years, depending on site access and specific research questions.

On each sampling visit, a 0.5-L water sample was collected in a polypropylene bottle for laboratory analysis of nitrate-nitrogen (NO_3-N), particulate nitrogen (PN), ortho-phosphorus (PO_4-P), dissolved phosphorus (DP), particulate phosphorus (PP), total inorganic carbon (TIC), dissolved organic carbon (DOC), and particulate organic carbon (POC) following methods detailed in Tockner et al. (1997). In the field, water turbidity (nephelometric
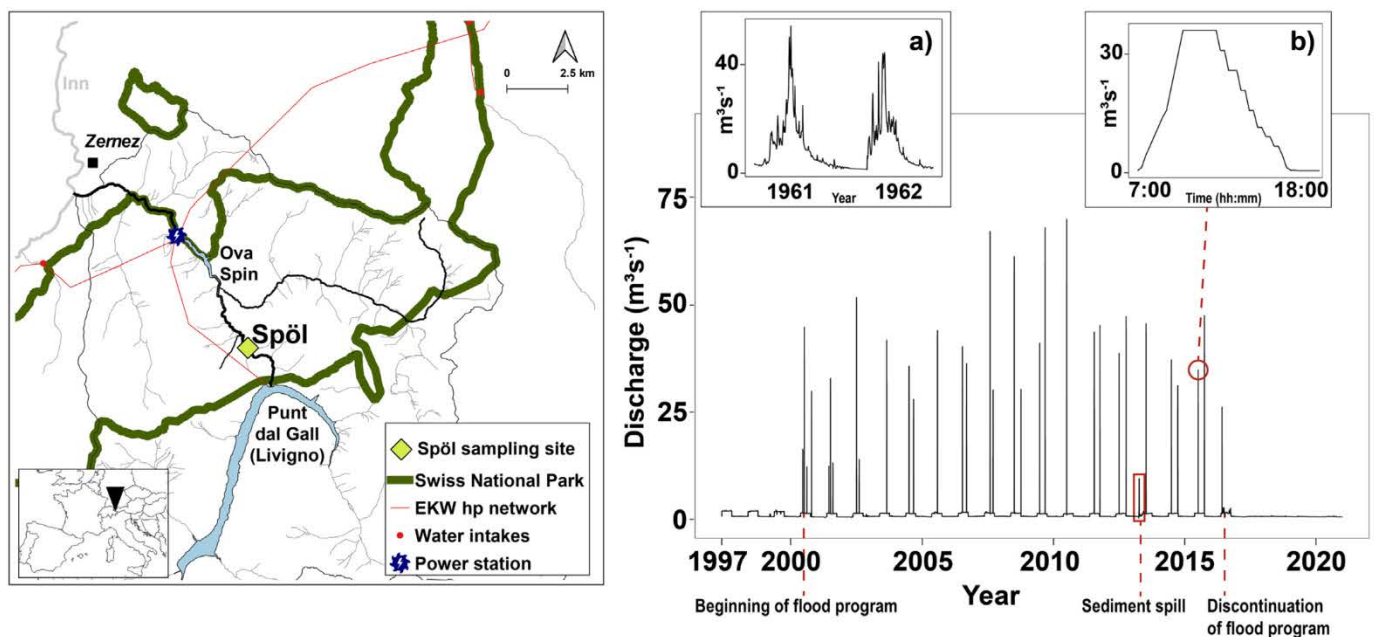

Fig. 1. Map showing the study site location in the Swiss National Park (left). The right graph shows the discharge regime during the study period showing the artificial floods used each year, including the sediment spill in 2013 and discontinuation of the flood program after 2016. Inset graphs display the natural flow regime over two years (1961, 1962) before the dam became operational in 1974 (a), and an example of a typical artificial flood (b).
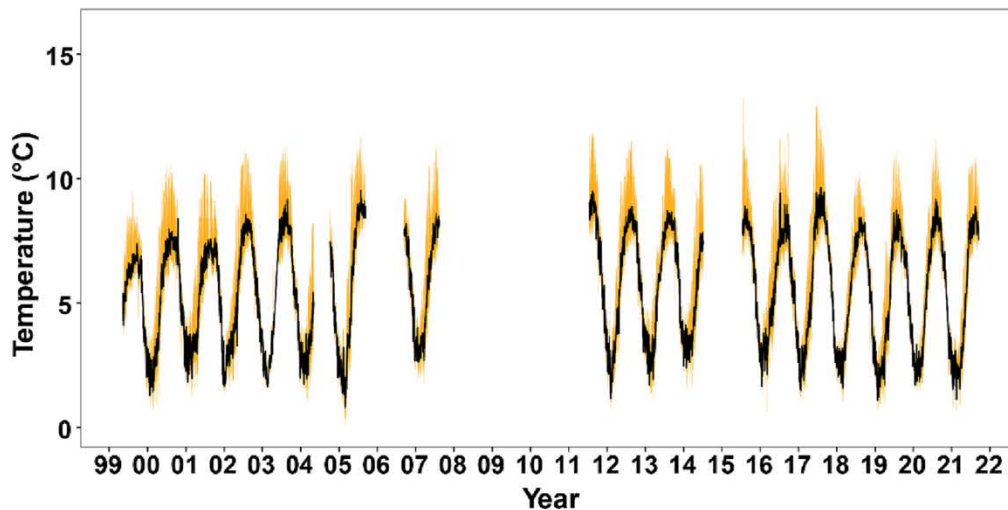
Fig. 2. Temporal patterns in water temperature (°C) over the study period (1999–2022), showing the daily mean, maximum and minimum. Temperature data were recorded hourly using a data logger; missing values were due to technical issues with the logger.

turbidity units; NTU) (Cosmos, Züllig AG, Switzerland), pH (WTW 3110, Weilheim, Germany), temperature and electrical conductivity (µS/cm at 20 °C) (WTW LF340, Weilheim, Germany) were measured using hand-held field meters.

Periphyton was quantified by randomly collecting 5–10 stones (cobble-size) within the study reach on each visit. The stones were placed in plastic bags, returned to the laboratory, frozen at −20 °C, and processed within 3–4 weeks after collection. Periphyton was removed from each stone by scrubbing the top surface of the stone with a wire brush into a pan with water; the area scraped was measured for quantifying periphyton biomass in g/m^2 (after Uehlinger, 1991). An aliquot of the periphyton suspension was filtered through a glass fiber filter (Whatman GF/F, pre-ashed at 450 °C) for determination of ash-free dry mass (AFDM). The AFDM of each sample was determined by drying the filter at 60 °C, weighing, burning the filter at 500 °C for 4 h in a muffle furnace, and then reweighing.

Benthic macroinvertebrates were collected (n = 3) from riffle/run habitats on each visit using a Hess sampler (0.045 m^2, 250-µm mesh). Samples were taken to a depth of 15–20 cm with all large stones scrubbed by hand to remove invertebrates before processing. Samples were stored in plastic bottles and preserved in the field with 70 % ethanol. In the laboratory, macro-invertebrates were handpicked from each sample using a dissecting microscope at 10×, identified to lowest practical taxonomic unit (usually genus), and counted. The remaining material from each benthic sample was then dried at 60 °C, weighed, burned at 500 °C for 4 h, and reweighed with the difference in weights used as estimates of benthic organic material (BOM as AFDM).

Trout abundance was estimated through the annual counting of spawning redds along the 2.6 km stretch below Punt dal Gall. Brown trout spawn in late autumn (November) and redds are easily seen (as denuded areas) and can be counted (J. Ortlepp, personal observation; Beland, 1996; Riebe et al., 2014). Redds were counted and mapped (GPS system) each autumn by Park officials under residual flow conditions (ca. 1.5 m^3/s) with water depths ca. 20–30 cm and water clarity typically good (<10 NTUs). Note that redd counts were used as an index of reproductive success of the trout over the study period and not an actual measure of trout abundance in the river, and assuming food was not limiting (see Beland, 1996; Riebe et al., 2014).

3.2. Data analysis

Continuous temperature data were plotted against time using the logger data (hourly records over the study period), including daily maxima and minima. Spot measures of selected physico-chemical parameters, namely nitrate-N (NO$_3$ + NO$_2$), phosphorous (PO$_4$-P), dissolved organic carbon

(DOC), particulate organic carbon (POC) and electrical conductivity, were plotted against time for the study period. The mean periphyton and benthic organic matter biomass (BOM) was plotted over time for the study period. Further, we correlated (Pearson correlation) the relative change (%) in biomass (periphyton, BOM) before and after individual floods against flood magnitude to examine whether the effects of flood magnitude on these parameters changed over the study period (Zar, 1984).

We used macroinvertebrate density and Simpson's evenness data to examine temporal response patterns during the study period. In addition, the relative change in density (as % change in density) before and after individual floods was correlated (Pearson correlation) against flood magnitude to examine whether the effects of flood magnitude changed over the study period. We also plotted the mean densities of 12 common and abundant taxa over time during the study period. Lastly, we used non-metric dimensional scaling (NMDS) of macroinvertebrate taxa densities (log-transformed) to examine temporal shifts in community composition during the study period (*vegan* package, R Core Team, 2021) followed by PERMANOVA using the '*adonis2*' function in *vegan* to test for differences among groups (Oksanen et al., 2019). Finally, we plotted the number of brown trout redds counted each year over the study period.

4. Results

4.1. Patterns in physico-chemistry

Temperatures showed fluctuations associated with season, being highest in summer and lowest in winter (Fig. 2). Inter-annual variation in temperature reflected annual differences in weather, being relatively colder during colder years and warmer during warmer years. No long-term trend in temperature was evident in the data.

Most measured physico-chemical parameters showed seasonal fluctuations with low values in winter and higher values in summer (Fig. 3). Peak values (or low values for electrical conductivity) often were associated with samples collected during a local precipitation event, especially dissolved organic carbon (DOC) and particulate organic carbon (POC) that likely arrived from small tributaries and valley side-slopes. Nitrate-N averaged 257 µg/L (SD = 47.1 µg/L) and ranged from a minimum 150 µg/L to a maximum 390 µg/L (Fig. 3). Phosphorous (PO$_4$-P) averaged 1.5 µg/L (SD = 1.2 µg/L) with minima below detection levels and a maximum 7.0 µg/L. Average DOC was 0.81 mg/L (SD = 0.44 mg/L) with a maximum 3.5 mg/L, and POC averaged 0.73 mg/L (SD = 0.57 mg/L) with a maximum 3.04 mg/L. Electrical conductivity averaged 256 µS/cm at 20 °C (SD = 31.6 µS/cm) and ranged from 127 to 348 µS/cm. There was a trend of increasing conductivity over the study period. Turbidity values
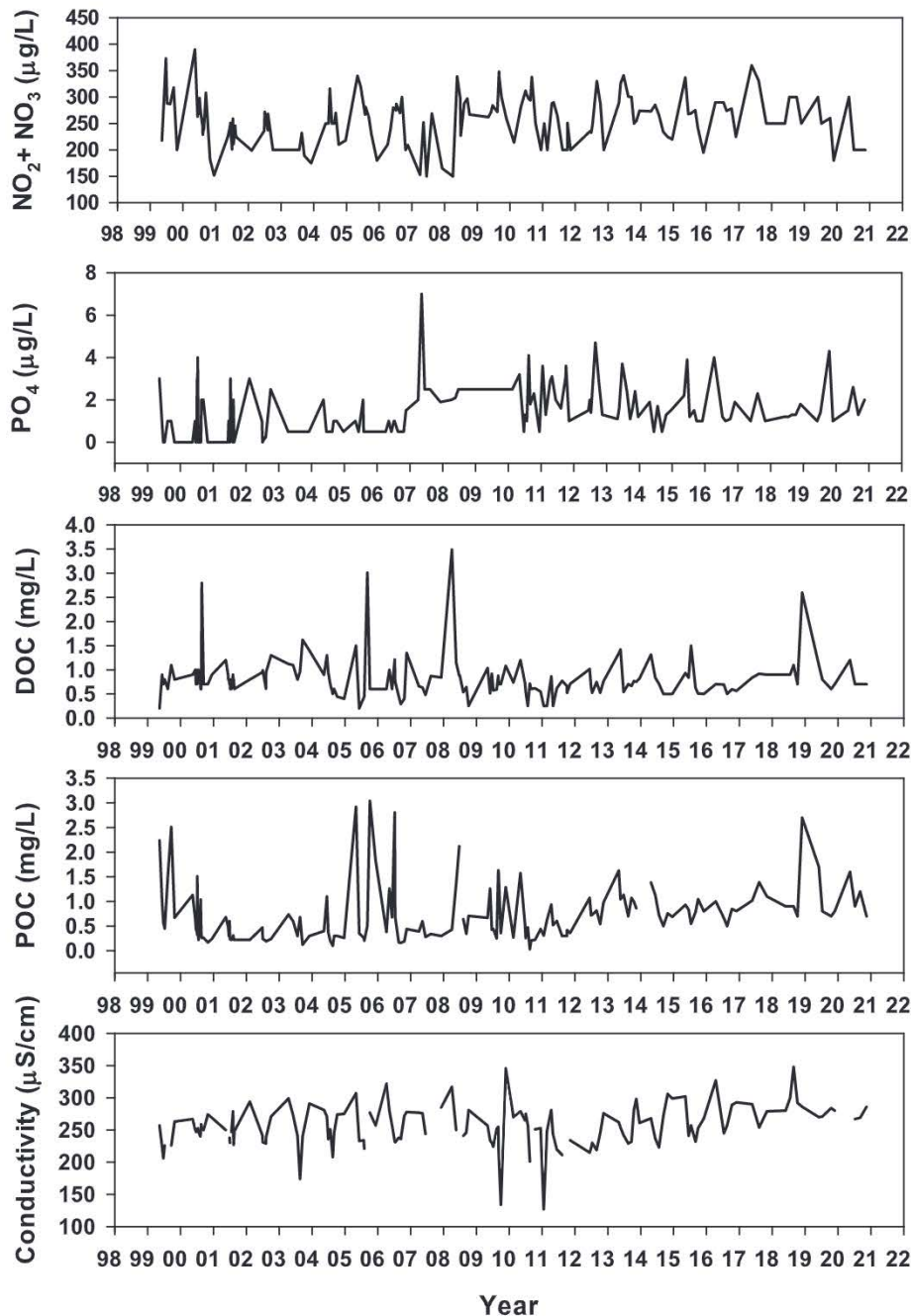
Fig. 3. Temporal patterns in selected physico-chemical measures during the study period (1999–2022). Values are spot measures collected for water chemical analysis or recorded using portable meters on each visit (see methods). Shown are nitrate-nitrogen ($NO_2 + NO_3$), phosphorus (PO_4), dissolved organic carbon (DOC), particulate organic carbon (POC), and electrical conductivity.

averaged 11.8 NTU (SD = 14.2) with a minimum 0.5 NTU and maximum 91.1 NTU. Discontinuation of the flood program in 2016 had no observable effects on measured physico-chemical parameters. However, there were substantial peaks in DOC and POC in 2019 that were likely associated with a rain event causing high inputs as mentioned above (see below regarding benthic organic matter values in 2019).

4.2. Patterns in organic matter resources

Periphyton biomass as AFDM averaged 30.7 g/m^2 (SD = 8.2 g/m^2) before the flood program, 19.6 g/m^2 (SD = 15.9 g/m^2) during the flood program, and 21.7 g/m^2 (SD = 10.1 g/m^2) after stopping the flood program in 2016. Periphyton showed a minimum 1.4 g/m^2 and maximum 100.5 g/m^2 during the study period, and peak values occurred between high flow

events and minimum values occurred after these events (Fig. 4). Floods actively mobilized bed sediments and scoured periphyton from stone surfaces with relative losses ranging from 20 % (low magnitude floods) upwards to ca 90 % (full range of flood magnitudes). There was a negative correlation between periphyton loss (as %) and flood magnitude ($r = -0.33$, $p = 0.022$), indicating large magnitude floods had no additional benefit to the ecology of the river (i.e., the water could be better used for hydropower production). Periphyton biomass was low in May 2020 likely due to flushing from snowmelt waters entering the river.

The biomass of benthic organic matter (BOM) averaged 16.1 g/m^2 (SD = 6.5 g/m^2) before the flood program, 5.1 g/m^2 (SD = 7.6 g/m^2) during the flood program, and 8.1 g/m^2 (SD = 4.8 mg/m^2) after stopping the program in 2016. BOM showed a minimum 0.2 g/m^2 and maximum 25.6 g/m^2 during the study period (Fig. 4). The effects of high flows
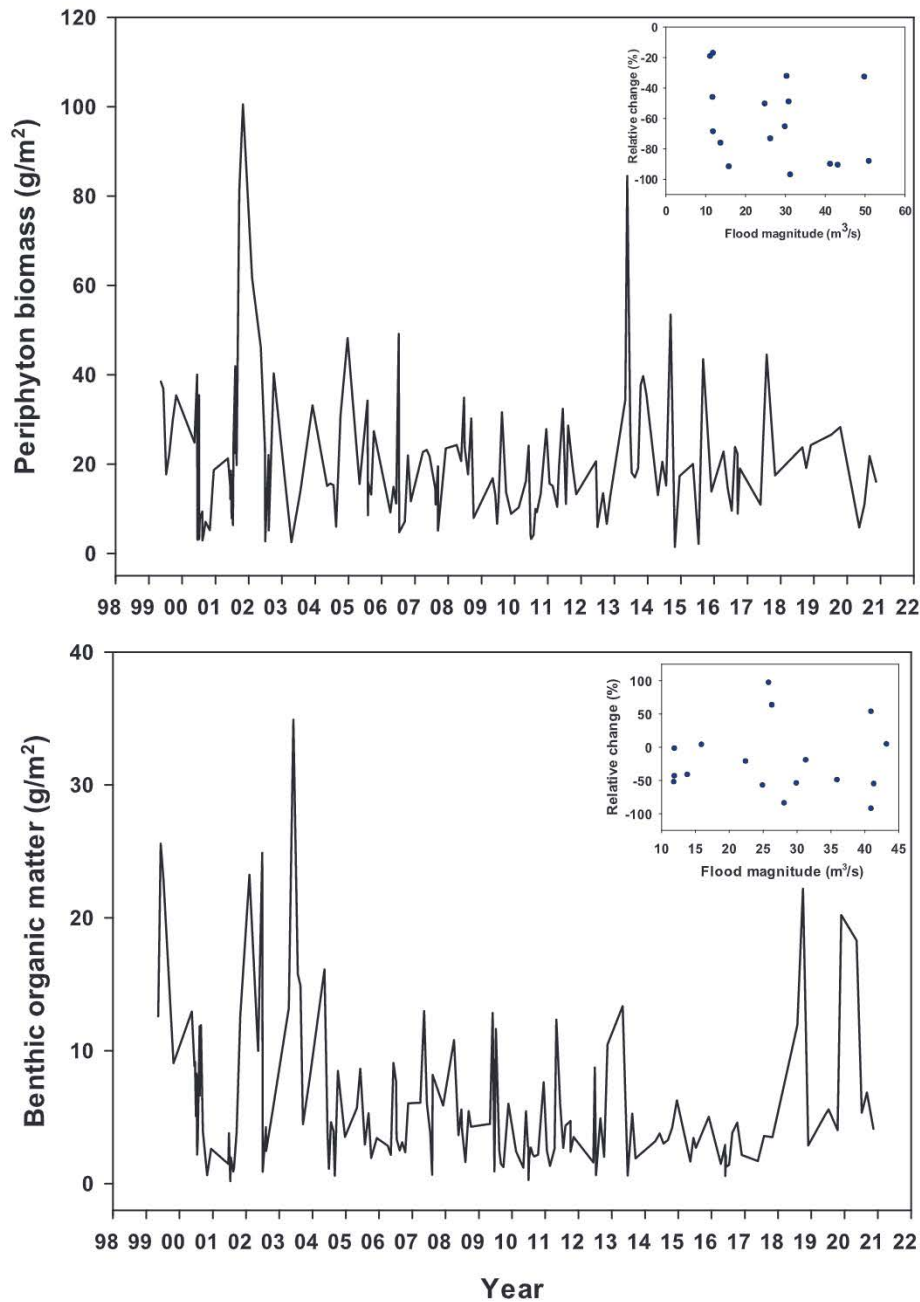
Fig. 4. Long-term measures of periphyton biomass (n = 5–10 per date) and benthic organic matter (BOM, n = 3 per date) as AFDM/m^2. Average values are presented without error bars for better illustration of temporal patterns. Inset plots show relative change in periphyton biomass or BOM before and after selected floods (see methods for details).

contrasted with that of periphyton, where relative BOM levels decreased ca. 50 % during some floods but increased between 50 and 96 % for 4 individual floods. There was no correlation between BOM loss (as %) and flood magnitude ($r = -0.005$, $p = 0.984$). Around 30 % of the floods showed no noticeable increase or decrease in BOM after the flood, whereas 60 % of the floods showed a 20 % decrease or more in BOM after the high flow event. BOM values decreased in 2019 (in contrast to DOC and POC) from a likely high flow caused by a rain event that flushed surface sediments in the main stem.

4.3. Patterns in macroinvertebrates

Macroinvertebrate density was quite high before the flood program, averaging 21,143 ind./m^2 (Fig. 5). The average density decreased during the flood program to 9142 ind./m^2 with peaks between individual flood events surpassing 20,000 ind./m^2 until after the sediment spill in 2013 where

peaks were between 10,000 and 20,000 ind./m^2. Following the discontinuation of the flood program in 2016, average densities decreased to 7820 ind./m^2 (Fig. 5). Individual floods directly impacted macroinvertebrate densities, typically reducing abundances by 60–96 % (Fig. 5 inset). There was a negative correlation between density loss (as %) and flood magnitude ($r = -0.403$, $p = 0.037$), indicating no additional benefits of large floods to the ecology of the river. Abundances showed no change after one low magnitude flood (16 m^3/s), which was the first flood implemented in the flood program. The second flood used in the program was 43.3 m^3/s and decreased macroinvertebrate densities by 96 %. Simpson's index averaged 0.37 (SD = 0.02) before the flood program, 0.34 (SD = 0.01) during the flood program, and 0.42 (SD = 0.03) after discontinuation of the program in 2016. Peaks in Simpson's index occurred between individual floods during the flood program, ranging between 0.50 and 0.60. A major peak in the index occurred in 2018 to near 0.80, but then decreased to <0.60 afterwards.
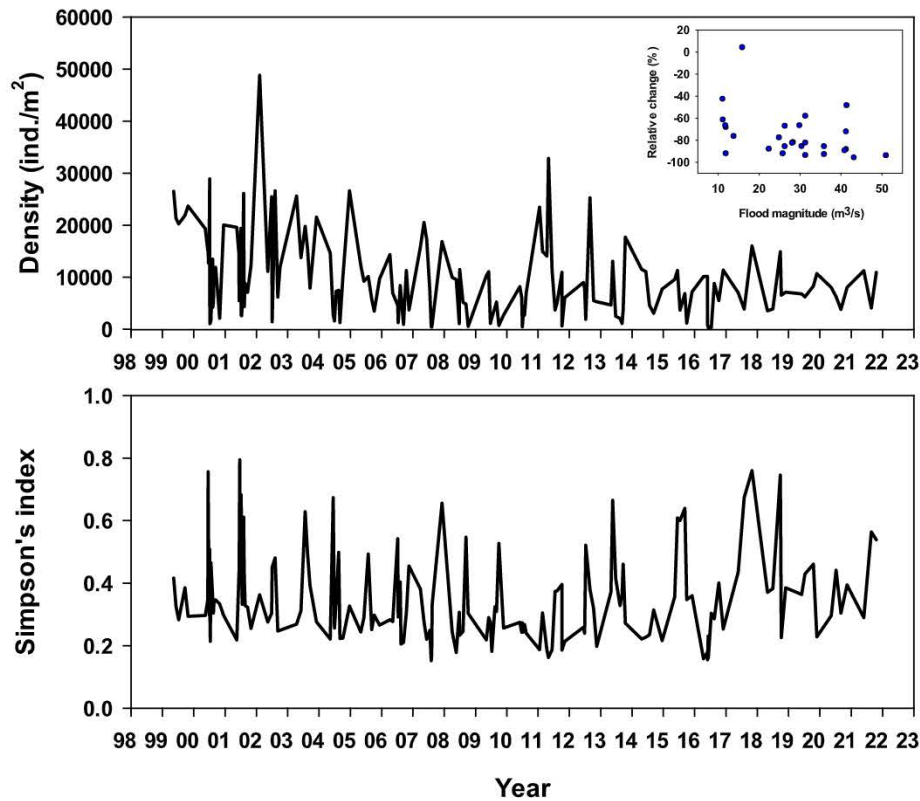
Fig. 5. Average macroinvertebrate densities (ind./m^2, n = 3 per date) and Simpson's index over the study period. Error bars are absent for better clarity of illustration. Inset plot show relative change in density before and after selected floods (see methods for details).

There were 12 taxa suitably abundant for illustrating response patterns during the study period. *Gammarus fossarum* was one of the most abundant macroinvertebrates in the Spöl at the study site prior to initiation of the flood program, reaching up to 15,000 individuals/m^2 and averaging ca. 8000 ind./m^2 (Fig. 6a). The floods were effective at reducing its numbers to <1000 ind./m^2 after most floods (average = ca. 2000 ind./m^2 during the flood period). However, *Gammarus* quickly rebounded after low magnitude floods or years (e.g., 2003) when only a single flood was released. Its numbers decreased after the sediment spill in 2013, but abundances recovered subsequently. Numbers again peaked after termination of the flood program in 2016 with an increasing trend from 2019 to 2021 (post flood average = 3350 ind./m^2). *Crenobia alpina* (turbellarian) was high in abundance before the flood program (average = 2365 ind./m^2), but decreased sharply during the flood program (average = 95 ind./m^2) and remained low after the flood program was discontinued (average = 35 ind./m^2) (Fig. 6b).

Baetis spp. (*B. alpinus* and *B. rhodani*) were abundant throughout the study period, averaging 1140 ind./m^2 before the floods, 1030 ind./m^2 during the flood period, and 1570 ind./m^2 after the floods were discontinued (Fig. 6c). *Baetis* showed an increase in the early part of the flood program (2000–2005), then lower numbers up to 2016 followed by an increase in abundance after 2016 in the absence of floods. Heptageniid mayflies (mostly *Rhithrogena* spp.) were low in abundance but with peaks often above 200 ind./m^2 (Fig. 6d); they averaged 24 ind./m^2 before the floods, 39 ind./m^2 during the flood program, and 40 ind./m^2 after the floods were discontinued.

The abundant stoneflies included *Nemoura* sp., *Protonemura* sp., *Perlodes* sp., and *Leuctra* spp. (Fig. 6e–h). *Nemoura* was low in abundance before the flood program (average = 56 ind./m^2), then increased dramatically between 2007 and 2012 (peaks 2000–6000 ind./m^2), followed by a decrease but with smaller peaks until 2016 (average = 310 ind./m^2 during flood program) and back to low numbers following 2016 (average =

43 ind./m^2) (Fig. 6e). *Protonemura* also was low in abundance before the flood program (average = 240 ind./m^2), followed by a substantial increase in abundance early in the flood program (peak up to 18,000 ind./m^2) with a gradual decrease until 2013 (average = 1010 ind./m^2 during flood program) and with low numbers from 2013 to 2021 (average = 72 ind./m^2 after 2016) (Fig. 6f). *Perlodes* showed no distinct pattern during the study period, averaging 50 ind./m^2 preflood, 90 ind./m^2 during the flood program, and 17 ind./m^2 after discontinuation of the floods (Fig. 6g). It showed two peaks over 1500 ind./m^2 in 2012 and 2016. Lastly, *Leuctra* was low in abundance before the flood program (average = 318 ind./m^2), showed a peak in 2001 (6000 ind./m^2), then was essentially absent until 2006 when abundances increased sharply again with peaks typically over 4000 ind./m^2, and with lower numbers after the floods were discontinued.

Abundant Trichoptera included *Allogamus* sp. and *Rhyacophila* spp. (Fig. 6i–j). *Allogamus* abundances increased in the early part of the flood program with peaks reaching 400 ind./m^2, but numbers dropped between 2008 and 2012, followed by another increase between 2013 and 2019 (Fig. 6i). *Rhyacophila* numbers also peaked when the flood program began, reaching over 500 ind./m^2 in 2002 (Fig. 6j). *Rhyacophila* was essentially absent between 2002 and 2007, increasing to ca 100 ind./m^2 after 2007 and peaking ca. 400 ind./m^2 in 2019–2020. *Rhyacophila* averaged 98 ind./m^2 before the flood program in 1999, decreasing to an average = 26 ind./m^2 during the flood program, and increased to 100 ind./m^2 after the flood program was discontinued post-2016.

Lastly, common dipterans included Chironomidae and *Dicranota* sp. (Fig. 6k–l). Chironomids averaged 8208 ind./m^2 before the flood program in 1999, decreasing to an average 2918 ind./m^2 during the flood program and decreasing further to an average 1909 ind./m^2 after the flood program was discontinued in 2016 (Fig. 6k). However, chironomid numbers peaked in various years to over 10,000 ind./m^2 (e.g., 2005, 2008, 2013) and reached over 20,000 ind./m^2 between 2001 and 2002.
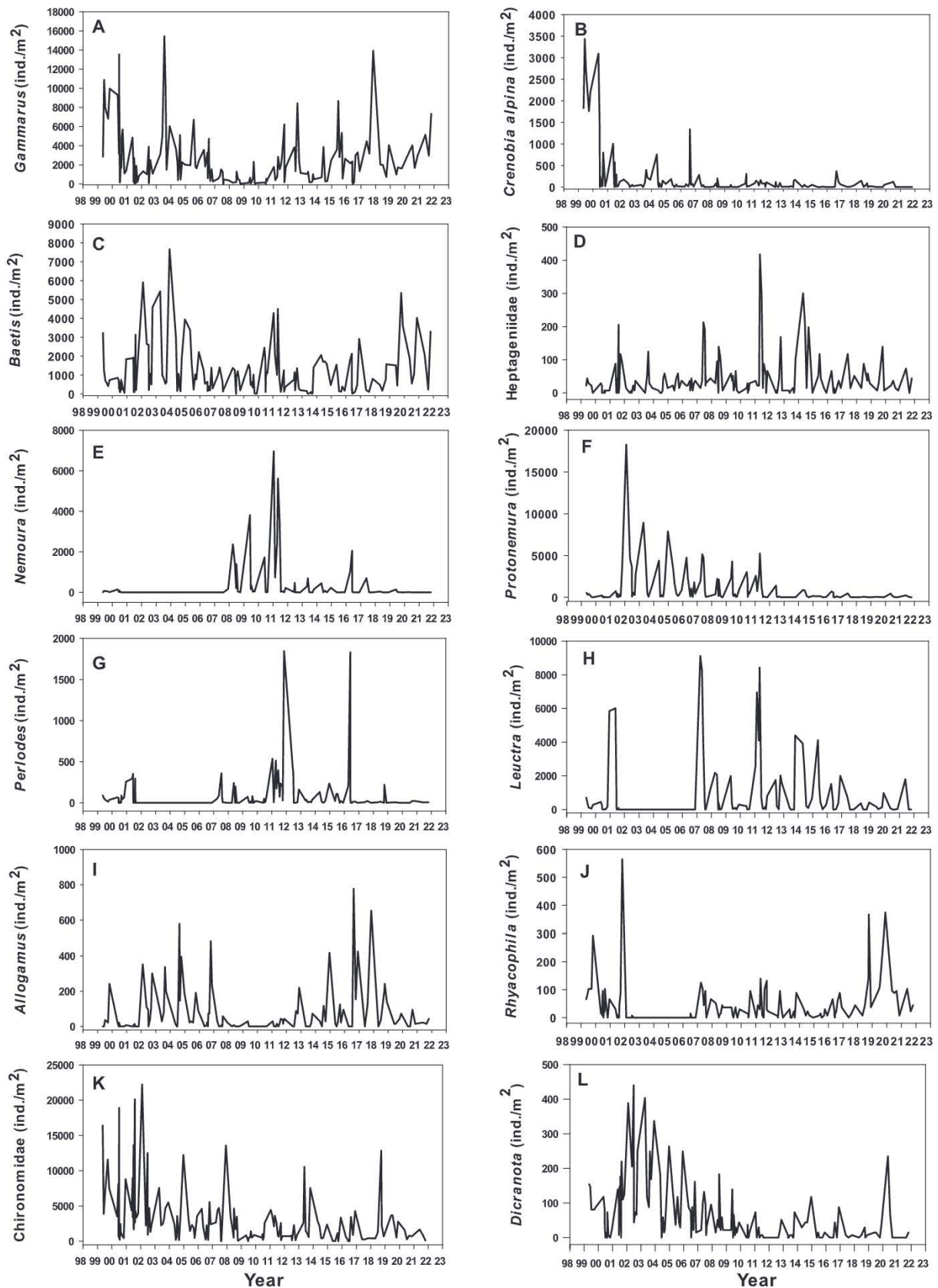
Fig. 6. Long-term density measures of 12 common macroinvertebrates collected in the Spöl on each visit. Presented are average values (n = 3 per date) without error bars for better clarity of illustration.
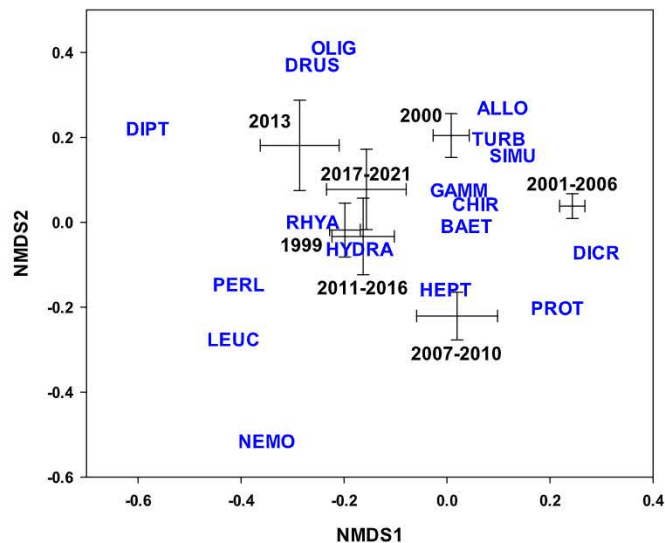
Fig. 8. Annual counts of brown trout redds in the Spöl between Punt Periv (long-term monitoring site in this study) and Punt dal Gall (dam) during the study period (see map Fig. 1).

Fig. 7. Scatterplot of the NMDS results using log(X + 1) transformed density data of macroinvertebrates collected in the Spöl on each sampling date. Different dates are pooled to represent different time periods of the study that generated distinct patterns in assemblage structure. ALLO = *Allogamus* sp., BAET = *Baetis* spp., CHIR = Chironomidae, DICR = *Dicranota* sp., DIPT = Diptera excluding chironomids and simuliids, DRUS = *Drusus* sp., GAMM = *Gammarus* sp., HEPT = Heptageniidae, HYDRA = *Hydracarina* spp., LEUC = *Leuctra* spp., OLIG = Oligochaeta, NEMO = *Nemoura* sp., PERL = *Perlodes* sp., PROT = *Protonemura* sp., RHYA = *Rhyacophila* spp., SIMU = Simuliidae, and TURB = Turbellaria (*Crenobia alpina*).

Dicranota abundances increased early during the flood program, attaining peaks ca 400 ind./m² between 2001 and 2004 (Fig. 6l). Abundances decreased over the study, averaging 61 ind./m² during the flood program, and only 25 ind./m² after 2016 when the program was discontinued (although a peak occurred in 2000 at over 200 ind./m²).

The results of the NMDS analysis revealed significant temporal patterns in assemblage structure of macroinvertebrates in the Spöl (PERMANOVA: F = 15.26, p < 0.001; Fig. 7). Assemblage structure shifted strongly the first year of the flood program in 2000 before transitioning to a rather stable assemblage structure between 2001 and 2006 that corresponded with increases in the abundances of *Baetis* spp., *Dicranota* sp., Simuliidae, *Allogamus* sp. and *Protonemura* sp. Another major shift in assemblage structure occurred in 2007 and lasted until 2010 with increases in the abundances of *Nemoura* sp., *Leuctra* spp., and *Perlodes* sp. in conjunction with decreases in the abundances of *Protonemura* sp. and *Allogamus* sp. (Fig. 7, and see Fig. 6 for changes in taxa densities). Assemblage structure shifted yet again in 2011–2016 with an exception in 2013, the year of the sediment spill in which numbers of most taxa were low until recovery in October of that year. The last assemblage shift was evident from 2017 to 2021 after discontinuation of the flood program, showing assemblage structure was most similar to that of 1999 before the flood program began.

4.4. Patterns in fish abundance

The number of brown trout redds in the monitored section was 58 in 1999 before the flood program began (Fig. 8). Redd numbers then increased incrementally to 239 in 2004 and remained relatively stable until 2013, ranging from a low of 150 in 2009 when counting under rather turbid water conditions (R. Haller, personal communication) to a high of 307 in 2008. The sediment spill occurred in 2013 and caused substantial mortality (>70 %; Task Force Spöl, 2015) of the trout population in the Spöl below the reservoir; redd numbers decreased to 38 and stayed low until increasing in 2016 to 153. In 2017 following the discontinuation of the flood program, redd numbers again decreased to a low of 35. Redd
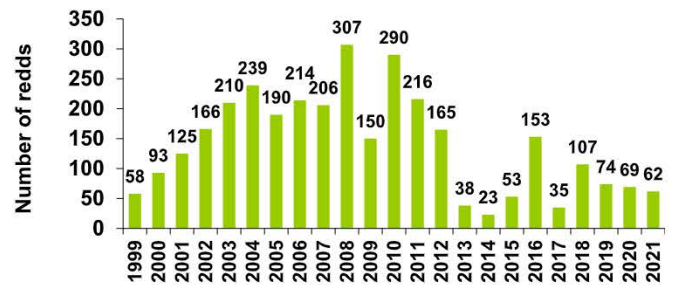
numbers then increased to 107 in 2018, before decreasing again in 2019, and reaching a low of 62 in 2021.

5. Discussion

Rivers below dams experience a multitude of perturbations or human-related disturbances, including alterations in flow, sediment and temperature regimes (Tofolon et al., 2010; Loire et al., 2021). For example, so-called flushing flows often are used to periodically flush sediments from reservoirs or to flush fine sediments that accumulate downstream of dams (Waters, 1995). In contrast, environmental flows are part of the river restoration toolbox (Williams et al., 2019) and include channel-forming releases that influence ecological properties (Olden et al., 2014). For instance, experimental or artificial floods are flow releases from dams used for environmental purposes (Gillespie et al., 2015). In this context, the Spöl flood program demonstrated positive responses in fish (brown trout abundances) and macroinvertebrates (Robinson, 2012; Robinson et al., 2018) to the release of 1–3 floods each year from 2000 to 2016. Fish abundance increased around 4–5 fold over pre-flood values. The macroinvertebrate assemblage, after passing through various transition states, became more alpine in character and resembled assemblages in natural streams in the region with the inclusion of more EPT taxa.

The Spöl also showed rapid recovery (fish and macroinvertebrates) to a pulse disturbance (major sediment spill) in 2013 (see Robinson et al., 2018), suggesting the flood program enhanced ecosystem resilience as expected from theory (Bunn and Arthington, 2002). For instance, fish abundances and macroinvertebrate assemblages quickly returned to pre-spill conditions following an artificial flood used to flush the deposited, fine sediments from the accidental spill (Robinson et al., 2018). The trout required 2 years to show recovery in concert with their reproductive cycle; i.e., brown trout reproduce after 2 years of development. In turn, macroinvertebrate assemblages demonstrated recovery by October 2013 (6–7 months after the spill), reflecting their short generation times and high reproductive potential, and potential recolonization from tributaries. In contrast, biotic assemblages demonstrated low resistance to changes in the habitat template once the flood program was discontinued in 2016 (a press disturbance; sensu Lake, 2000), returning to structural properties (fish abundances, macroinvertebrate composition) observed before the flood program in 1999 (this study). In the context, climate-related ramp disturbances such as prolonged drought also can substantially alter environmental flow release programs from dams, e.g., Colorado flood program on Lake Powell (Korman et al., 2023), and test the resilience of rivers to further perturbations (not tested in this study).

Environmental flows, such as flow releases, have been suggested as one pillar in the arsenal for restoring the endangered biodiversity of fresh waters (Tickner et al., 2020). Flow releases must be considered with a long-term perspective and include long-term monitoring to be effectively adaptive as a management tool (Holling, 1978; Williams and Brown, 2014). For example, long-term objectives, over 26 years involving five different adaptive releases, were adopted in the flow release program for improving fish recruitment in the Bridge River, Canada (Bradford et al.,

2022). The experimental releases on the Colorado River at Lake Powell also included long-term management objectives and temporal monitoring to be adaptive to ongoing changes in the ecosystem (Melis et al., 2015). Here, managers are now facing a new challenge in facilitating the release program under constraints imposed by prolonged drought (Korman et al., 2023). The Spöl study also highlights the benefits of long-term monitoring for understanding ecosystem state changes to long-term, multiple intra-annual flow releases (Robinson, 2012) and also response patterns, e.g. resilience or colonization dynamics, to novel perturbations (Robinson et al., 2018, this study). Further, monitoring data from various studies can be used for predicting response patterns in other rivers to periodic flow releases, e.g. through meta-analysis (Konrad et al., 2011; Gillespie et al., 2015). Another potential use of flow release monitoring data is forecasting river response to dam removal, especially dams used for flow regulation or those affecting sediment dynamics (Loire et al., 2021), and relevant today as more dams are decommissioned.

Dams decouple the multi-dimensional coherence of rivers in both space and time. Dams, and dam cascades, also isolate and disconnect populations (Nilsson et al., 2005), thereby affecting ecosystem structure (meta-population/community processes; Cross et al., 2013) and function (primary/secondary production, metabolism; Kennedy et al., 2016; Deemer et al., 2022). Flow releases are expected to increase the resilience of dammed rivers by simulating a natural flow regime (Olden et al., 2014) as well as improving sediment dynamics (Wohl et al., 2015) and increasing the lateral connectivity with adjacent floodplains (Bunn and Arthington, 2002). Flow releases are used to enhance the heterogeneity of riverine habitats, including rejuvenation of the hyporheic zone, thereby facilitating the development of refugia and increasing surface/subsurface exchange (Mathers et al., 2021). The Spöl study has demonstrated some of these positive effects, such as increasing hyporheic exchange to provide refugia (Mathers et al., 2021), increasing the availability of spawning habitat for fish recruitment by increasing the porosity of bed sediments (Mürle et al., 2003), and showing high resilience by fish and macroinvertebrates to a pulse disturbance (major sediment spill; Robinson et al., 2018).

In contrast, most flow release studies show that rivers have low or lack resistance to both disturbance and perturbation (see Olden et al., 2014). The present study highlights this lack of resistance with both fish abundances and macroinvertebrate assemblages returning to pre-flood values following the discontinuation of flow releases. The lack of periodic flow releases allows habitats to return to the homogeneous condition caused by flow regulation, through the disruption of flow and sediment dynamics associated with flow releases. The lack of high flows causes streambeds to fill with fine sediments via tributary and side-slope inputs, thereby decreasing bed porosity and thus spawning habitat for fish. The lack of flow disturbance also decreases hyporheic refugial habitats in the same fashion and allow competitive dominants, such as *Gammarus* in the Spöl (Robinson et al., 2018), to reach high abundances even though also being affected by the loss in refugial habitats (e.g., Mathers et al., 2021).

The response to flow-release discontinuation reflects patterns found when newly built flow-regulatory dams begin operation; the similarity in response is a general pattern well-documented in rivers below dams (Ward, 1989). The flood discontinuation on the Spöl was due to PCB contamination of bed sediments following dam renovation with intentions to restart the flow release program once sediments near the dam are cleaned of PCBs; this being a rather costly procedure (R. Haller, personal communication). Another example is the Colorado system, which has been affected by a prolonged drought impeding any future dam releases until reservoir levels return to pre-drought levels (Korman et al., 2023). Here, managers expect a serious ecosystem transition in the fisheries resulting from the drought in relation to changes (substantial increases) in river temperatures that likely will transfer through food webs and alter ecosystem functioning (Cross et al., 2011; Kennedy et al., 2016). Both systems, Spöl and Colorado, can be viewed as experiments in disturbance ecology and especially the resilience of regulated rivers to novel disturbance (e.g., drought) and perturbations (e.g., human-related extreme events). In the Spöl, based on response patterns to an earlier perturbation (Robinson et al., 2018), we expect that the system will show quick recovery once flow releases resume (and at the previous periodicity).

The importance of the temporal dimension in flow release programs cannot be overstated. The effects of dams have both short-term and long-term consequences on the structure and function of rivers (Ward and Stanford, 1983), and short-term effects can influence long-term dynamics in abiotic and biotic properties (Loire et al., 2021). Furthermore, alterations and changes that have occurred over the long-term can influence short-term responses to pulse as well as press disturbances. For example, flow releases in the Spöl have altered riverbeds by reducing moss coverage and mobilizing bed sediments, thereby increasing the porosity of the riverbed that improved recruitment capacity for trout as well as adding refugia for macroinvertebrates to pulse perturbations such as the sediment spill in 2013. Refugia provide a mechanism of resilience for biota to disturbance and are integral in the habitat template of rivers.

The long-term changes in the riverbed from the flow releases also were evident in the response of the Spöl system to the discontinuation. Indeed, the response patterns following discontinuation suggest a legacy effect of the flow releases on the river. For instance, although community assembly has returned to a preflood composition (e.g., *Gammarus* now dominates assemblages as before the flood program), densities of *Gammarus* remain low as well as other macroinvertebrates in the system. This result indicates that the habitat template, here meaning the embedded nature of the river bottom covered with mosses, fine sediment and filamentous algae found before the flood program (Uehlinger et al., 2003), has not returned to preflood conditions. Mosses, in particular, likely provided important habitat for gammarids (Stream Bryophyte Group, 1999; Consoli, 2023), allowing densities to reach high levels (10–30,000 ind./m^2; Robinson et al., 2003) and being an important food resource for trout. Consoli (2023) also found that secondary production of macroinvertebrates in the Spöl has not reached preflood levels, which was dominated by *Gammarus* production.

6. Conclusions

The response patterns of fish and macroinvertebrates clearly indicate that ecological conditions of the Spöl River have degraded since discontinuation of the flood program in 2016. Fish abundances have returned to low pre-flood numbers, likely in response to a loss in reproductive areas suitable for redds. Further, the structural composition of macroinvertebrates also have returned to a pre-flood representation, albeit at lower densities. Periphyton and benthic organic matter levels have remained relatively low compared to pre-flood levels, although bands of filamentous algae occur along shorelines and fine sediments have noticeably increased in depositional areas along the river (authors, pers. observation). Prior to the flood program, mosses and filamentous algae covered the stream bottom (Uehlinger et al., 2003), providing habitat for a high density of *Gammarus* (Robinson et al., 2003). Moss coverage is still low in the river and likely explains the currently low abundance of gammarids (Consoli, 2023), although they currently dominate the macroinvertebrate assemblage. We expect gammarid densities to increase as mosses become more abundant in the river. However, the system is quite resilient, as evident after the 2013 sediment spill, and thus should respond quickly once the flood program resumes.

CRediT authorship contribution statement

CTR conceived the study, summarized the results, wrote the paper; GC summarized the results, wrote the paper, JO conceived the study, summarized results, wrote the paper.

Data availability

Data will be made available on request.

Declaration of competing interest

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