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Summer is in winter: disturbance-driven shifts in macroinvertebrate communities following hydroelectric power exploitation

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Abstract

In Alpine streams, humans have strongly modified the interactions between hydraulic processes, geomorphology and aquatic life through dams, flow abstraction at water intakes and river channel engineering. To mitigate these impacts, research has addressed both minimum flows and flow variability to sustain aquatic ecosystems. Whilst such environmental flows might work downstream of dams, this may not be the case for water intakes. Intakes, generally much smaller than dams, are designed to abstract water and to leave sediment behind. Sediment accumulation then results in the need to flush intakes periodically, often more frequently than daily in some highly glaciated basins. Sediment delivery downstream is then maintained through short duration floods with very high sediment loads. Here we tested the hypothesis that sediment flushing, and the associated high frequency of bed disturbance, controls in-stream habitat and macroinvertebrate assemblages. We collected macroinvertebrates over a 17-month period from an Alpine stream as well as a set of lateral unperturbed tributaries that served as controls. In contrast to established conceptual models, our results showed that the stream is largely void of life during summer, but that populations recover rapidly as the frequency of intake flushing falls in early autumn, producing richer and larger populations in winter and early spring. The recovery in autumn may be due to the recruitment of individuals from tributaries. We conclude that intake flushing in summer inverts expected summer-winter macroinvertebrate abundances, and questions the extent to which environmental flows in intake-impacted Alpine streams will lead to improvements in instream macrofauna unless sediment also is managed.

Keywords

Alpine stream, water intake, flushing, macroinvertebrates, environmental flows, sediment

1 Introduction

The management of Alpine rivers requires the balancing of two competing uses: water supply for hydropower production and sustaining instream flora and fauna. Much attention has been given to securing both the sustainability of reservoir operations and improving aquatic ecosystems (e.g. WFD CIS, 2015) through flow regulation and environmental flows, so-called “e-flows”. E-flows recognise the need for regulated streams to have not only minimum flows but also flow variability, including flow magnitude, frequency, duration, timing, and rate of change (Poff et al., 1997). In this context, ecosystem impacts downstream of dams have been widely studied (e.g. Ligon et al., 1995; Petts & Gurnell, 2005; Childs, 2010) to identify the volume of water that should be released downstream, and its variability, as a compromise between exploitation and ecosystem needs (King et al., 2003; Acreman, 2016). In contrast, there has been much less attention given to the ecosystem impacts downstream of water intakes (Gabbud & Lane, 2016). In sediment terms, dams are at one end of a spectrum of sediment disconnection: sediment tends to be retained behind a dam for a long time period, although occasional flushing may be required (a typical frequency of many years). Water intakes are at the other extreme. They are designed to allow the abstraction of water for within- or between-valley transfer by separating out sediment from water. They commonly have a smaller sediment storage capacity and need to be emptied more frequently in “flushing” events. In basins with high erosion rates, such as glaciated basins, flushing frequency may even be sub-daily at certain times of the year. Flushes feed the river with solid material as well as the flow needed to evacuate the intake of sediment. However, after flushing, as abstraction recommences, sediment transport capacity is reduced. As waves of sediment move more slowly than waves of water, downstream locations typically receive a short duration flood with an exceptionally high sediment load (Petts & Bickerton, 1994; Lane et al., 2014) followed by deposition of sediment. The following flush may then erode some of this sediment, especially if the water wave becomes separated from the sediment wave within this following event, a probability that increases with distance downstream. This event-scale cycle of deposition-erosion in the short-term leads to net long-term river bed aggradation, notably in catchments with a high proportion of glaciation (Koppes & Montgomery, 2009; Lane et al., 2017; Bakker et al., 2018). The long term effect of flow abstraction coupled with continued sediment delivery leads to the accumulation of "legacy" sediment (James, 2013) and long-term bed level rise (e.g. Bakker et al., 2018). Unlike dams, intakes maintain sediment connectivity from source to sink (Lane et al., 2014; 2017).

Research has found that flushing may have a significant impact on downstream river morphology, habitat conditions (Kondolf et al., 2014; Wohl et al., 2015) and potentially flora and fauna. Both coarse and fine sediments can impact aquatic life (Jones et al., 2012) and both their excess and shortage can have negative impacts (Wood & Armitage, 1997; Milhous, 1998; Jones et al., 2012; Extence et al., 2013). For example, increases in fine sediment concentration in the river flow can trigger a suite of responses such as downstream invertebrate drift (Culp et al., 1986) in order to escape the negative effects of high turbidity (Ciborowski et al., 1977). This may cause a local diminution of invertebrate abundance and alter community composition (Ehrhart et al., 2002; Jones et al., 2012), allowing more resistant species to survive and more rapidly establishing species to quickly return. While some macroinvertebrates have developed adaptations to disturbance (Matthaei et al., 1996), it appears that river morphodynamics that are slightly balanced towards erosion may allow sufficient transport and nutrient mixing to reverse fine sediment accumulation provided that there is not so much erosion that habitat is destroyed (King et al., 2003).

In glacier-fed rivers, macroinvertebrate assemblage composition varies seasonally, according to dominant water source (glacial, snowmelt and groundwater, respectively, kryal, nival and krenal systems (Ward et al., 1999; Füreder et al., 2001; Brown et al., 2003). The hydrology of these systems leads to snow- and glacier-driven flood pulses (Malard et al., 2006; Cauvy-Fraunié et al., 2014). The origin of water, and these pulses, influence population dynamics (Malard et al., 1999; Brown et al., 2003; Gabbud & Lane, 2016). At high altitudes, macroinvertebrates depend more on channel stability, water source and temperature than on longitudinal trends due to altitude (Maiolini &

Lencioni, 2001). Habitat diversity has been defined as maximal when these water sources are mixed (Brown et al., 2015).

Following from these hydrological observations, macroinvertebrate biomass, species richness and abundance tend to be higher in spring and autumn in nival systems (e.g. Burgherr & Ward, 2001; Füreder et al., 2001; Robinson et al., 2001; Schütz et al., 2001). For systems with kryal influence, these seasonal windows may be complicated because glacially-fed rivers commonly have summer water temperatures less than 10°C (Milner & Petts, 1994) for some kilometres downstream from the glacier. They also may have a very distinctive sediment regime with particularly elevated suspended sediment concentrations in summer (Gurnell, 1987; Milner & Petts, 1994; Brown et al., 2003), relatively low organic matter supply and nutrient loading, and high rates of morphodynamic disturbance (Gabbud & Lane, 2016). Milner & Petts (1994) proposed a spatially-explicit conceptual model for glacier-fed streams that reflects this pattern, suggesting that the abundance and diversity of species tend to be low close to glaciers and increase with rising water temperature and increasing channel stability downstream. Individual species may differ in their adaptation to colder temperatures (Robinson et al., 2001) and it has been noted that higher macroinvertebrate abundance and diversity can be found at different times of the year, with taxa absent in summer being present during other seasons (Milner et al., 2001; Brown et al., 2015).

Hydroelectric operations associated with flow intakes may complicate this conceptual model for a number of reasons (see Gabbud & Lane, 2016). First, flow abstraction leads to long periods of minimum or no flows, depending on the policy regime in place in the basin (for instance, in Swiss streams, there remain examples where there is still no minimum flow applied). These periods shorten in duration as glacier melt increases, and it is necessary to flush the intakes with growing frequency. Second, flushes lead to short duration flow peaks with very rapid flow rise and fall (typically 15 to 30 minutes from minimum to maximum), more rapid than that associated with normal diurnal discharge rise and fall in glaciated basins (typically > 6 hours from minimum to maximum depending on catchment buffering effects). Third, these flow peaks are often accompanied by peaks in suspended load and bedload (Gurnell & Warburton, 1990; Lenzi et al., 2003), with peak sediment concentrations that range from 20 to 100 mg/l in the downstream channel due to water abstraction to concentrations greater than 6500 mg/l directly below the intake during flushing (Gurnell, 1983). Fourth, the increased flow during flushes, coupled to high rates of sediment transport, may lead to channel instability (both erosion and deposition), but with a bias towards long-term deposition at the scale of decades if flow abstraction leads to a reduction in sediment transport capacity to levels lower than the rate of sediment delivery (Bakker et al., 2018).

Whilst perturbation, whether of flow or sediment, may have positive effects on aquatic ecosystems (Ryan, 1991; Poff et al., 1997), it is less clear that they are positive for perturbations associated with intake flushing because of the rate of discharge rise and the extreme sediment concentrations and bed disturbance that result, at a potentially very high frequency (daily or sub-daily in summer). Critical here is the high turbidity linked with bed instability (Munn & Brusven, 1991; De Jalon et al., 1994; Milner & Petts, 1994; Gislason et al., 2001), the ability of instream fauna to find refugia during rapid flow change and the disturbance of triggers of different life stages (Poff et al., 1997). Relatively little research has investigated the effects of flow and sediment pulses on macroinvertebrate assemblages in high altitude rivers (Petts & Bickerton, 1994) until more recently (e. g. Brown et al., 2015; Espa et al., 2015; Gillespie et al., 2015; Quadroni et al., 2017; Schneider & Petrin, 2017). More generally, sediment considerations are often overlooked in the setting of e-flows (see Wohl et al., 2015) or have focused on the management of dams (see Gabbud & Lane, 2016).

In this study, we investigated the disturbance-driven shifts in macroinvertebrate communities following hydropower exploitation. We surveyed the ecosystem impacts downstream of Alpine water intakes in a glaciated basin, over an entire year. We included a set of lateral unperturbed tributaries that served as controls, but recognising that such tributaries might have different ecosystem characteristics to those that might naturally be found in the main stream. We tested the hypotheses that (1) it is sediment flushing, and the associated high frequency of bed disturbance, that controls in-stream habitat and macroinvertebrate assemblages; and (2) macroinvertebrates are able to recolonise the stream as soon as the disturbance rate is reduced, due in part to supply of macroinvertebrates from lateral tributaries. We use the evaluation of these hypotheses to identify how environmental flows might be better designed for Alpine catchments where the river is regulated by water intakes.

2 Study site – The Borgne d'Arolla

This study was conducted in an Alpine glacier-fed stream, the Borgne d'Arolla (hereafter, the Borgne) in the south-west Swiss Alps. Geologically, the catchment is part of the Dent Blanche Nappe essentially composed of gneiss and granites (Steck et al., 2001). The surrounding vegetation is generally pioneer or secondary successional species (shrubs, larch (*Larex* sp.), alpine grasses, etc.) (Stampfli, 2015) and the current tree line is at ca. 2'100-2'200 m. The river reach considered consists of wider zones (see Bakker et al., 2018), where there is enough valley bottom width for the development of braided channels and associated alluvium and local habitat potentially suitable for macroinvertebrate populations; and narrower and steeper zones, generally with bedrock or semi-alluvial cover, unlikely to provide suitable macroinvertebrate habitat. The elevation of the river reach considered in this study is between 1'815 and 2'215 m a.s.l. with a mean slope of 20%. The Borgne is surrounded by a set of valley glaciers and is fed by a series of both kryal and nival streams, some temporary (T01, T02, T06, T07 and T15) and the others permanent (Figure 1a) (Gabbud et al., in review).

Groundwater and direct precipitation can contribute to runoff depending on the tributary under consideration (Petts & Bickerton, 1994). The Borgne is fed by several glaciers, notably the Haut Glacier d'Arolla, the Glacier de Collon, the Glacier de Pièce and the Glacier de Tisjiore Nouve, whose water is used for hydropower production. The climate in the area is temperate. Annual precipitation is generally between 900 and 1300 mm (Micheletti et al., 2015, based on Meteosuisse, 2014). Daily air mean temperature data (Figure 1d) were provided for the study period 2016-2017 by the Swiss Institute for Snow and Avalanche Research (WSL).

The water of the Borgne and some of the tributaries is abstracted at water intakes (Figure 1b, c) and pumped to a neighbouring valley as part of large hydroelectric power scheme, Grande Dixence SA (Grande Dixence SA, 2010). Over the 6 km reach of stream studied here, there are 3 main intakes that influence the Borgne: Bertol Inférieur in the Borgne itself (2115 m a.s.l.), and Pièce (2497 m a.s.l.) and Tsijiore Nouve (2124 m a.s.l.) on the two main left valley tributaries (Figure 1a). They abstract water from May to November (the water supply is too low in winter for abstraction) and are flushed as a function of sediment accumulation. The frequency of flushes by day changes over the seasons. There is no minimum flow at any of the intakes at present and thus instream flows are driven by recharge from either nival or krenal sources.

The investigated reach was defined to cover the four wider braiding zones, named A, B, C and D (Figure 1), impacted by the flow intakes in the valley and also to repeat an earlier study of this system by Petts & Bickerton (1994). The first Borgne site (A0) was upstream of the Bertol Inférieur intake (Figure 1a). Although this site is impacted by flushes from three upstream sites (Vuibé, Haut Glacier d'Arolla and Bertol Supérieur), part of its basin is unexploited for hydropower and it has continuous stream flow throughout the summer and normally the winter. Two sites (A1 and A2) lie between the Bertol Inférieur intake and the Pièce and Tsijiore Nouve tributaries and are referred to as being in the upstream reach. Both sites experience a very low baseflow component during summer due to flow abstraction, primarily associated with krenal sources. The final four sites (B1, C1, D1 and D5) were downstream of the Pièce/Tsijiore Nouve tributaries and are referred as being in the downstream reach.

The Borgne is of particular interest, as Petts & Bickerton (1994) undertook macroinvertebrate sampling in the 1990s, based on the Milner & Petts (1994) model. They hypothesised that the abstraction of water for hydroelectric operations should cause the macroinvertebrate gradient to steepen with distance downstream from the intakes. They found that the abstraction of kryal sourced water due to intakes would increase the contribution of nival and krenal sources and improve in-stream habitat conditions (a warmer, clearer and more stable stream), such that the development of macroinvertebrate populations with distance from the glacier would be more rapid. That said, by comparing their data with an older study of the Borgne before hydropower development (Dorier, 1937), Petts & Bickerton (1994) found that *Diamesa*, the only species colonizing glacial tributaries above 1500 m according to Doria (1937), had decreased in number in the Borgne since flow abstraction began. Petts and Bickerton's (1994) data collection was undertaken in 1993, a year with very few flushes (89 at Bertol Inférieur) as compared with present: data for Bertol Inférieur suggest that since this date there has been a progressive increase in flushing frequency from 2003 onwards to consistently > 180 flushes per year since 2010, and in 2015 > 300 (Figure 9c in Bakker et al., 2018).

3 Methodology

Sampling stations were chosen along the Borgne by selecting one representative site within each Petts and Bickerton (1994) defined sub-reach. Petts & Bickerton (1994) undertook sampling over a single period in June 1993. In this paper, we report measurements made monthly between June and October 2016 and in January and March 2017 at 7 sites in the Borgne and also in 15 relatively unperturbed tributaries shown in Figure 1. Given all the tributaries flow into the Borgne, these inputs are considered as the primary source of water, sediment and macroinvertebrates for the main river. Gabbud et al. (in review) analysed the main drivers of macroinvertebrate assemblages over the year for the tributaries. Here, we assume that the tributaries will partially serve as reference to what we might expect in unregulated Alpine streams in glaciated basins, as we recognise that these streams have a natural variation in daily flow and sediment load. Additional monthly measurements were made between May and October 2017 in the main Borgne. Tributary sites T01, T03 and T05 are excluded from the analyses as these could not be sampled on all occasions. Site D5 could not be sampled in October 2017 due to in-channel engineering works, the only ones affecting the Borgne during the study. All sample sites were between 1’815 and 2’215 m a.s.l. No data collection was undertaken during flushing.

3.1 Physical data: sample site parameters

Temperature was point measured at the time of macroinvertebrate sampling at each sample site using a ProfiLine Cond 3110 multi-parameter sampler. During 2016 and winter 2016-17, the macroinvertebrate sampling took two days and so temperature measurements weren’t necessarily made on the same day. Temperature measurements were within day when sampling focused on the Borgne alone from May 2017. The latter allowed calculation of the downstream gradient in temperature in the main channel; i.e., the slope of the regression plot of temperature versus distance downstream, under the assumption of minimal within-day temperature variation except during flushing.

3.2 Physical data: flushes

Fifteen-minute resolution discharge data for each water intake were provided by HYDRO Exploitation SA and ALPIQ SA, responsible for the hydroelectric power scheme, for the three main intakes: Bertol Inférieur, Pièce and Tsijiore Nouve. The discharge abstracted is recorded to meet regulatory requirements. During flushing, abstraction falls to near zero, and this allows us to identify: (1) the total and daily number of flushes (frequency); (2) their respective duration; and (3) the time that had passed between macroinvertebrate sampling and the last flushing.

3.3 Macroinvertebrate sampling and statistical analyses

Macroinvertebrates were collected using a kick-sampling method (25x25 cm kicknet, net mesh size of 1 mm). Three replicates from different representative substrates were randomly surveyed each time in the same reach (see Gabbud et al., in review). Invertebrates were sorted and stored in 97 % ETOH. They were identified using a binocular microscope in a laboratory using Tachet et al. (2010) to at least genus level as often as possible, and family level otherwise, except for Oligochaete that were identified to the order level. The abundance (number of individuals of each family at each station) and richness (number of taxa at each station) were determined. According to the Swiss IBCH guidelines (see OFEV, 2010), the standard practice recommends considering as a representative community, a population containing at least 3 individuals, and at least 10 individuals for the following taxa: Limnephilidae, Ephemerellidae, Baetidae, Caenidae, Elmidae, Gammaridae, Chironomidae, Asellidae, and Oligochaeta. Below this number, abundance is considered as null or zero individuals.

Diversity was calculated using the Shannon Index (*H*):

$$H = -\sum_{i=1}^{s} p_i \ln p_i \qquad [1]$$

where p_i is the proportion of individuals of one particular species (*n*) divided by the total number of individuals (*N*) and *s* the number of species of the sample. This index allows characterisation of the structure of the biotic community taking into account the number of individuals by species (Shannon & Weaver, 1949). The range varies from 0, when the population consists of only one species, to $\log_2 s$ when all species present have the same number. A value of 0 indicates zero diversity while a value of 1 reflects maximum diversity (several species with a similar number of individuals for each species).

Statistical analysis used the Bray-Curtis Dissimilarity Index to assess how the (dis)similarity of the abundance and diversity of macroinvertebrates between sites. The Index (*BC*) was calculated from log-transformed (i.e. log(*x*+1)) abundances to avoid extreme spreading and null values, using:

$$BC_{jk} = 1 - \frac{2\sum_{i=1}^{p} \min(N_{ij}, N_{ik})}{\sum_{i=1}^{p}(N_{ij} + N_{ik})} \quad [2]$$

with N_{ij} = abundance of a species *i* in sample *j* and N_{ik} = abundance of a species *i* in sample *k* (Bray & Curtis, 1957). Following [2], a value of 0 indicates a perfect similarity between the two stations (same species and abundances), and a value of 1 indicates zero similarity. Dendrograms were constructed from the similarity results, where the more representative node level of 5 was chosen to insure relevant and sufficient groups of similarities and so common characteristics to be highlighted (Bray and Curtis, 1957). This analysis was applied twice: (1) for all sites (Borgne and tributaries) and all time periods together, except for those with zero invertebrates that are by definition identical and whose group were added manually; and (2) by "zone", where for each site we considered the similarity between it and the tributary upstream for all time periods combined. Sites A0, A1 and A2 were not considered in the latter analysis as no sampled tributary fed these parts of the main channel.

4 Results

4.1 Temperature evolution

Water temperature of the Borgne varied between 0°C and 16.2°C with season (Annex 1). The arithmetic mean of measured values per station passed from 2.2°C upstream of the intake at A0 to 3.9°C at around the same distance downstream at A1. Given low baseflow, A1 was frozen in January 2017. A2 was frozen in March 2017 and dry in September and October 2016 and 2017 (Annex 1): A1 has a small baseflow related to seepage around the intake gates; but this had infiltrated into the stream bed by A2 during the autumn and winter.

Figure 2 shows stream temperature evolution during 2017, using data collected on the same day from June onwards, plus the data sampled over two days for January and March 2017. The distances of the measurement stations from the Bertol Inférieur intake are also provided, from A0 at -0.15 km (upstream) to D5 at 5 km downstream. A2 was excluded from the figure because it was particularly shallow and regularly dry or frozen. The slope of each regression line is also shown.

June was the hottest month measured. A0 has the lowest within-year temperature variation, between 1.5 and 3.2°C. Due to water abstraction effects at the intake, a decoupling between A0, the coldest (glacial) site upstream of the intake and sites downstream of the intake was noted, with temperature increasingly notably rapidly with distance downstream during spring and summer (May, June, July and August). This gradient is largely correlated with insolation patterns, with significant durations of valley shading by September and October.

4.2 Flushing frequency and duration

A total of 521 flushes occurred in 2016 and 554 in 2017 (Annex 2), with 56% from Bertol Inférieur, 14% from Pièce and 30% from Tsijiore Nouve in 2016, and 60%, 10% and 29%, respectively, in 2017. This confirms that Bertol Inférieur provides the main disturbance to the Borgne river. Figure 3 shows the number of flushes classed by duration (between 15 minutes and 255 minutes). Annex 2 shows that, respectively, 72 % of the flushes in 2016 and 73 % in 2017 lasted for 45 minutes or less. Flow attenuation means that with distance downstream from the intakes, the duration of flushing impacts should be longer. The maximum travel time between the onset of flushing at an intake and the most downstream site was less than an hour. The cumulative number of flushes was higher in 2017 (Figure 3), when flush duration also shifted to being shorter (Annex 2). Short duration flushes are normally caused by flushing the sand trap (Figure 1c) and so we can conclude that 2017 had more of these events.

The numbers of flushes that affected the upstream reach (sites A1, A2, Bertol Inférieur only, marked in black, Figure 3) and the downstream reach (all other sites, impacted by all intakes, marked in grey) are shown for 2016 (Figure 4a) and 2017 (Figure 4b). There were no flushes in either winter or early spring, and so these periods are excluded from the plots. For all sites, there was almost continuous periods with daily flushing from mid-June to mid-September in both years. During such periods, the main difference between the upstream reach and downstream reach was the within-day flushing frequency, which for most days was higher, sometimes considerably higher, for the downstream sites.

Bertol Inférieur had: (1) the highest flushing frequency, at least twice daily from 19 June until 15 September 2016 and 16 May to 15 September 2017; and (2) the longest period when at least daily flushes were present, from 15 May to 17 October 2016, and from 9 May to 7 October 2017. Tsijiore Nouve flushes started on 22 May 2016 and on 16 May 2017, and Pièce started to flush later, reflecting the high altitude of its intake (c. 2600 m a.s.l.). The longer flushing periods of 2017 reflected the warmer summer of this year (Figure 1d).

The horizontal bars on Figure 4 show when there were at least 4 days without disturbance, reflecting the finding of Brooks & Boulton (1991) that after an experimental disturbance, the mean number of taxa and individuals reached almost its pre-disturbance densities in 4 days (for substratum generalist macroinvertebrates). These windows are only found outside of the mid-June to mid-September period.

In summary, Table 1 links the days of macroinvertebrate sampling to the flushing data. The number of days since last flushing indicated that winter sampling occurred more than 100 days after the last flushing, as there was no flushing between late autumn and early spring. For June, July, August and September samples, in both 2016 and 2017, there was generally never more than a few hours between flushing events and the level of disturbance was very high, at a much higher rate than the natural daily disturbance cycle in a glacial river (1 flow peak per day). Downstream sites were disturbed almost twice as frequently as upstream sites.

4.3 Borgne macroinvertebrate assemblage trends over a seasonal one-year survey

The abundance (number of individuals by order present - in colours) and diversity (Shannon Index, Equation [1]) in the Borgne main channel for 7 dates out of the 13 sampled are shown in Figure 5 (detailed numbers in Annex 3): June, August and October 2016, and January, March, August and October 2017. To help visualisation and to represent the respective seasons, not all months are shown. The map below the graph indicates the location of the sampling stations, the streams impacted by Pièce and Tsijiore Nouve (yellow bar) and the position of Bertol Inférieur intake (yellow star). Table 2 summarises each site's evolution. The variation in both abundance and diversity was high. Diptera (in purple) represented the dominant order, and particularly Chironomidae.

Table 2: Site evolution (abundance and diversity) description according to Figure 5, from upstream to downstream

A0	Upstream of the intake, this site had only a few Diptera in June 2016, and no populations in August. In October, abundance in Diptera increased markedly, and in January there were a considerable number of Diptera, as well as Ephemeroptera in March. Then, no populations were found in June, August and October 2017. The diversity index was equal to zero (only Diptera - Chironomidae) except in October and March when it stayed below 0.5.
A1 / A2	Immediately downstream of the intake, the two sites were void of life for the entire period of study, except for 3 Plecoptera found in June 2016 in A1. A1 was frozen in January, A2 was frozen in March 2017 and dry during October in both years.

B1	No individual was found in June and August 2016. Then an increase and diversification was visible from autumn to winter: a few Diptera in October 2016, slightly more in January 2017 joined by Ephemeroptera, increasing in March 2017 and joined by some Plecoptera and Trichoptera. The diversity index increased correspondingly and significantly, as Baetidae, Nemouridae, Limnephilidae, Chironomidae and Limoniidae were present in March 2017. This richness dropped afterwards as this station was void of life in June and August 2017. In October, a higher abundance and diversity was measureable.
C1	Some Diptera and Plecoptera were present in June 2016, before disappearing by August 2016. Both orders recovered in autumn 2016. January 2017 had the maximum diversity as Diptera, Ephemeroptera, Plecoptera and Trichoptera were present. Only a few Diptera and some Plecoptera were measurable in March. The stream was void of life in June and August 2017, with Diptera recovering by October 2017. The diversity index was high in June 2016 as Diptera included some Chironomidae, Simuliidae and Limoniidae, and Plecoptera contained Leuctridae and Nemouridae. In January 2017, Baetidae, Perlodidae, Limnephilidae, Chironomidae, Limoniidae and Simuliidae were present, which explains the high Shannon index value.
D1	This site was inhabited by Diptera, Ephemeroptera and Plecoptera in June 2016 but void of life by August 2016. In October 2016, Diptera were present and during January and March 2017 both Diptera and Plecoptera were measurable. During June and August 2017 the site was void of life, and the two previous orders had recovered by October 2017. The presence of Oligochaete, Leuctridae, Nemouridae and Simuliidae in June 2016 increased the diversity index. In January 2017, families present were Leuctridae, Perlodidae, Chironomidae and Limoniidae, as well as in March except for Limoniidae.

D5	Diptera and a few Plecoptera were measured in June 2016, no life was detected in August 2016, and Diptera and Trichoptera recovered by October 2016. During January 2017, Ephemeroptera, Plecoptera and several Trichoptera were present. Maximum abundance was detectable in March 2017, through the presence of Diptera and many Plecoptera. June and August 2017 were void of life, and sampling was not possible in October 2017 due to river engineering. The diversity index was quite stable between October 2016, January 2017 and March 2017 and stayed around 0.7.

These results allow six key points to be made. (1) There were more macroinvertebrates upstream (A0) of the most frequently flushed intake (Bertol Inférieur, Figure 4) than downstream, even though diversity was lower. A0 is affected by upstream flushing but less frequently (less than weekly) than sites below Bertol Inférieur. (2) The two stations immediately downstream of the intake, A1 and A2, illustrated the most severe depletion, as they were almost void of life for the whole year, although these sites are often dry between July and September, notably A2, and so it is possible that this lack of life reflects either the presence of either no minimum flow or too frequent perturbation. (3) In general, there was more life in the Borgne in late autumn (October), winter (January and March) and early spring (June) when flushing frequency was low, although for June there was a difference between 2016, when frequent flushing started, and 2017 when flushing started earlier (Figure 4). Higher abundance was found in June 2016 than June 2017 for sites C1, D1 and D5. (4) The Borgne was void of life in summer (August) of both years and there was no recovery in populations with distance downstream from the intake. (5) At sites B1, C1, D1 and D5, as soon as flushing frequency fell, life recovered, firstly predominantly through the presence of Diptera and Trichoptera (October in 2016 and 2017), then joined by Ephemeroptera in January 2017, and finally Plecoptera, one of the most sensitive families, notably present in March 2017. (6) The diversity (Shannon index) reached its maximum during winter and early spring.

4.4 Possible macroinvertebrate supply from tributaries

The abundance and families present in both the Borgne and its main nival and glacial surrounding tributaries are shown in Figure 6 for five representative dates when both the Borgne and its tributaries were sampled: June, August and October 2016, and January and March 2017.

Tributaries supply the Borgne downstream of station A2, that is stations A1 and A2 receive no tributary supply. In June 2016, the Borgne had fewer invertebrates than the surrounding tributaries, even if the number of individuals tended to increase with distance downstream. In August, the majority of tributaries had their maximum abundance and number of families present, potentially serving as source of macroinvertebrates for the Borgne, but the Borgne was void of life. In October, the invertebrates were less numerous in the tributaries even if most groups were present, while recovery in the Borgne had begun, predominantly due to Diptera and some Trichoptera in D5. In January 2017, the permanent tributaries were still active and some had a good abundance and mix of families present (T05, T12, T13) whilst other streams were less abundant (T09, T10), and the Borgne richness was higher than in the latter. Borgne communities increased and became even more diversified in March, while surrounding permanent streams showed no significant changes in abundance compared to January, except for T05. Sensitive species such as Plecoptera became established in winter, particularly in March 2017 as they were present in all tributaries and Borgne stations downstream of the intake (except A1 and A2).

What is shown through these results is that: (1) the main channel was potentially continuously supplied by the surrounding tributaries; but (2) species were not able to establish themselves in the Borgne in summer; then (3) the Borgne recovery was rapid in autumn, and increased to reach maximum abundances in winter, with abundances higher than in some tributaries; and (4) some species present in the tributaries never significantly colonised the Borgne, notably Turbellaria and Oligochaeta, possibly reflecting habitat condition dissimilarities.

4.5 Intercomparison of site similarities

The Bray-Curtis Dissimilarity Index (Equation [2]) examined inter-site similarities, shown in Figure 7, by comparing communities of the stations in the Borgne and surrounding tributaries from June to October 2016 and January and March in 2017, at the family level. Five dominant groups (coloured to help visualisation) were highlighted, based on the relevant dendrogram node level of 5, flagging that: (1) the main Borgne sites are only found in the yellow, green and blue groups; (2) the yellow group is dominant in the main Borgne but less apparent in the tributaries; (3) the next major group in the Borgne is green, but is only ever found in the Borgne in late autumn, winter and early spring, whilst green membership is most common in summer in the tributaries; and (4) some tributary groups are never found in the main Borgne.

Figure 8 shows the dendrograms resulting from the Bray-Curtis Dissimilarity Index to further analyse the longitudinal connections between the main stream and its tributaries (Equation [2]), performed by looking at groups of tributaries and their associated Borgne site directly downstream for all time periods. A0, upstream of the intake of Bertol Inférieur, as well as A1 and A2, not supplied by any tributaries, are not considered. Months were colour-coded according to two periods: (1) summer and early autumn, i.e. June, July, August and September; and (2) late autumn, winter and early spring, i.e. October, January, March and May. The first branch, in italics, shows stations with zero invertebrates. Stations of the Borgne (A, B, C and D) are highlighted by asterisks.

The results show that in zone 1, winter communities in the Borgne in January, March and October 2017 were similar to macroinvertebrate assemblages in the surrounding tributaries during spring, summer and autumn (T02 in June, July, August and October, and T05 in June and July). This trend is also true in zone 2, where C1 had similar composition in June and October 2016, and in March and October 2017, close to T06 in June and T09 in January; C1 in January was similar to T06 in July, August and October, and T09 in March. In zone 3, D1 macroinvertebrate compositions were all analogous, except D1, and similar to T11 in June. D1 in June was comparable to T10 from June to October 2016 and in January and March 2017. Afterwards, the signal is less clear and tributaries constitute groups by themselves. Hence, along the upstream-downstream gradient, communities in the Borgne during winter are closely similar to the populations of the surrounding tributaries during spring and summer.

5 Discussion

We showed that the aquatic fauna in the Borgne is highly sensitive to changes in flushing frequency; the dramatic drop of life by August (Figure 5) matches with flushing frequency intensification (Figure 4). Some portions of the Borgne are impacted by these short-term (mainly between 30 and 45 min; Figure 3, Annex 2) inundations as many as 17 times over 24 hours, and at least 2 times a day from mid-June to mid-September (Figure 4), which represents a rate of disturbance much higher in frequency than the natural diurnal discharge peak commonly found in glacial rivers. Whilst discharge would have risen and fallen in the Borgne in the absence of water abstraction, due to daily cycles in glacier melt, these flushing events are different because of the exceptional concentrations of suspended load and bedload associated with them and the speed with which flow rises and falls. The comparison between communities in the Borgne in June 2016 and 2017 is a clear example: in 2016, sampling took place 2 days after flushing and 3 flushes in total had occurred within the previous 4 days (Figure 4, Table 1); invertebrates were measurable in the Borgne (Figure 5). In 2017, flushes had occurred fewer than 24 hours before sampling and 7 flushes had occurred within the previous 4 days, and no individual was found.

Flushing can reduce light penetration, can clog or bury stream sediments, can bury organic matter making it less accessible, and can erode habitat, all of which reduce available resources and lead to habitat degradation (Quinn et al., 1992; Jones et al., 2012). Stream temperatures are certainly also affected by flushing. It increases from May to June with stronger solar radiation, but decreases afterwards by July and August, the warmest months, probably in response to flushing that re-introduces cold water into the river. The drastic morphological alterations during the intensive flushing period make habitat conditions very harsh, even completely unsuitable. Even the attenuation of flushing with distance downstream is not always sufficient to maintain habitats, such that the recovery of macroinvertebrates, whilst present (notably in June and October when flushing was still occurring, Figure 4), was slower than expected. No life was recorded at any site in the Borgne in August, the month of highest flushing frequency, even though stream temperatures were relatively warm (Figure 2) and macroinvertebrates could have been supplied to the main channel from tributaries at least for sites in the downstream reach (Figure 6). While macroinvertebrates may have developed adaptations to disturbance (Matthaei et al., 1996), it appears that the return-time between flushes is too short to allow them to survive (Table 1). This supports our hypothesis that sediment flushing, and the associated increased frequency of bed disturbance, controls in-stream habitat and the macroinvertebrate populations that develop.

In contrast to expectations, our results show that whilst the stream is largely void of invertebrates during the summer (Figure 5), populations recover rapidly as soon as the frequency of intake flushing falls in early autumn (Figure 4, Table 1) even though in other senses this may be a less optimal period for invertebrates (e.g. temperatures are lower, Figure 2). Macrofauna are able to recolonise the Borgne, but it is mainly the species better adapted to disturbance and harsh habitat conditions that arrive first (Ilg & Castella, 2006; Brown & Milner, 2012), most commonly Diptera (Figure 5). The latter are well known to be ubiquitous, opportunistic and resilient species, with rapid turn-over, drift ease and high mobility (Armitage & Cannan, 2000; Jones et al., 2012; Cauvy-Fraunié et al., 2014; Espa et al., 2015). Rapid recovery after flow disturbance has been reported by others (Robinson et al., 2001, 2004; Brown, 2012; Espa et al., 2013). The recovery is attributed to the ability of the main stream to recruit individuals from tributaries (Figure 6). For instance, A1 and A2 are not supplied by any tributary and were void of life for the whole period of study (Figure 5) even when flushing frequency was reduced. For zones in the downstream reach (i.e. B1 and downstream), communities in the

Borgne reflect the communities of the surrounding tributaries (Figure 6), although sometimes only partially (Figure 7, Figure 8).

Most surprisingly, these communities develop and become more diverse, with richer and more abundant populations in winter and early spring (Figure 5, Figure 6), at the lowest temperatures (Figure 2), and begin to include sensitive species such as Plecoptera. Increases in macroinvertebrate diversity during winter have been reported elsewhere (e.g. Burgherr & Ward, 2001; Füreder et al., 2001; Brown et al., 2015), explained by more stable diurnal conditions because less disturbance in winter.

It may be that Alpine macroinvertebrate resilience (Brown et al., 2006) can be higher than expected (Milner & Petts, 1994). Our results show that macroinvertebrate populations in winter are more numerous and richer than in summer, as well as more similar to what is found in unregulated tributaries in summer (e.g. B1 communities in winter are similar to T02 and T05 in spring and summer; Figure 7, Figure 8). Thus, we conclude that intake flushing in summer may tend to invert the expected summer-winter abundance of macroinvertebrate populations in this context. This issue has practical implications and reinforces the importance of the debate regarding sampling strategies for assessing the biological quality of running waters, especially at high altitude, which rarely advocates winter sampling. Indeed, sampling strategies and protocols for assessing biological water quality in high altitude streams advocate sampling during spring and summer, sometimes in autumn and rarely in winter, based on the statement that this period will not present a river health representative in the abundance of macroinvertebrates.

In 1993, negative ecological impacts were concentrated near the most frequently purged water intake (zone A; sites A1 and A2 in this study) (Petts & Bickerton, 1994). In downstream zones (B through D), even though the macrofauna were regularly impacted by sediment purges, the loss of organisms was quickly compensated by the drift of invertebrates from nearby tributaries, thus maintaining a rich ecosystem. By contrast, in 2016 and 2017, the frequency of flushing was substantially increased compared with 1993 and we identified little life in these downstream zones. It suggests that macrofauna may be able to adapt to a certain frequency and magnitude of purges, but above a certain level, purges destroy the biotic community (Figure 5, Table 1).

Questions regarding the extent to which environmental flows themselves will lead to improvements in instream macrofauna then follow. It appears that in this kind of high altitude system, with water intakes that are flushed, the effects of sediment load and frequency of flushing surpass the effects of water abstraction itself. Introducing a minimum flow will in that sense probably improve the upstream reach (sites A1 and A2) in autumn most notably, although it is here that temperature limitations might remain dominant. The downstream sites have minimum flows through krenal contributions in mid-summer. However, our data suggest that minimum flows are unlikely to impact any site in the summer months unless flushing frequency is reduced. As the only option for flushing these kinds of intakes is through opening of the sediment traps, whether gravel or sand, it is highly unlikely that the benefits of higher flows with lower sediment loads may be realised. Even then, as sediment laden flushing will still be required, newly-created refugia are likely to be refilled and sediment remobilisation may maintain habitat instability. The key challenge is to reduce the frequency with which it is necessary to flush the intakes, this is the number of daily/weekly flushes, without eliminating them completely: a certain number of perturbations may be valuable for these freshwater ecosystems (Resh et al., 1998) and macroinvertebrates are tolerant of a certain level of disturbance frequency and high altitude species are particularly adapted (Robinson et al., 2001, 2004; Brown, 2012; Cauvy-Fraunié et al., 2014; Espa et al., 2015). The current frequency is too high to support life. A frequency reduction, even if the respective volume of evacuated sediment by flushing is maintained, might allow more developed community establishment as well as the development of other biogeomorphic processes (e.g. increases in organic matter loading) that would improve habitat and potentially increase macrofauna abundance and diversity. Hence, the impact of a lower frequency high magnitude flushing regime might be less severe. However, it is also possible that a less frequent but higher magnitude flushing event, as with when dams are flushed, would have more severe negative impacts, and this remains an unresolved issue. Further, it is perhaps also important to reflect upon the way the ways that intakes are flushed. Whilst this paper does not address the reasons that macrofauna sensitive to flushing, it is possible that the flushes cause water level rises and falls that are too rapid for macrofauna to adapt, whether by seeking refuge within stream bed sediment or through drift whether during flow rise into areas that become more suitable at higher flow or during flow fall into areas that return to being suitable at lower flow. Further research should investigate whether changes in the way flushes are managed might maintain sediment evacuation from intakes whilst introducing flow rises and falls that better allow macrofauna to adapt.

Both Lane et al. (2017) and Bakker et al. (2018) have reported on the drivers of the high flushing rates in the study system and shown that flushing rate increased markedly with the onset of rapid glacier recession in the late 1980s and, in particular, from the late 1990s. Thus, what we may be seeing in the Borgne at present, when compared with the earlier study of Petts & Bickerton (1994), is the effects of rapid climate change upon flushing frequency, such that there is now even less life in the Borgne than they found in 1993. The frequency of flushing is a direct rate of sediment delivery to the intakes, which is itself correlated to the volume of water supplied to the intake (and hence a function of glacier melt) (Lane et al., 2017). There are two solutions here. First, since 2008, the hydropower operator has introduced night time flushes if the intake is half full or more, to reduce the frequency of daytime flushes which pose a risk to tourists visiting the area. An alternative risk management framework might reduce flushing frequency by as much as 20%. A second, practical solution is to propose sediment management in tributaries with intakes where flushing frequency has risen to levels that negatively impact downstream flora and fauna. For instance, increasing the retention of sediment in proglacial margins, whose areal extent is increasingly markedly following glacier recession, might be achieved with negligible engineering. Data showed that the volume of sediment supplied delivered downstream of Bertol Inférieur intake between 2010 and 2015, the period of highest flushing frequency, was between 2 and 5 x 10^4 m^3y^{-1} (Bakker et al., 2018). If we consider just one of the upstream basins, the Haut Glacier d'Arolla, with minimal engineering through making use of a terminal moraine, the braid plain could provide enough storage, enough to reduce flushing frequency to that in the year (1993), when Petts and Bickerton (1994) found much more developed macroinvertebrate populations in the Borgne, for 20 years.

Such a solution could be particularly interesting because it would reduce, without completely stopping, the amount of sediment entering the basins of the intake, and thus diminish the frequency of flushes required. This reduction in disturbance would allow the establishment of more sustainable and more stable habitats downstream that could then be quickly recolonized by macroinvertebrates from surrounding natural tributaries. Macrofauna would then be more able to survive this lower rate of disturbance. Reduced flushing frequency will also mean less loss water loss and so make the introduction of minimum flows less economically costly. However, this type of solution causes landscape modifications that must also be considered. It may also be necessary to make a clearer legal distinction between dams that retain sediments behind a wall for long periods of time, and water intakes that maintain sediment connection regularly through flushes, as their sediment dynamics, and therefore management needs, are very different. Currently, in Switzerland, all types of hydropower, dams or intakes, are subject to the same regulations, particularly in terms of ecological restoration measures (LEaux, 1991). This requires hydropower companies to mitigate the impacts of their activities on downstream streams and rivers. The law requires a minimum flow but also generic mitigation to deal with sediment related problems. In 2012, the Swiss Confederation produced a guide as to what sediment mitigation might involve (OFEV, 2012). The guidance does not mention flow intakes. It treats dams, encouraging measures to re-establish sediment flux through one or more of: sediment transfer tunnels, flushing flows or mechanical. removal and transfer of sediment from upstream of dams to downstream (OFEV, 2012, 49). Where this is not possible, it suggests artificial floods to reactive the river bed (OFEV, 2012, 49). This national level advice is reflected in implementation: before the investigation reported here, responsible authorities were advocating floods to rework the river-bed, even though the nature of water abstraction means that these were occurring regularly. Our work herein not only emphasises the dangers of overlooking sediment management in Alpine streams impacted by hydropower but the need to look carefully at the extent to which hydropower impacts sediment flux as such impacts might not conform to the dominant view that hydropower (dams) cause sediment disconnection.

6 Conclusions

This research assesses the effects of water intake abstraction and their associated sediment flushes on Alpine instream habitat and macroinvertebrate communities. The study stream had two main reaches. Downstream of a major intake, the upstream reach was void of life throughout the study period and had negligible flows. Here, we cannot eliminate the possibility that the lack of water is responsible for the lack of life. However, the downstream reach had a permanent variable minimum flow associated with nival and krenal sources. Yet, it also was largely void of life during the summer months (June through August), when flushing frequency is highest (up to 17 times a day, Figure 4). Sampling showed that populations recover rapidly as the frequency of flushing falls in early autumn, to produce richer and more numerous populations in winter and early spring. It appears that the community richness and diversity expected in summer was more typically found in winter. Rapid recovery once flushing frequency decreased was attributed to the ability of the main stream to recruit individuals from the tributaries. Thus, we conclude that (1) sediment flushing, and the associated increased frequency of bed disturbance, controls in-stream habitat and macroinvertebrate assemblages that develop; and (2) intake flushing in summer inverts the expected summer-winter abundances of macroinvertebrate populations. In the downstream area, the problem is less the lack of water than the disturbance frequency and sediment load of flushes, as well as the rate of change of flow and sediment transport conditions within each flushing event. As compared with a previous study (Petts and Bickerton, 1994) there is now much less life in the Borgne in summer and we related this to a dramatic increase in flushing frequency, attributable to climate change (Lane et al., 2017; Bakker et al., 2018).

Others have highlighted Inconsistent or negligible effects of environmental flows on macroinvertebrate assemblages downstream of reservoirs at high altitudes. Brown et al. (2015) for example, found that even if discharge and water temperature were increased, invertebrate assemblages did not significantly improve. Even if we cannot generally conclude that the effects of minimum flow introduction are negligible, this study shows that, following Wohl et al. (2015), sediment related issues linked to hydropower need to be addressed as well as flow requirements. In Switzerland, and possibly characteristic of the European Alps in general, intakes regulate more than 50% of hydropower impacted rivers by basin area; yet legislation remains dominated by the assumption that hydropower disconnects sediment flux in river basins, leading to river bed degradation and coarsening, collimation, and degraded habitat. In the case of intakes, as sediment connection is maintained, improving habitat will need sediment management as well as flow management.

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8 Figure and table captions

Figure 1: a) The Borgne and surrounding tributaries in the Arolla catchment, with the three water intakes of interest for this study in black; b) The water intake of Bertol Inférieur; c) A typical water intake scheme with sediment management with two basins (after Lane et al., 2017); d) Temperature data for 2016 and 2017 (provided by the WSL, Swiss Institute for Snow and Avalanche Research, from the automated meteorological station Les Fontanesses (2'600'558, 1'097'471, 2847 m a.s.l., LV95))

Figure 2: Slope of the regression plot of temperature 2017 versus distance downstream with y = slope reported; A2, being particularly shallow, is not shown; D5 was not sampled in October 2017 because of local disturbance in the channel

Figure 3: Number of flushes according to flushing duration at respective intakes: Bertol Inférieur (Bertol), Pièce and Tsijiore Nouve (Tsijiore); solid line for 2016, dotted line for 2017; cumulative number of flushes are in black for 2016, grey for 2017

Figure 4: Number of flushes for the period of flushing, between 1 May and 20 October, impacting only the downstream part of the channel (Pièce plus Tsijiore Nouve intakes, in grey) and impacting the whole channel (Bertol Inférieur intake, in black); up, in 2016; down, in 2017; from Grande Dixence SA discharge data; in green, windows of theoretical possible life with 4 consecutive days without disturbance (Brooks and Boulton, 1991)

Figure 5: Macroinvertebrate abundance (number of individuals; vertical; right axis), grouped at the order level (colours), in the Borgne for the 7 instream stations, from upstream (left) to downstream (right), from June 2016 to October 2017; black crosses indicate the diversity calculated through the Shannon Index, using family level (left axis); lower map shows the locations of stations, the streams impacted by Pièce and Tsijiore Nouve (yellow bar), and the position of Bertol Inférieur intake (yellow star)

Figure 6: Macroinvertebrate abundance (number of individuals; horizontal) and families present (level of orders; colours) in the Borgne (A, B, C, D, marked in red) and the surrounding tributaries (T, marked in black); in a) June 2016, b) August 2016, c) October 2016, d) January 2017, e) March 2017; The y axis sorts the tributaries into their order with respect to the Borgne, for example, tributaries T2 and T5 enter the Borgne upstream of site B1

Figure 7: Bray-Curtis Dissimilarity Index groups of similarities; 5 groups were highlighted; 0 indicates that no individual was present in the stream; in bold black, stations in the Borgne main channel; stations presented from upstream to downstream, showing where the tributaries (T) join the main channel

Figure 8: Dendrograms from Bray-Curtis Dissimilarity Index analysis; the analysis was performed by looking at groups of tributaries and their associated Borgne site directly downstream, for all time periods; A0, upstream of the intake of Bertol

Inférieur, plus A1 and A2, not supplied by any tributaries, were not included. The first branch presents the stations with zero invertebrates, in italics; A, B, C and D with asterisks are the stations in the main stream of the Borgne, T represents the tributaries; my = May (pink), jn = June (yellow), jl = July (light orange), a = August (dark orange), , s = September (garnet), o = October (purple), jv = January (light blue), ma = March (dark blue); months colour-coded to help visualisation according to season and to highlight the correspondence; respective year 2016 and 2017 are written as 16 or 17

Table 1: Time since the last flushing for each date of macroinvertebrate sampling, where 0 indicates that a flushing occurred fewer than 24 hours before the collection, respectively, for the upstream (A1 and A2) and downstream (B1, C1, D1, and D5) sites; Mean number of flushes within the last 4 days, detected as minimum time recovery by Brooks and Boulton, 1991; from Grande Dixence SA discharge data

9 Appendices

Date	A Time	A Temp (°C)	A Time	A Temp (°C)	A Time	A Temp (°C)	B Time	B Temp (°C)	C Time	C Temp (°C)	D Time	D Temp (°C)	D Time	D Temp (°C)	
13.06.2016	10:30	2.7	11:00	5.2	13:15	8.6	16:00	7.2							
14.06.2016									17:00	6.9	15:00	6	09:30	6	
11.07.2016	08:50	2.3			11:45	10.5	13:00	9.2							
12.07.2016			08:40	2.8					09:15	6.5	13:45	7.6	09:45	7.1	
08.08.2016	15:30	4.6	16:10	9	19:00	16.2									
09.08.2016							10:15	6.6	15:15	7	14:00	8.6	12:00	8.4	
13.09.2016	14:00	4	14:15	8.2	14:30	0	14:45	8.3			17:15	8			
14.09.2016									09:00	6.3			11:30	8.6	
10.10.2016	10:15	1.8	10:45	2	11:00	0	14:30	3.7							
11.10.2016									09:15	2.6	15:00	5.2	11:00	2.9	
Mean (°C)		3.1		5.4		7.1		7.0		5.9		7.1		6.6	**6.0**
30.01.2017	11:50	1.5	12:30	0	11:00	0	15:45	2.8							
31.01.2017									10:10	2.3	12:30	2.4	14:30	2.2	
28.03.2017	10:00	1.6	10:30	1.1	11:00	0	13:00	4.7							
29.03.2017									09:30	1.7	12:30	5.8	16:00	7.1	
Mean (°C)		1.6		0.6		0.0		3.8		2.0		4.1		4.7	**2.4**
25.05.2017	08:50	1.6	09:15	2.7	10:00	6.5	10:45	4.3	12:40	7.5	13:15	8.5	14:00	9.0	
19.06.2017	10:00	3.2	10:15	6.1	10:30	11.5	10:45	8.2	13:20	9.5	13:45	11.3	14:00	12.5	
24.07.2017	10:15	2.8	10:30	4.1	11:00	8.2	12:30	6.9	14:00	0.6	14:30	9.0	15:00	9.9	
21.08.2017	10:15	2.4	10:20	4.0	10:30	8.2	11:15	6.4	12:30	7.4	13:00	8.8	13:15	9.5	
18.09.2017	10:00	0.4	10:15	2.7	10:30	0.0	11:00	5.2	11:15	5.6	12:15	6.7	12:30	7.2	
20.10.2017	11:30	2.6	11:45	3.6	12:15	0.0	12:30	5.7	14:00	6.6	14:45	7.0	-	-	
Mean (°C)		2.2		3.9		5.7		6.1		6.2		8.6		9.6	**6.0**
St Dev		± 1.0		± 1.3		± 4.7		± 1.4		± 3.0		± 1.7		± 4.3	

Annex 1: Temperature of the Borgne main channel over the 13 survey periods for each station (A0, A1, A2, B1, C1, D1, D5) with the time of sampling; from June to October 2016 with the seasonal mean by station; in January and March 2017 with the winter mean by station; from May to October 2017 with the seasonal mean by station and standard deviation (relevant only for 2017 as all data collected within the same day)

Flushing duration	# Bertol Inférieur		# Pièce		# Tsijiore Nouve		Total (#)		Total (%)	
(min)	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017
15	2	9	3	5	1	11	6	25	1	5
30	36	113	26	14	61	88	123	215	24	39
45	134	98	32	31	79	35	245	164	47	30
60	30	18	11	4	9	10	50	32	10	6
75	11	12	2	1	3	11	16	24	3	4
90	13	21	0	1	0	2	13	24	2	4
105	17	18	0	0	2	1	19	19	4	3
120	18	13	0	1	1	3	19	17	4	3
135	11	19	0	0	0	1	11	20	2	4
150	8	5	1	0	0	0	9	5	2	1
165	4	6	0	0	0	0	4	6	1	1
180	2	1	0	0	0	0	2	1	0	0
195	1	1	0	0	0	0	1	1	0	0
210	1	0	0	0	0	0	1	0	0	0
225	0	0	0	1	0	0	0	1	0	0
240	1	0	0	0	0	0	1	0	0	0
255	1	0	0	0	0	0	1	0	0	0
270	0	0	0	0	0	0	0	0	0	0
285	0	0	0	0	0	0	0	0	0	0
300	0	0	0	0	0	0	0	0	0	0
Number of flushes	**290**	**334**	**75**	**58**	**156**	**162**	**521**	**554**		
Contribution (%)	56	60	14	10	30	29				

Annex 2: Number of flushes of respective duration (min) by intake, respectively Bertol Inférieur, Pièce and Tsijiore Nouve, in 2016 and 2017; In horizontal, combined sum of each flushing duration in 2016 and 2017, and percentage of each duration; in vertical, total number of flushes by intake and contribution of each intake to the flushing frequency; from Grande Dixence SA discharge data

	Ephemeroptera	Plecoptera	Trichoptera	Diptera	Sum	Shannon
A0_0616	0	0	0	12	12	0
A0_0816	0	0	0	0	0	0
A0_1016	0	0	0	143	143	0.15
A0_0117	0	0	0	89	89	0
A0_0317	30	0	0	141	171	0.46
A0_0617	0	0	0	0	0	0
A0_0817	0	0	0	0	0	0
A0_1017	0	0	0	0	0	0
A1_0616	0	3	0	0	3	0
A1_0816	0	0	0	0	0	0
A1_1016	0	0	0	0	0	0
A1_0117	0	0	0	0	0	0
A1_0317	0	0	0	0	0	0
A1_0617	0	0	0	0	0	0
A1_0817	0	0	0	0	0	0
A1_1017	0	0	0	0	0	0
A2_0616	0	0	0	0	0	0
A2_0816	0	0	0	0	0	0
A2_1016	0	0	0	0	0	0
A2_0117	0	0	0	0	0	0
A2_0317	0	0	0	0	0	0
A2_0617	0	0	0	0	0	0
A2_0817	0	0	0	0	0	0
A2_1017	-	-	-	-	0	0
B1_0616	0	0	0	0	0	0
B1_0816	0	0	0	0	0	0
B1_1016	0	0	0	23	23	0
B1_0117	19	0	0	31	50	1.07
B1_0317	42	8	15	57	122	1.33
B1_0617	0	0	0	0	0	0
B1_0817	0	0	0	0	0	0
B1_1017	32	7	22	95	156	1.15
C1_0616	0	10	0	19	29	1.43
C1_0816	0	0	0	0	0	0
C1_1016	0	3	0	36	39	0.27
C1_0117	19	3	37	34	93	1.52
C1_0317	0	4	0	13	17	0.55
C1_0617	0	0	0	0	0	0
C1_0817	0	0	0	0	0	0
C1_1017	0	0	0	140	140	0.39
D1_0616	20	23	0	4	47	1.26
D1_0816	0	0	0		0	0
D1_1016	0	0	0	91	91	0
D1_0117	0	6	0	34	40	1.1
D1_0317	0	33	0	63	96	0.85
D1_0617	0	0	0	0	0	0
D1_0817	0	0	0	0	0	0
D1_1017	0	6	0	59	65	0.67
D5_0616	0	3	0	52	55	0.21
D5_0816	0	0	0	0	0	0
D5_1016	0	0	65	37	102	0.65
D5_0117	11	4	64	0	79	0.6
D5_0317	0	124	0	51	175	0.76
D5_0617	0	0	0	0	0	0
D5_0817	0	0	0	0	0	0
D5_1017	0	0	0	0	0	0

Annex 3: Detailed number of individuals detected at each station (letter) by month (number) used in Figure 5; abundance (sum) and Shannon index (Shannon) added as well.