Flow Sediment Interactions in Managed Rivers: Influence on Ecosystem Structure and Function

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FLOW SEDIMENT INTERACTIONS IN MANAGED RIVERS:

INFLUENCE ON ECOSYSTEM STRUCTURE AND FUNCTION

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Summary

Flow and sediment regimes are two of the main abiotic factors driving riverine ecosystems, interacting at different temporal and spatial scales. These interactions have a strong influence on habitat composition, ecosystem processes and community composition. Nowadays, flow and sediment regimes are highly altered due to anthropogenic modifications of rivers and floodplains, such as dams or river channelization, which disrupt the main properties of both regimes. The primary goal of this thesis was to understand the role of flow and sediment interactions on ecosystem structure and function in managed rivers and evaluate different techniques that mitigate the impact of rivers regulation. Hyporheic sediment respiration, periphyton biomass and chlorophyll-a were used as indicators of ecosystem function, whereas macroinvertebrates assemblages were used as a structural indicator.

The first chapter studied the variability of different indicators of ecosystem structure and function under different flow and geomorphology conditions. The study took place in a section of the river Thur, where a widening restoration was implemented by removing 1 km of lateral protections. This widening section characterized by newly established habitats such as gravel bars is fringed upstream and downstream by channelized sections. Channelized sites showed higher rates of sediment respiration, periphyton and macroinvertebrates compared to restored sites. Restored sites showed a greater temporal and spatial variability in the measured indicators due to the influence of flow disturbance, which was lower in channelized sites. Overall, sediment respiration and macroinvertebrate richness were related to flow variability and geomorphology, whereas periphyton and macroinvertebrate density was influenced mainly by flow variability.

The second chapter investigated the influence of flow regulation (residual flows and hydropeaking) on aquatic life stages that can persist in sediments during dry phases (i.e. macroinvertebrate seedbanks). Gravel bars affected by hydropeaking showed greater densities of organisms due to the high frequency of inundations, which increased the drift of animals onto gravel bars. The opposite trend was found in residual flow rivers, where there is a lack of flood occurrence.

The third chapter assessed the ecological impact of a Sediment Bypass Tunnel, a structure that routes upstream sediment input around dams, reducing the accumulation of sediments in the dam. Operations of the tunnel create a general decrease in measured indicators (sediment respiration, periphyton and macroinvertebrates), the decrease being related to the magnitude of flow and sediment released at the tunnel.

The fourth chapter described the interactions of flow and sediment inputs in two rivers with contrasting management programs (experimental floods and sediment bypass tunnel). Sediment lateral inputs caused local interactions with flow, generating morphological and biotic heterogeneity in the streambed, whereas upstream sediment inputs together with high flows by sediment bypass tunnel created a general decrease in biotic indicators in the system, reducing spatial variability.

The results from this thesis showed that each of the measured ecosystem properties is influenced in a specific way by flow-sediment interactions. The results indicated that different techniques can be used to mitigate the negative consequences of flow and sediment regime alterations on ecosystem functioning and structure, highlighting the important role of integrative objectives in river management.

Zusammenfassung

Das Abfluss- und das Sedimentregime eines Fliengewässer verbunden und gehören zu den wichtigsten abiotischen Faktoren, die Ökosysteme formen beide Regime sind miteinander zeitlich und räumlich verbunden. Hierdurch haben sie einen wesentlichen Einfluss auf die Habitatzusammensetzung, auf Ökosystemprozesse und auf die Zusammensetzung der Lebensgemeinschaften. Aufgrund menschlicher Eingriffe wie dem Bauen eines Dammes oder der Korrektur eines Flusses sind beide Regime in Fluss- und Auenlandschaften heutzutage stark beeinträchtigt.

In diesem Zusammenhang war das Hauptziel dieser Arbeit, die Wechselwirkung von Abfluss- und Sedimentregimen auf Ökosystemstrukturen und -funktionen in regulierten Flüssen zu untersuchen sowie Ansätze und Techniken zu bewerten, die den negativen Einfluss der Regulierung mindern sollen. Als Indikatoren zur Charakterisierung von Ökosystemfunktionen dienten hierbei die Sedimentrespiration im Hyporheos sowie der benthische Algenaufwuchs inklusive dessen Chlorophyll-a-Gehalt. Als Indikator zur Bewertung der Ökosystemstruktur dienten Lebensgemeinschaften von Makroinvertebraten.

Das erste Kapitel dieser Arbeit beschäftigt sich mit der Variabilität der strukturellen und funktionellen Indikatoren bei unterschiedlichen morphologischen und Abflussbedingungen. Durchgeführt wurde diese Studie an der Thur, deren kanalisierter Flusslauf durch eine etwa ein Kilometer lange Aufweitungsstrecke (Entfernung der Seitendämme) unterbrochen wird. Im Gegensatz zur kanalisierten Strecke konnten sich in der Aufweitungsstrecke neue Habitate wie Kiesbänke bilden, die aufgrund der Abflussvariation ständigem Wechsel unterlegen sind. Im Vergleich zeigte die kanalisierte Strecke hinsichtlich Sedimentrespiration und benthischem Algenaufwuchs sowie Makroinvertebraten höhere Raten bzw. Abundanzen. Hingegen war die aufgeweitete Strecke aufgrund der grösseren abflussbedingten Störung durch eine erhöhte zeitliche und räumliche Variabilität in den oben genannten Parametern geprägt. Insgesamt wurden die Sedimentrespiration und die Anzahl der Makroinvertebratenarten wesentlich durch die Abflussvariabilität und die Flussmorphologie beeinflusst, wohingegen der benthische Algenaufwuchs und die Makroinvertebratendichte vornehmlich durch die Abflussvariabilität alleine gesteuert wurden.

Das zweite Kapitel untersuchte den Einfluss der Abflussregulierung (Restwasser und Schwall-Sunk) auf aquatische Lebensstadien derjenigen Makroinvertebraten, die während

Trockenphasen in Schotterbänken (Macroinvertebrate seedbanks) überdauern können. Schotterbänke, die durch Schwall-Sunk-Dynamiken ständigem aquatisch-terrestrischen Wechsel ausgesetzt waren, zeigten höhere Organismendichten aufgrund der hohen Überflutungsfrequenz, welche die Drift der Invertebraten auf die Schotterbänke erhöht. In der Restwasserstrecke, in der Wasserstandsschwankungen weitgehend fehlen, konnte ein entgegengesetzter Trend aufgezeigt werden.

Thema des dritten Kapitels war der ökologische Einfluss von Sedimentumleitstollen. Sedimentumleitstollen leiten Geschiebe aus dem Einzugsgebiet um den Damm herum, wodurch die Sedimentakkumulation im Stausee vermindert wird. Dieser Durchlass von Geschiebe und Abfluss führte generell zu einer Abnahme in allen gemessenen Indikatoren (Sedimentrespiration, Algenaufwuchs und Makroinvertebraten) in Abhängigkeit von der Stärke und Dauer der Abfluss- und Geschiebedurchleitung.

Im vierten Kapitel wurden die Wechselwirkungen von Abfluss- und Sedimenteintrag in zwei Flüssen mit unterschiedlicher hydromorphologischer Bewirtschaftung (experimentelle Hochwasser und Sedimentumleitstollen) untersucht. Die Sedimentzufuhr über Seitenerosion bei experimentellen Hochwassern verursachte eine morphologische und biotische Heterogenität im Flussbett, wohingegen Sedimentzugaben flussaufwärts über Sedimentumleitstollen generell zu einer Abnahme der biotischen Indikatoren im System sowie zu einer reduzierten räumlichen Variabilität führten.

Insgesamt zeigen die Resultate dieser Arbeit, dass jede der gemessenen Ökosystemeigenschaften in spezifischer Weise von den Interaktionen des Abfluss- und Sedimentregimes beeinflusst werden. Massnahmen zur Vermindeung den negativen Konsequenzen eines beeinträchtigten Abfluss- und Sedimentregimes auf Ökosystemsstrukturen und -funktionen können in verschiedener Weise angewandt werden. Voraussetzung dafür ist jedoch eine integrative Sichtweise dieser Bewirtschaftungsformen.

Introduction

Importance of flow and sediment interactions

Flow and sediment regimes (FSR) are intertwined abiotic features that primarily regulate riverine ecosystems (Poff *et al.*, 1997; Bunn & Arthington, 2002; Lytle & Poff, 2004). Flow regime is described by flow magnitude, frequency, duration, timing, and rate of change of floods (Poff *et al.*, 1997), whereas sediment regime is characterized by sediment input, output, storage and transportation of sediment itself (Figure 1) (Wohl *et al.*, 2015). These different components interact at different temporal and spatial scales influencing geomorphic and ecological processes (Yarnell *et al.*, 2015). For instance, at the catchment scale, annual seasonal floods transport significant sediment and nutrients loads, and disperse seeds and organisms (Ahearn *et al.*, 2006; Petts & Gurnell, 2013) whereas at reach scale, the same flood restructure the channel and floodplain landforms, creating morphological variability (Florsheim & Mount, 2002).

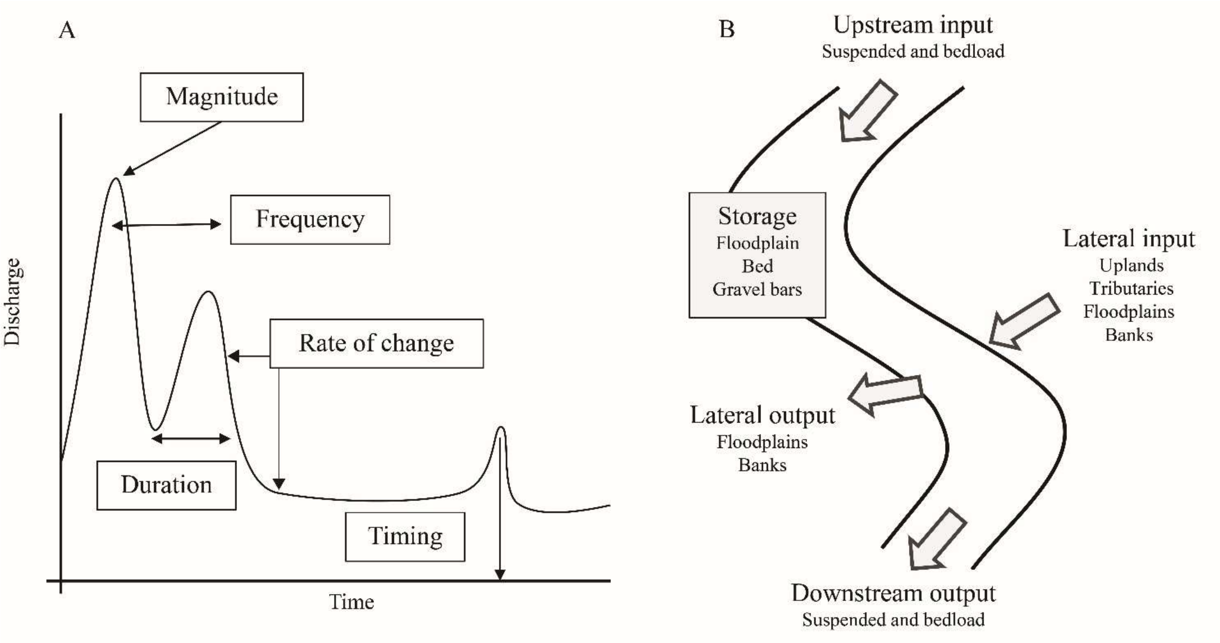

Figure 1: Conceptual overview of flow (A) and sediment (B) regimes and their components. (from Poff et al., 1997 , Bunn and Arthington, 2002, and Wohl et al. 2015).

The importance of flow variability and disturbance for riverine ecosystems was brought into attention few decades ago (Resh *et al.*, 1988; Junk *et al.*, 1989; Poff & Ward, 1989; Poff et al., 1997). These studies laid down the foundations of the importance of natural flow regime as a major determinant of habitat and biotic composition, and longitudinal and lateral connectivity of populations (Naiman *et al.*, 2008). Furthermore, these studies were crucial for assessing hydrological alteration in rivers and thus, the first river conservation and restoration issues (Richter *et al.*, 1996; Stanford *et al.*, 1996; Poff et al., 1997). Yet, the connection between flow and sediment dynamics in river research and management programs overlooked sediment regime for many years, focusing on flow regime as the main actor in ecosystem integrity. However, the significance of the sediment regime was highlighted recently, motivated by the important interactions of sediment dynamics with ecosystem processes and organisms. For instance, sediment dynamics play an important role in biogeochemical processes in streambed surface and in the transition zone between groundwater and streams (i.e hyporheos) (Brunke & Gonser, 1997). Sediment composition and physical heterogeneity at fine-scale determines periphyton growth, nutrient uptake and microbial respiration (Singer *et al.*, 2005; Singer *et al.*, 2010; Haggerty *et al.*, 2014). Moreover, sediment-related processes, such us erosion or deposition of sediment, drive physical habitat configuration of rivers and floodplains (Southwood, 1977). Likewise, some organisms, such as some aquatic insects, are adapted to timing of bed disturbances (Lytle *et al.*, 2008; Jones *et al.*, 2012), and some other, salmonids, require specific streambed conditions for spawning (Riebe *et al.*, 2014).

Managed rivers; services and impacts

Rivers have undergone significant changes for human purposes for the last 10,000 years (i.e. Holocene). Since the ancient Egyptians, Romans and Mayas, humans have managed rivers with similar goals such as irrigation, land reclamation, navigation, and power generation (Healy, 1983; Fahlbusch, 2009). Indeed, river management is considered as a catalytic force in the rise of prehistoric into developed societies (Brown, 1997). Over the centuries, the methods employed for river management have greatly evolved, from small weirs and rivers diversions to large dams and river basis planning. Nowadays, more than 50,000 large dams exist worldwide, with additional constructions expected in the next decades (Nilsson *et al.*, 2005; Lehner *et al.*, 2011; Zarfl *et al.*, 2014), and more than 63,000 km or canals have been constructed globally (Abramovitz, 1996). Dams are mainly used for hydropower energy, which contributes to 16% of the total world energy production. Specifically, 11 countries use hydropower to produce more than 90% of their electricity need (The World Bank Database, 2016). Concurrently, dams store water runoff, rain and snow melt, playing an important role not only in water supply but also in global food production and floods mitigations (Lehner et al., 2011). Channelization of rivers locally reduces the risk of floods of nearby agricultural lands or human settlements. In addition, the increased depth of straightened channels is also more suitable for navigation.

Together with societal benefits, river management disrupt the aforementioned components of FSR, which in turn generate numerous and varied ecosystem and morphology modifications. On one hand, the presence of dams creates a sediment deficit in the receiving waters, as they can trap about 99% of upstream sediment delivery (Williams & Wolman, 1984), generating erosion in the streambed, a reshape of channel and floodplains, and a shift in distribution of habitats, which may bring to species loss (Brandt, 2000; Bunn & Arthington, 2002). Dams also avoid natural flow disturbance, which shape evolutionary and ecological processes (Bunn & Arthington, 2002; Lytle & Poff, 2004), threatening native species of rivers and floodplains, facilitating at the same time the invasion and succession of exotic species adapted to the new flow regime and habitat conditions (Kingsford, 2000; Bunn & Arthington, 2002). On the other hand, lateral protection of rivers avoid lateral connectivity between rivers and floodplains during floods, disrupting input and output of nutrients, and populations connectivity (Petts & Amoros, 1996). Also activities not directly related to rivers can modify the input and transport of sediments in a region, such as the increase of agriculture, forest harvest, or urbanization in a catchment (Wohl, 2014). In summary, numerous anthropic activities can alter FSR at different spatial scale, from basin to reach, degrading riverine ecosystems dramatically.

Due to the negative consequences of FSR modifications, many efforts have been made to minimize the impact of dams and river channelization by managing flow and sediments (Konrad *et al.*, 2011; Tonkin *et al.*, 2014; Yarnell et al., 2015; Yin *et al.*, 2015), and/or by directly improving ecosystem integrity of impacted sites via restoration (Hart *et al.*, 2002; Bernhardt *et al.*, 2005; Jähnig *et al.*, 2009). One of the most common techniques used to re-establish flow variability is experimental flows (E-flows), which simulate natural floods by releasing water from dams (Mürle *et al.*, 2003; Konrad et al., 2011), whereas many different methods can be used to improve altered sediment regime conditions, depending on the specific issues to solve. For instance, to reduce lack of sediment downstream dams, sediments can be routed around or through the dam using sediment by pass tunnels or “sluicing” respectively, or can be dredged from the reservoir and placed in the receiving waters (Kondolf *et al.*, 2014). These strategies are of special importance due to the global problem of decrease storage capacity of dams. In order to re-establish lateral connectivity, lateral protections can be removed to allow water overflow floodplains in case of floods.

Investment in river management and restoration strategies, however, not always achieve to stop habitat quality and ecosystem function declining, in some cases due to a lack of flow-sediment interaction considerations (Bernhardt et al., 2005; Wohl *et al.*, 2015). In the light of the complexity of flow-sediment interactions, together with the expected dam production and river channelization, the need of new FSR integrative management plans that meet both ecosystem and society needs has to be highly considered (Arthington *et al.*, 2010; Wohl et al., 2015).

Goals of the thesis and Outline

This thesis was conducted as part of the practice-oriented project “Sediment and habitat dynamics”, funded by the Swiss Federal Office for the Environment (FOEN/BAFU). The main purpose of this project was to study the importance of sediment dynamics on Swiss rivers from an ecological, engineering, geomorphologic and managerial perspective, identify the main threats to sediment regime, and the solutions to alleviate human river alterations.

The primary goals of this thesis were to understand the role of flow and sediment interactions on ecosystem structure and function and assess the efficiency of different techniques used to re-establish the natural occurrence of both regimes under anthropogenic alterations. This study focused on ecosystems with different levels of alteration (from near-natural to highly altered) and different management strategies. To gain insights into how ecosystem are influenced by flow-sediment interactions, this thesis emphasized the study of three pillars of the ecosystem in terms of structure and function: heterotrophic respiration, periphyton and benthic macroinvertebrates. Heterotrophic respiration is a key process in the carbon cycle, the main path of carbon loss to the atmosphere (Andrews & Schlesinger, 2001) and integrates energy flow through aquatic and terrestrial compartments. In rivers, heterotrophic respiration mainly occurs in hyporheic sediments (Grimm & Fisher, 1984; Naegeli & Uehlinger, 1997), where bacterial community process organic matter (Uehlinger & Naegeli, 1998). Thus, this process is strongly affected by organic matter content and other factors that influence bacterial growth such as temperature (Savage & Davidson, 2001; Tang *et al.*, 2006). Periphyton − the complex mixed community of algae, bacteria, archaea and fungi (Lock *et al.*, 1984) − uptakes nutrient and carbon (Battin *et al.*, 2003) and is the cornerstone of food webs in rivers (Mulholland *et al.*, 2000; Finlay, 2001). Last, benthic macroinvertebrates represent the most common animal group in rivers and are ecologically important. Indeed, benthic macroinvertebrates metabolize energy inputs along river–floodplain extension (Vannote *et al.*, 1980), being the main prey for numerous species of fish, birds and other animals (Nakano & Murakami, 2001; Baxter *et al.*, 2005). Moreover, some macroinvertebrates can inhabit gravel bars in floodplains, surviving via interstitial moisture content (active seedbank) or as resistant forms (dormant seedbank) (Tronstad *et al.*, 2005; Stubbington & Datry, 2013), playing an important role for community recovery and in the river-floodplain food web (Paetzold *et al.*, 2005). These three pillars are considered as appropriate functional or structural indicators as they show an integrated response to environmental change and are regulated by processes and mechanisms operating at different spatial and temporal scales (Vinson & Hawkins, 1998; Euskirchen *et al.*, 2003; Feio *et al.*, 2010).

In **Chapter 1**, the spatio-temporal variability of different indicators of structure and functional indicators were investigated at five sites with contrasting flow-sediment interactions. A restored river section with an enhanced flow-sediment interaction was compared to a channelized one, where sediment dynamics were diminished. Within the restored section, sites with different sediment processes were investigated in detailed.

In **Chapter 2**, the influence of flow regulation on aquatic macroinvertebrate seedbank (i.e. aquatic life stages that can persist in bed sediments during dry phases) was investigated. Macroinvertebrate seedbank plays a very important role in the recovery of communities in rivers after big disturbances so its alteration may cause a loss of community resistance and capacity of recovery after extreme events.

Chapter 3 assessed the ecological impact of a recently implemented sediment bypass tunnel (SBT) in Switzerland. We evaluated the ecological impact of the operations and the suitability as a flow and sediment replenishment strategy.

In **Chapter 4**, the interactions between sediment inputs and managed flow regimes were investigated in two rivers with contrasting flow management programs. The influence of sediment inputs and flow on different ecological indicator were investigated at habitat scale, as well as any longitudinal pattern after flow events in both rivers.

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Chapter 1

Title: Integrating spatio-temporal variability in ecosystem function and structure into river restoration

Short title: Integrating spatio-temporal variability into river restoration

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Abstract

Hydrological and morphological variability that drives river ecosystem structure and function has been severely altered worldwide by human regulation, such as via channelization. Removal of lateral protection, as a primary river restoration action, has become increasingly important, but little is known about how de-channelization together with a natural flow regime influences fluvial ecosystems. Here we examined the spatio-temporal variability of ecosystem functional and structural indicators under flow and morphology changes in a restored (de-channelized) section of a Swiss river with a natural flow regime. We measured hyporheic sediment respiration, periphyton biomass and chlorophyll-a content, and macroinvertebrate density, richness and community composition approximately monthly over two years at restored and non-restored sites. Spatially, we found greater sediment respiration rates and macroinvertebrate density and taxa richness in non-restored sites, while primary production was similar among restored and non-restored sites. In contrast, we found higher temporal variation of respiration and macroinvertebrate density in restored sites than in non-restored sites. Intra-annual change in flow was the main driver affecting periphyton biomass and macroinvertebrate density, while morphological processes influenced mainly sediment respiration. Community composition shifted similarly in restored and non-restored sites, mainly driven by changes in flow. We also found flow-morphological interactive effects on sediment respiration and taxa richness. We conclude that different ecosystem properties are affected in different ways by flow, geomorphology, and their interaction, with temporal variability being the main restoration element in this river. These empirical findings emphasize the importance of integrating flow and sediment regimes in river restoration to maintain dynamic ecosystem properties.

Keywords: Flow regime, sediment regime, heterogeneity, sediment respiration, periphyton, macroinvertebrates.

Introduction

Over the last 25 years, it has become well accepted that natural hydrologic variability sustains riverine ecosystems (Resh *et al.*, 1988; Poff & Ward, 1989; Bunn & Arthington, 2002). Flow variability influences physical habitat conditions, maintains patterns of longitudinal and lateral connectivity and has a strong influence on instream and riparian organisms that show adaptations to flow regime dynamics (Richter *et al.*, 1996; Lytle & Poff, 2004; Wood & Armitage, 2004). More recently, the sediment regime also has been acknowledged as a key factor sustaining the ecological integrity of river/riparian ecosystems. Natural sediment regime can be defined as the natural conditions, prior to human disturbances on topography and land cover, of input and output of mobile sediment from channels and storage of sediment within channels and floodplains over time (Wohl *et al.*, 2015). A natural sediment regime is crucial for many sediment related processes, such as channel morphology and riverbed heterogeneity (Southwood, 1977). The sediment regime structures aquatic and riparian communities by affecting sediment size distributions (Jones *et al.*, 2012), modifying zones of scour in relation to substrate size (Merritt, 2013), and influencing organism life histories (e.g. some organisms are adapted to riverbed disturbance timing (Lytle *et al.*, 2008)). Flow and sediment regimes mutually interact, as streamflow transports sediment and river morphology that is formed by sediment transport determines hydrodynamics. Therefore, both regimes and their interaction play a decisive role in maintaining habitat structure and ecosystem heterogeneity. Until recently and rather surprisingly, flow and sediment regimes have been studied separately (Benke, 2001; Surian & Rinaldi, 2003), and few studies considered their interactive effects in the context of river management (Wohl et al., 2015). One reason for this phenomenon is the difficulty to characterise the sediment regime. In this respect, different metrics can indirectly help towards assessing sediment dynamics, such as cross-sectional and channel geometry measures, grain size distributions or channel development.

Due to human alterations, many ecological requirements of rivers worldwide have been compromised at present for human needs, mostly through the alteration of flow and sediment regimes and their inherent variability. For example, longitudinal connectivity of water and sediment is dramatically reduced by dams and weirs, which reduce flow and sediment transport variability and lowers physical complexity (Brandt, 2000; Tena & Batalla, 2013). Another major alteration is river channel modification with artificial levees, embankments or different concrete structures for flood control or navigation purposes. For example, more than 14,000 km (22%) of the rivers in Switzerland have been channelized (Zeh *et al.*, 2009), severely altering river and riparian integrity and connectivity. Such artificial structures increase flow velocity and river incision, inducing river-floodplain disconnection (Lach & Wyzga, 2002; Tockner & Stanford, 2002). In addition, river morphology is simplified by eliminating many hydro-geomorphic processes, reducing sinuosity and homogenising instream habitats among others (Gregory, 2006). In short, human regulation has severely modified flow and sediment regimes in rivers.

Reflecting a recent mandate to achieve good ecological status of water bodies, re-naturalization of laterally protected rivers and/or channel reconfiguration has been established as a priority in different restoration programs (European-Commission, 2000). The main goal of these actions is to restore river hydromorphology, resulting in increased habitat heterogeneity for organisms and eco-evolutionary processes. Through restoration actions, areas with wider channels that foster local sediment deposition and gravel bar development, or areas with sediment inputs that increase sediment heterogeneity of streambeds, can create and sustain ecological hotspots with enhanced habitat diversity (Yarnell, 2008). Assessment at medium geomorphic scales (10^2–10^3 m), such as the reach scale, is crucial since many geomorphic processes such as erosion or deposition occur at this scale, creating specific characteristics that sustain various biological processes and organism distributions and abundances (Richards *et al.*, 2002). Temporally, assessment at the intra-annual scale is important because flow variability can completely modify ecosystem structure and function in a matter of weeks-months in newly restored channels. Since most current restoration studies were limited in time and space (Palmer *et al.*, 2010), much less is known about the spatial and temporal heterogeneity or the interactive effects of sediment and flow regimes on ecosystem structure and function. To understand these interactive processes is crucial to manage and restore river reaches in a more effective and holistic way.

The main goal of our study was first to capture a comprehensive overview of the effects of a sediment restoration action on habitat diversification and the associated changes in ecosystem structure and function at medium spatio-temporal scales. More specifically, we investigated the influence of different hydro-geomorphic processes (as a metric of sediment regime) and intra-annual flow variability in habitat conditions (physico-chemistry, hyporheic attributes) as well as ecosystem function (organic matter processing, primary production) and structure (macroinvertebrate density, community composition). We expected that restoration of hydro-geomorphic processes under a natural flow regime would restore physical, chemical, and hyporheic attributes towards natural dynamics and thus be distinct from adjacent non-restored habitats. We hypothesized that higher organic processing rates, higher values of primary production and more diverse and abundant macroinvertebrate assemblages would be found in restored areas than in channelized areas, being dependent on antecedent flow conditions. Further, we expected that the re-establishment in hydro-geomorphic heterogeneity under a natural flow regime would help restore certain taxa and increase the spatio-temporal variability in ecosystem structure and function.

Methods

Study site

The study was conducted on the Thur river, the largest river in Switzerland free of retention basins. The Thur is a 7th order perialpine river draining a catchment of 1730 km^2 (Figure 1a), originating in the north-east alpine region of Switzerland from Mount Säntis (2502 m a.s.l.). Catchment land use is dominated by fields/pastures (61% of land area) and forest (25%), while urban land use represents 8% of the area (Uehlinger, 2000). The river was channelized with stone rip-rap in the 1890s for flood protection. In the 1990s, the rip-rap from different channel sections of 1-3 km in length was removed to allow the formation of new gravel bars and increase the hydrological connectivity between the river and riparian zones. In the 2002, one km of channel protection was removed along both banks of the river (the stretch used in the present study). The study reach was located in the lower part of the river (370 m a.s.l.), 12 km upstream of the confluence to the river Rhine. The 2-km long study area comprised the restored reach (subject to river widening) and channelized areas upstream and downstream of the restored section (Figure 1b). Due to the lack of large retention structures, the flow regime of the Thur is naturally dynamic, fluctuating from 3 to 900 m^3/s with an average discharge of 47 m^3/s (1995–2016 records). Channel width in the channelized reaches was ca. 50 m while the maximum width in the restored area was 160 m. We selected five sampling sites in the study area (Figures 1b and 1c), expecting them to respond differently to changes in flow/sediment pulses. Two sampling sites were located in the channelized reaches: one upstream (Site 1) and one downstream of the restored reach (Site 5). Three sampling sites were located along the main gravel bar in the restored reach: an erosional site (Site 2), a point bar site (Site 3), and a depositional site (Site 4).

Field sampling and flow regime classification

Field surveys were conducted six times per year, approximately monthly in 2014 and 2015, from early spring to late autumn. Surveys were conducted when the water level was safe for access into the main channel, but after flow pulse events of different magnitude to account for temporal and hydrological variability (Figure 2). To characterize the intra-annual flow regime, we used a daily discharge record from a gauging station located 7 km downstream of the sampling sites, at the municipality of Andelfingen.

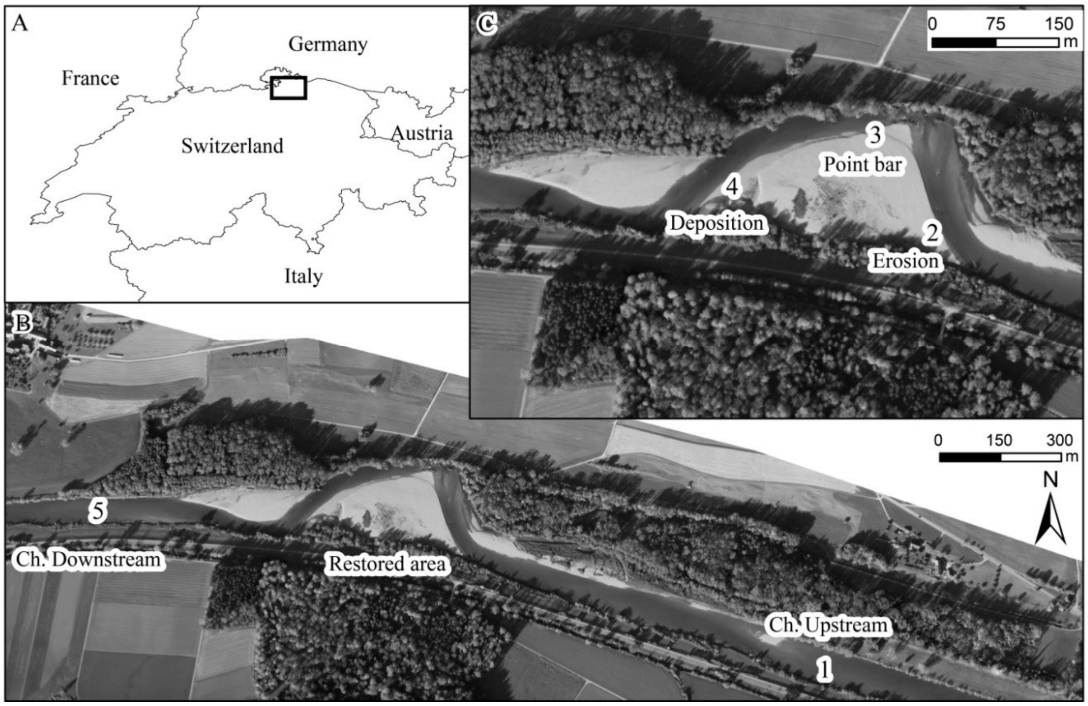

Figure 1: A = Location of study site in Switzerland. B = general view of the study reach, including channelized areas upstream (Site 1) and downstream (Site 5) of the restored area. C = Detail picture of the main restored gravel bar. Ch = channelized. Flow direction: Right to left.

In order to study the effects of flow variation affecting each sample collection, the previous flow period associated with each field survey was defined as the time elapsed between sampling dates. As no defined period can be given for the first sampling date in both years, we used the average flow value from the previous 41 days (average duration of all periods). For each period, we calculated 9 hydrological descriptors using the daily discharge record: mean, median, skewness, maximum, minimum, coefficient of variation, number of days flow was below the 1st quartile (low-flow events), number of days flow was above the 3rd quartile (high-flow events), and number of days flow was above the sediment motion threshold (150 m^3/s). The 1st and 3rd quartiles (20 and 60 m^3/s, respectively) were calculated from the 20-year record (Richter et al., 1996), while the sediment motion threshold value was taken from a previous study at the same site (Uehlinger, 2000).

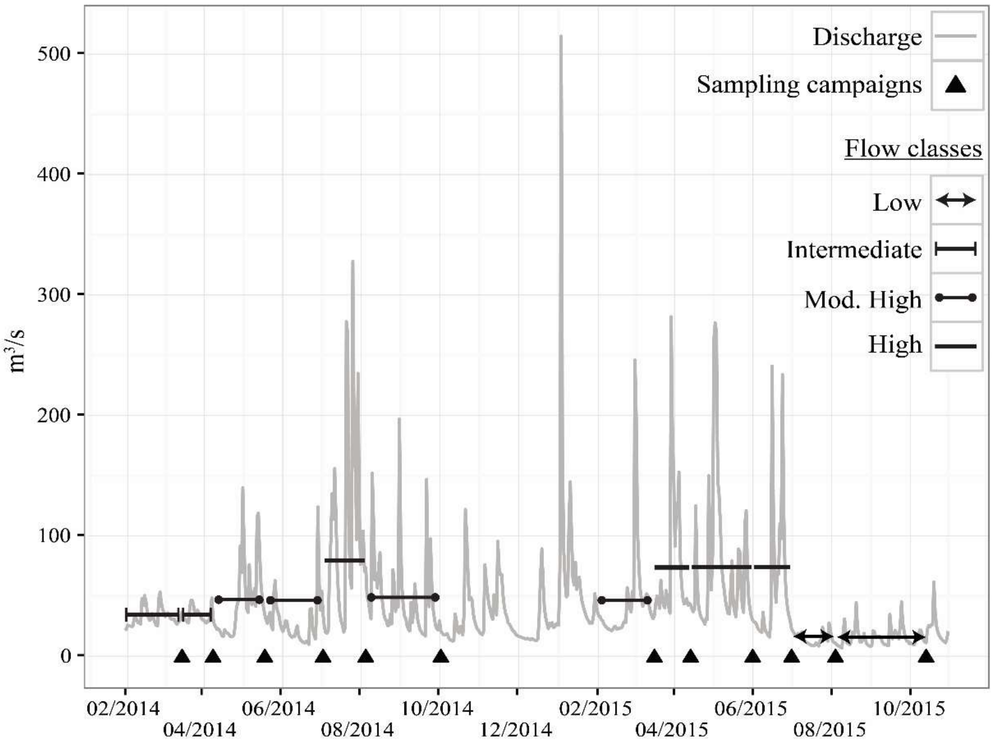

Figure 2: Hydrograph of Thur river in 2014 – 2015. Black lines represent flow classes of the period affecting each sampling campaign (Mod. High = Moderately High).

The 9 hydrological descriptors were used to cluster the 12 flow periods into 4 flow classes according to similarity in flow attributes using hierarchical cluster analysis (Ward's method): High, Moderately High (Mod. High), Intermediate, and Low. We determined the number of the classes from an inspection of the cluster dendrogram in a preliminary analysis to reasonably represent the flow regime in the study area (see *Results*). The measured functional and structural ecosystem attributes were compared among sites among the 4 flow classes (see below).

Abiotic factors: physical, chemical, and hyporheic attributes

We measured local abiotic conditions including physical, chemical, and hyporheic attributes at each site on each sampling date. Physical attributes were represented by 3 variables: water depth (cm), velocity (cm/s), and median grain size of streambed sediments (stream d50 mm). Velocity at 0.6 depth was measured using a portable velocity meter (MiniAir2, Schiltknecht AG, Gossau, Switzerland). Sediment size distribution was estimated by measuring b-axis of 50 randomly-collected stones per site (Wolman, 1954). Further, a 0.5-litre water sample was collected at each site, returned to the laboratory, and analysed for dissolved organic carbon (DOC), total nitrogen (TN), nitrate-N (NO_3-N), total phosphorus (TP), and electrical conductivity at 20°C (Cond) following methods in (Tockner *et al.*, 1997).

Hyporheic attributes were represented by 4 variables: fine and coarse particle organic matter (FPOM and CPOM, respectively), median grain size of sediments (hypo d50) of hyporheic material used in the incubation experiments for sediment respiration (see below), and vertical hydraulic gradient (VHG). Material from each incubation chamber used for sediment respiration measures was stored in a plastic bag and kept frozen (−20°C). In the laboratory, CPOM from this material was separated using a 2 mm sieve. A CPOM subsample and main sediment sample (including organic particles finer than 2 mm, FPOM) were dried at 60°C, weighed, burned at 450°C for 4 h, and reweighed to determine ash-free dry mass (AFDM kg^{-1}) of sediment. Ashed sediments were then sieved through a sieve column separating grain size fractions >8 mm, 8–4 mm, 4–2 mm, 2–1 mm,1–63 µm and <63 µm. Median grain size (mm) was calculated using Gradistat v8 (Blott & Pye, 2001). Vertical hydraulic gradient was measured *in situ* to characterize groundwater-stream water exchange direction and magnitude. Minipiezometers were driven to a depth of approx. 50 cm into the streambed (Baxter *et al.*, 2003). Positive values above stream-water surface levels indicated upwelling conditions, while negative values indicated downwelling conditions.

Ecosystem function

To assess ecosystem function, we used sediment respiration in the hyporheic zone and periphyton biomass on the riverbed. Hyporheic sediment respiration (SR), as a proxy for hyporheic organic matter processing, was measured *in situ* following methods in Uehlinger *et al.* (2002). Change in O_2 concentration was measured overtime in sealed Plexiglas tubes (n = 3) half-filled with hyporheic sediments (sieved <8 mm as standard protocol) and then filled with stream water. Surface sediments were excluded to avoid effects on respiration by autotrophs (Doering *et al.*, 2011). A portable oxygen meter (Hach HQ40d connected to a LD0101 oxygen probe) was used to measure oxygen concentration and temperature in each tube before and after incubation. Hyporheic sediment respiration was calculated based on the consumption of O_2 in the tube and the weight of sediment (*R*, mg O_2 kg^{-1} sed h^{-1}) and then normalized by a reference temperature (20°C) to account for seasonal variation (Naegeli & Uehlinger, 1997).

Periphyton biomass and chlorophyll concentration were measured from five random cobbles collected from the streambed, stored in plastic bags, and kept frozen at −20°C until processed. Periphyton was scrubbed from the surface of each stone using a metal brush, the slurry collected, volume measured, and divided into two sub-samples. Both sub-samples were filtered using Whatman GF/F filters. One filter was dried at 60°C, weighed, combusted at 450°C and reweighed for biomass estimation as AFDM, expressed as g AFDM m^{-2}. Surface area of each stone was calculated by wrapping the stone with aluminum foil and using a weight to area relationship (Bergey & Getty, 2006). The second filter was extracted for 7 min in 90% ethanol at 70°C, and chlorophyll concentration measured by High Performance Liquid Chromatography (Meyns *et al.*, 1994).

Ecosystem structure

We evaluated benthic macroinvertebrates to assess ecosystem structure. Benthic macroinvertebrates were collected (n = 3 per site and date) using a Hess sampler (250-um mesh, 0.04 m^2 area) and preserved with 70% ethanol. In the laboratory, the sampled individuals were hand-picked and identified to family level (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Coleoptera, Gastropoda, Crustacea, Isopoda, and Odonata) or subclass level (Oligochaeta) and their abundances counted using a stereomicroscope (10x magnification). The density (individuals m^{-2}) and taxa richness were calculated from the dataset.

Data analysis

The effect of geomorphic processes and flow classes on each variable was first tested using analysis of variance (Vischer *et al.*) with sites (1, 2, 3, 4, 5) and flow classes (High, Moderately High, Intermediate, Low) as factors, following data transformation ($\log_{10}(x+1)$).

For better interpretation, sites were then re-grouped as restored (sites 2, 3, and 4) and non-restored areas (sites 1 and 5), and the coefficient of variation (CV) was used to examine the temporal variation of each variable within areas. To determine the relative importance of sites and flow classes on the variation in ecosystem function and structure (except macroinvertebrate community composition), variation partitioning was used, separating the variation among dependent factors. The main ecosystem variables were explained individually by linear regression using "varpart" function (Peres-Neto *et al.*, 2006) in the "vegan" package of R software (R Development Core Team, 2015). An ANOVA-like permutation test using function "anova.rda" then was used to evaluate the different partitions of each variable. A non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance and calculated on $\log_{10}(x+1)$ transformed densities was used to examine changes in macroinvertebrate community composition followed by an analysis of similarity (ANOSIM), to test for among-group differences. All analyses were carried out using the R statistical computing software.

Results

Flow class

The cluster analysis grouped the 12 periods into four flow classes (Figure 1b, Table 1): High, Moderately High, Intermediate, and Low. Based on the variance inflator factor (VIF < 10), the mean, median and maximum discharge were excluded from the cluster analysis to avoid multicollinearity. Flow classes differed in the main flow indicators. Class High (n = 4) showed the greatest values of almost every indicator except for minimum discharge and low-flow events. Class Moderately High (n = 4) showed the second highest values. Class Intermediate (n = 2) showed medium values for all indicators and the highest value of minimum discharge and lowest for coefficient of variation. Class Low (n = 2) showed the lowest values for all indicators and the highest value for low-flow events (Table 1). Flow characterization showed that the river Thur had high intra-annual streamflow variability, mainly driven by seasonality, although inter-annual differences between wet and dry years also contributed to distinguish flow classes. Flow class High included seasonal events such as snowmelt high flows but also irregularly high rain events (as in 2014). In contrast, Low events in 2015 were characteristic of a dry year, showing extreme dry conditions for the river.

Table 1. Summary of characteristics of the hydrological indicators of each flow class (average ± standard error). Note that mean, median and maximum discharge were not used for classification to avoid multicollinearity. Days < 1st q = numbers of days discharge below 1st quartile; Days > 3rd q = numbers of days discharge above 3rd quartile; CV = coefficient of variation; Days disrupt = numbers of days discharge above sediment motion threshold

	Flow classes			
	High	**Mod. High**	**Intermediate**	**Low**
n	4	4	2	2
Mean (m^3/s)	76.4±7.2	41.2±3.9	32.7±0.6	14.1±0.2
Median (m^3/s)	49.7±7.8	32.4±3.0	31.0±0.4	12.8±0.5
Skewness	1.6±0.1	1.3±0.0	1.1±0.0	1.1±0.0
Max (m^3/s)	281.0±15.5	175.8±24.2	49.9±1.7	35.5±6.2
Min (m^3/s)	23.5±3.8	15.1±2.0	23.7±2.2	6.8±0.5
Days < 1st q	1.8±0.9	7.5±3.0	0.0±0.0	41.5±8.1
Days > 3rd q	15.5±2.8	8.0±2.3	0.0±0.0	0.0±0.0
CV	0.9±0.0	0.8±0.1	0.2±0.0	0.4±0.1
Days disrupt	3.8±1.0	1.0±0.5	0.0±0.0	0.0±0.0

Abiotic factors

Based on the observations (Table 2), the two-way ANOVA indicated differences among sites and flow classes in physical attributes (Table 3). Water velocity significantly differed among flow classes ($p = 0.04$), being faster under high flow conditions (0.39 ±0.1 m s^{-1}, average in space, Table 2) than under low flow conditions (0.22 ±0.1 m s^{-1}). Depth did not significantly differ among sites and flow classes ($p = 0.71$), but varied substantially (e.g., temporal average ranging between 18.3 ±1.3 cm at Site 5 and 37.8 ±3.7 cm at Site 1). Streambed d50 significantly differed among sites and flow classes ($p < 0.01$), as depositional site 4 had the lowest (2.0 ±0.3 cm, average in time) and erosional site 2 had the largest (4.2 ±0.5 cm) sediment size. Streambed d50 showed the same temporal pattern among flow classes, being greatest in the Low class and lowest in the Moderately High and High classes. CV of streambed d50 was double in restored sites (41%) than in non-restored sites (22%)

Table 2. Characterization of the study sites: physical, chemical and hyporheic zone (average ± standard error).Vel= velocity; Stream d50 = streambed median sediment size; DOC= dissolve organic carbon ; TN = total nitrogen; NO3-N = Nitrate-N; TP = total phosphorus; Cond = electrical conductivity; FPOM = Fine particulate organic matter; CPOM = Coarse particulate organic matter; Hypo d50 = hyporheic median sediment size; VHG = vertical hydraulic gradient; n.a. = not available

	Vel	Depth	Stream d50	DOC	TN	NO_3-N	TP	Cond	FPOM	CPOM	Hypo d50	VHG
Site	m/s	cm	cm	mg C/L	mg N/L	mg N/L	µg P/L	µS/cm 20°C	g/kg sed	g/kg sed	mm	cm/cm
1	0.35±0.1	37.81±3.7	3.44±0.3	2.27±0.1	2.38±0.1	2.20±0.1	37.49±3.5	422.33±13.3	4.0±0.1	0.18±0.02	4.8±0.1	0.12±0.06
2	0.55±0.1	25.04±2.2	4.18±0.5	2.27±0.1	2.41±0.1	2.21±0.1	37.93±3.8	423.77±13.3	4.5±0.2	0.10±0.02	3.8±0.2	−0.06±0.03
3	0.21±0.1	27.50±3.1	3.08±0.3	2.29±0.1	2.40±0.1	2.21±0.1	38.34±3.8	425.38±13.1	4.0±0.1	0.24±0.05	3.2±0.2	0.08±0.03
4	0.27±0.1	27.24±2.7	1.98±0.3	2.32±0.1	2.38±0.1	2.21±0.1	37.53±3.8	423.37±13.4	4.2±0.1	0.16±0.03	3.0±0.2	0.04±0.03
5	0.23±0.1	18.33±1.3	3.53±0.3	2.20±0.1	2.36±0.1	2.19±0.1	39.65±3.8	423.97±13.0	4.1±0.1	0.15±0.02	4.4±0.2	0.22±0.03
Flow class												
High	0.39±0.1	27.11±2.3	2.69±0.2	1.98±0.1	2.23±0.1	2.08±0.1	38.36±1.8	421.75±8.3	3.9±0.1	0.14±0.02	3.9±0.2	0.11±0.02
Mod. high	n.a.	31.21±2.6	2.97±0.2	2.40±0.1	2.27±0.1	2.16±0.1	45.14±2.3	421.10±8.7	4.4±0.1	0.15±0.02	3.8±0.2	0.04±0.03
Intermediate	n.a.	n.a.	n.a.	2.56±0.1	2.77±0.2	2.54±0.1	43.99±2.8	421.00±22.3	3.9±0.1	0.10±0.02	4.0±0.2	n.a.
Low	0.22±0.1	21.30±1.7	4.20±0.3	2.28±0.1	2.53±0.1	2.27±0.1	18.16±0.7	435.80±12.4	4.6±0.1	0.31±0.05	3.6±0.3	0.08±0.04

Chemical attributes showed no significant differences among sites ($p > 0.9$), but DOC, TN, and TP differed among flow classes, being related to seasonality ($p < 0.01$) (Table 3). DOC varied between 1.9 and 2.7 mg C L^{-1}, being lowest in the High class (2.0 ±0.1 mg C L^{-1}, average in space, Table 2) and greatest in the Intermediate class (2.6 ±0.1 mg C L^{-1}). TN showed similar trends, with lowest values in the High class (2.2 ±0.1 mg N L^{-1}, averaged in space) and greatest in the Intermediate class (2.8 ±0.2 mg N L^{-1}). TP was greatest in the Moderately High class (45.1 ±2.3 µg P L^{-1}, average in space) and lowest in the Low class (18.2 ±0.7 µg P L^{-1}). FPOM and CPOM significantly differed among sites ($p = 0.01$) and flow classes ($p < 0.01$), and their interaction for CPOM ($p < 0.01$). FPOM levels were an order of magnitude greater than CPOM (e.g., FPOM 3.9 ±0.1 g kg^{-1} sed and CPOM 0.14 ±0.02 g kg^{-1} sed in the High class). On average, FPOM was greatest in the Mod. High and Low classes (4.4 ±0.1 and 4.6 ±0.1 g kg^{-1} sed, respectively), whereas CPOM was highest in the Low class (0.3 ±0.05 g kg^{-1} sed). The hyporheic d50 and VHG significantly differed among sites ($p < 0.01$). Hyporheic d50 was greatest in non-restored sites 1 and 5 (on average, 4.8 ±0.1 and 4.4 ±0.2 mm, respectively). VHG upwelling was greatest in non-restored sites (0.12±0.06 and 0.22±0.03 cm cm^{-1}), whereas restored site 2 showed negative or near 0 values, indicating downwelling (−0.06±0.03 cm cm^{-1}).

Ecosystem function

Sediment respiration (SR) ranged from 0.10 to 1.39 mg O_2 kg^{-1} sed h^{-1} and differed significantly among sites, flow classes and its interaction (all $p < 0.01$, Table 3), being highest in the Low class and lowest in the High class (Figure 3). SR at non-restored sites (1 and 5) showed less variation among flow classes than restored sites (2, 3, and 4) (CV = 40% and 71%, respectively). Among restored sites, the temporal variability of SR was highest at the point bar site (site 3) (Figure. 3). Variation partitioning explained 45% of the variation in SR: 11.2% by sites and 33.8% by flow classes (Figure 4).

Table 3. Two way ANOVA results of the effects of site and flow class on all measured variables. Bold numbers indicate statistical significance (α = 0.05). Stream d50 = streambed median sediment size; DOC= dissolve organic carbon; TN = total nitrogen; NO_3-N = Nitrate-N; TP = total phosphorus; Cond = electrical conductivity; FPOM = Fine particle organic matter; CPOM = Coarse particle organic matter; Hypo d50 = hyporheic median sediment size; VHG = vertical hydraulic gradient; SR= Sediment respiration; Chla = periphyton chlorophyll; Density = macroinvertebrate density; and Richness = macroinvertebrate taxonomic richness.

		Site	Flow class	Site*Flow class
Abiotic factors				
Physical	Velocity	0.07	**0.04**	0.36
	Depth	0.71	0.71	0.5
	Stream d50	**<0.01**	**<0.01**	0.43
Chemistry	DOC	0.99	**<0.01**	0.99
	TN	0.99	**<0.01**	1
	NO_3-N	0.99	0.08	1
	TP	0.98	**<0.01**	0.99
	Cond	0.99	0.86	1
Hyporheos	FPOM	**0.01**	**<0.01**	0.91
	CPOM	**0.01**	**<0.01**	**<0.01**
	Hypo d50	**<0.01**	0.55	**<0.01**
	VHG	**<0.01**	0.06	**0.03**
Ecosystem function				
	SR	**<0.01**	**<0.01**	**<0.01**
	Biomass	0.93	**<0.01**	0.49
	Chla	0.39	**<0.01**	0.82
Ecosystem structure				
	Density	**<0.01**	**<0.01**	0.32
	Richness	**<0.01**	**<0.01**	**0.02**

Periphyton AFDM and Chl-a were significantly different among flow classes ($p < 0.01$). Greatest values of both periphyton measures occurred in the Low class, up to 22 g m^{-2} AFDM and >500 mg Chl-a m^{-2}, and extremely low values near 0 in the Intermediate, Mod. High, and High classes. There were no differences in CV among restored and non-restored site (AFDM CV = 150% and 140%, and Chl-a CV = 190% and 200%, respectively). These trends were also confirmed by variation partitioning: The variations in AFDM and Chl-a were explained best by flow class (68 and 63%, respectively) and not by site (0%)(Figure 4).

Ecosystem structure

Macroinvertebrate density and taxa richness were significantly different among sites and flow classes ($p < 0.01$). Taxa richness also differed in the interaction ($p = 0.02$). Densities ranged from <100 to over 25,000 ind m^{-2} (Figure. 3). Erosional and point bar (sites 2 and 3) had lower density and taxa richness than the other sites, while non-restored sites (sites 1 and 5) had slightly higher densities and richness than restored sites (especially in the Intermediate class) (Figure. 3). Density CV was higher in restored sites (176%) than in non-restored sites (124%), whereas CV of richness was the same for both (38%). The variation in macroinvertebrate density and richness was explained best by flow class (55 and 15%, respectively) and site (8 and 5%, respectively) (Figure. 4).

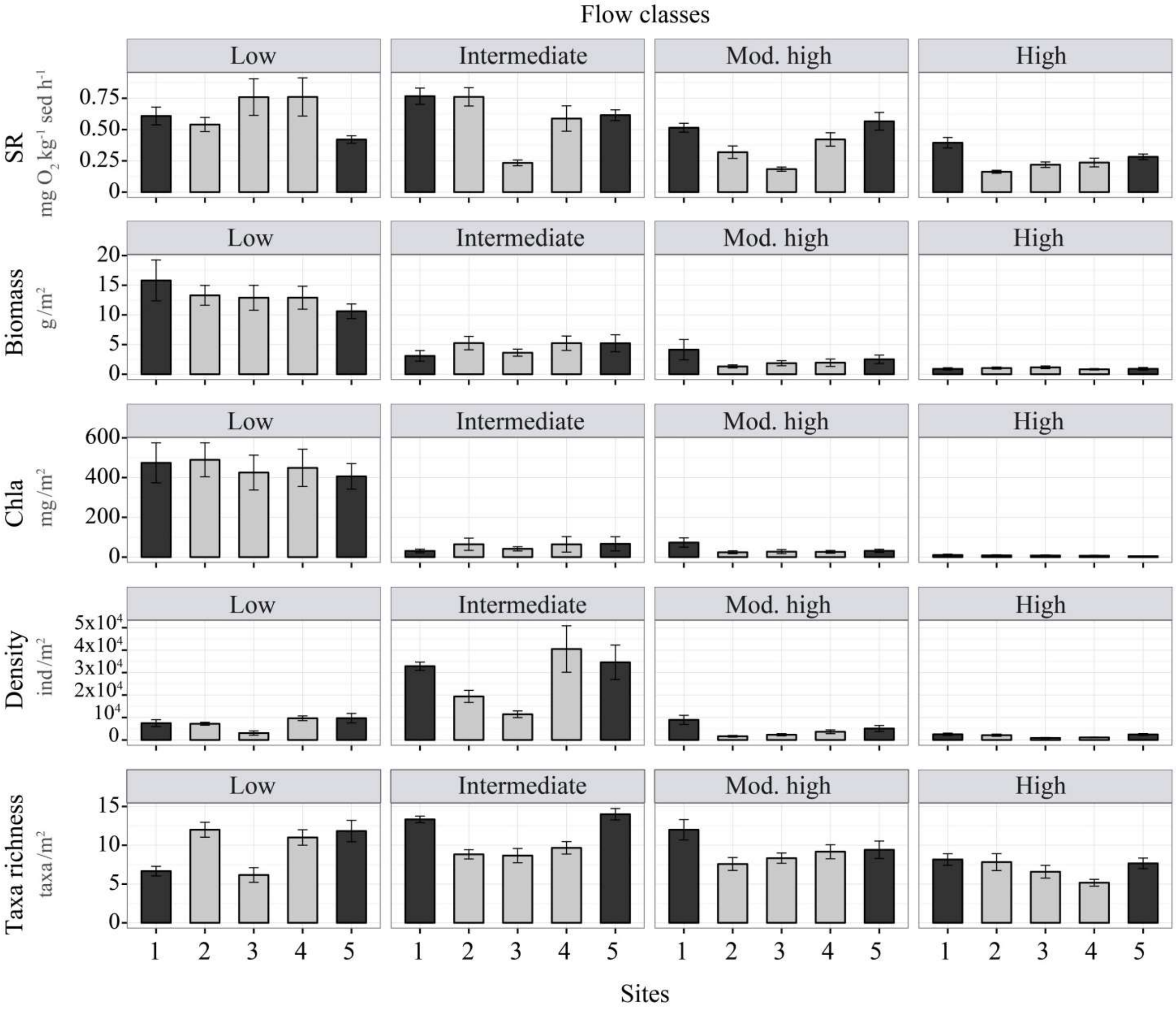

Figure 3: Rates by site and flow class of the main ecosystem function and structure (average ± standard error). Black bars (site 1, site 5) represent non-restored sites, while grey bars (site 2, site 3, site 4) represent restored sites. SR= Sediment respiration; Chla = periphyton chlorophyll; Density = macroinvertebrate density; and Richness = macroinvertebrate taxonomic richness.

NMDS analysis (stress = 0.21; Figure 5) showed a difference in macroinvertebrate composition in the different flow classes (ANOSIM by groups, R = 0.37, p = 0.001). In particular, assemblages clearly shifted in composition from the High class to Mod. High class to the Intermediate class along both NMDS axes, with the Low class assemblages falling outside this pattern of change. The Low class was dominated by families of snails (Hydrobiidae, Valvatidae and Planorbidae), Odonata (Gomphidae, Corduliidae) and isopods (Ashellidae), these groups being absent in the other flow classes. Restored and non-restored site assemblages were similar in each flow class (ANOSIM, R = 0, p = 0.5), although restored sites were shifted to the right along axis-1 for the higher flow classes (Figure. 5).

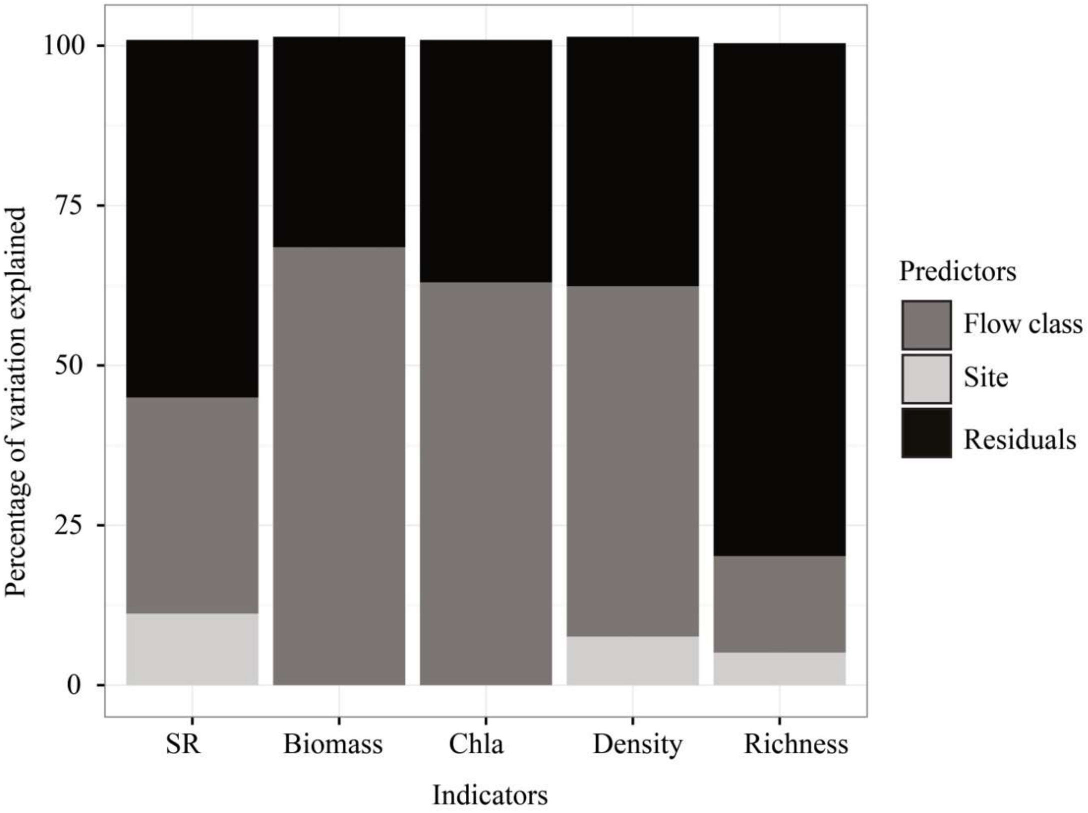

Figure 4: Partitioning variation of the ecosystem function and structure (percentage of variation explained by flow class and site). All proportions of explained variance were significant ($p < 0.05$). SR= Sediment respiration; Chla = periphyton chlorophyll; Density = macroinvertebrate density; and Richness = macroinvertebrate taxonomic richness.

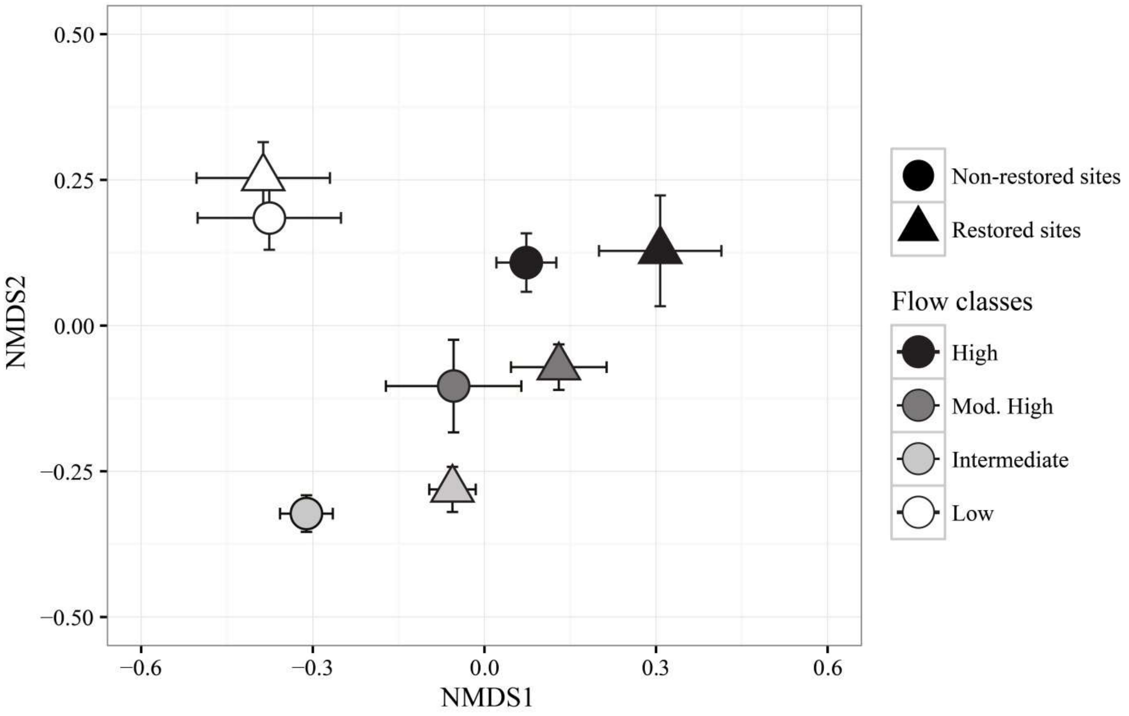

Figure 5: Community composition in NMDS ordination space based on macroinvertebrate densities. Symbols represent samples affected by different flow classes and restored or non-restored sites.

Discussion

We demonstrated that channel protection removal and re-activation of geomorphic processes in the Thur influenced the spatio-temporal variability in ecosystem function and structure, partially reflecting streamflow variation at the reach and intra-annual scales. The different restored sites in the study reach also showed differences in ecosystem function measures and their variability, especially in response to natural flow variability. A primary goal of river restoration is often to restore hydro-morphology, which usually leads to habitat diversification (abiotic attributes) with little attention to biota (Muotka *et al.*, 2002; Lepori *et al.*, 2005; Jähnig *et al.*, 2010; Palmer et al., 2010). Our results clearly indicate the need of designing restoration projects with a more holistic perspective, as in the Thur case study (Schirmer, 2014), that considers multiple temporal (monthly to several years) and spatial habitat to reach) scales. In this study, we focused specifically on how flow and sediment regimes in space and time influence ecosystem function and structure and its variation.

Most changes in water chemistry were related to the flow regime, thus to larger scale processes such as snowmelt water inputs or catchment response to major precipitation events. Water quality was the same among the different sites on any specific date, contrary to expectations and as was shown in other studies (Boulton *et al.*, 1998; Fernald *et al.*, 2006). The presence of large gravel bars in the restored area did not have an effect on water quality. Exchanges between the water column and channel bed and river banks (vertical and lateral linkages) can affect water quality, as these are biogeochemically active areas where organic matter decomposition and nitrogen removal occurs (Findlay, 1995; Battin *et al.*, 2003). The degree of exchange and transformation are driven by streambed topography and heterogeneity as well as coarse-scale patterns in river morphology, e.g. meander presence (Gomez-Velez & Harvey, 2014). Here, the length of the restored stretch (ca. 500 m,) where these spatial properties were enhanced, may have been too short to detect changes in exchange based on surface water physico-chemistry. The relatively high discharge of the Thur also might have over-ridden various exchange properties, being proportionally a much greater contributor (in terms of volume) to water quality. Nevertheless, we observed an increase in the variability in stream-bed physical properties in restored sites due to high flow events that were absent in non-restored sites.

Organic matter decomposition in the hyporheos, inferred from sediment respiration (SR) estimates, and primary production (periphyton AFDM and Chl-a) also showed different responses to flow events, and related sediment processes, among sites. The non-restored sites displayed stable conditions through time in terms of SR relative to restored sites. The lack of natural disturbance in long river sections may have general consequences leading to an ecosystem regime shift (Scheffer *et al.*, 2001), characterised by an increase of organic matter transformed into inorganic forms, with less organic carbon transported downstream (Aristi *et al.*, 2014). The presence of dynamic restored areas where SR varies according to flow regime (greater CV), may re-establish the natural organic matter processing at the reach-basin scale (Robinson & Uehlinger, 2008). Surface biofilms (periphyton cover), however, showed a clear response to flow events, likely reflecting a restriction to surface sediments and greater susceptibility of physical disturbance from scouring (Uehlinger, 2000; Uehlinger *et al.*, 2003). The fact that this response occurred in restored and non-restored sites suggests a remarkably low resistance of surface biofilms to spates (Uehlinger, 2000), despite differences in river morphology and bed heterogeneity.

Surprisingly, and despite the lack of bed surface alterations, macroinvertebrate densities at all sites were low under low flows. Abnormally low discharge conditions in summer, which caused high temperatures and physical changes in surface velocities and depth, may have caused these low densities, favouring communities more characteristic of lentic systems (e.g., Low class assemblages compared to other flow classes). Similarly, the fact that there was a more abundant and richer assemblage under intermediate flows suggests assemblages comprised taxa adapted to the Thur flow regime (Robinson & Minshall, 1998). Contrary to our hypothesis, we found a more abundant and richer assemblage on average in non-restored than restored sites. Other studies also have shown minor changes in macroinvertebrate assemblages in restored reaches despite enhanced habitat heterogeneity (Bernhardt & Palmer, 2011; Violin *et al.*, 2011). The higher disturbance in restored sites, in terms or sediment movement and deposition, may be one explanation for these differences in our study, although various other explanations have been offered for this lack of response, such as irrelevant spatial scales of management actions, time limitations for assemblages to show a response, or ignoring other stressors in the same river (Haase *et al.*, 2012). The study by Tonkin *et al.* (2014) showed that dispersal distance and regional taxa pools are also primary factors driving the colonization of restored rivers by benthic macroinvertebrates (also see Baumgartner & Robinson (2016)). The present study may be a good example of the interaction of a higher disturbance and a poor source population, since much of the lower section of the Thur is affected by lateral protections, constraining development of community assembly in restored habitats. This homogenization of the taxa source pool may explain the similarity between assemblages among the study sites in this study.

Overall, our study showed that both flow and morphology variability play an essential role in ecosystem function and structure. The fact that flow and morphology heterogeneity differ in their influence on ecosystem components emphasizes the importance of integrating both regimes when planning and evaluating restorations. Further, our study demonstrated the importance of considering intra-annual flow patterns in managing regulated rivers, especially in respect to current strategies in restoring sediment dynamics. In conclusion, considering how flow-sediment regimes interactively influence ecosystem function and structure at the riverscape scale enhances success potential in river management. Maintaining the inherent variability in flow-sediment interactions must be a priority when managing and restoring river reaches (Richards et al., 2002).

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Chapter 2

Title Macroinvertebrate seedbanks of gravel bars in flow regulated rivers

Short title: Aquatic macroinvertebrate seedbanks

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Abstract

Gravel bars along unregulated rivers undergo inherent wet-dry phases that shape local faunal assemblages that comprise mostly terrestrial spiders and beetles. Much less is known about the role of gravel bars as temporary habitats for aquatic macroinvertebrates, surviving via interstitial moisture content (active seedbank) or as resistant forms (dormant seedbank) during dry periods. Macroinvertebrate seedbanks are an important subsidy for terrestrial organisms as well as a source of immigrants to surface waters following gravel-bar inundation. In flow-regulated rivers, natural wet-dry periods have been artificially altered, e.g., through an increase or decrease in the frequency and magnitude of wet-dry periods (residual flows, hydropeaking). In this study, we investigated the presence/absence, density, taxa richness and assembly of active and dormant aquatic macroinvertebrates of gravel bars in five floodplains in Switzerland with different flow regimes (natural, residual, hydropeaking). We sampled the sediments of gravel bars and then incubated them in the laboratory to assess active and dormant seedbanks after a period of wetting. We found that several taxa inhabited gravel bars as both active and dormant seedbanks, mostly Oligochaeta and Chironomidae. The presence of macroinvertebrates showed high variability among sites, suggesting site dependent conditions influence seedbank properties. The density of active seedbanks was greater at rivers affected by hydropeaking, and lower in residual-flow than natural-flow rivers. These results emphasize the importance of gravel bars as habitats for aquatic macroinvertebrates and thus their inclusion in flow management schemes as well as conservation/restoration programs.

Keywords: hydropeaking, residual flow, active seedbank, dormant seedbank.

Introduction

The role of floodplains in driving biological complexity has been well documented, being referred to as biological hotspots due to their spatial (terrestrial-aquatic interface) and temporal (expansion and contraction cycles) heterogeneity (Naiman *et al.*, 1993; Naiman & Décamps, 1997; Robinson *et al.*, 2002). Floodplain complexity is primarily driven by flow components (magnitude, frequency, duration and timing of floods) that regulate habitat heterogeneity, spatial configuration and habitat connectivity (Poff *et al.*, 1997; Stanley *et al.*, 1997; Malard *et al.*, 2006; Doering *et al.*, 2007; Poff & Zimmerman, 2010). However, numerous anthropogenic alterations such as habitat degradation, pollution, invasion of exotic species, and flow regulation have modified floodplains worldwide, thus making them one of the most threatened ecosystems (Malmqvist & Rundle, 2002; Tockner & Stanford, 2002).

Anthropogenic flow regulation often alter the frequency and magnitude of natural floodplain expansion-contraction cycles creating disconnect between rivers and adjacent floodplains. For example, water abstraction and levee construction typically reduces natural flow fluctuations, thereby homogenizing floodplain habitats and channel complexity (Doering *et al.*, 2012). Similarly, residual flows below dams used for hydropower production usually lack wet-dry cycles associated with natural flow regimes (Richter *et al.*, 2003). In contrast, hydropeaking for electrical production dramatically increases the frequency of expansion-contraction cycles (daily fluctuations with up to 10-fold differences in flow) in affected rivers with negative consequences for flora and fauna (Moog, 1993; Førsund, 2015), creating an extensive artificial intertidal zone to which lotic organisms are poorly adapted (Ward & Stanford, 1979; Moog, 1993). For instance, Glen Canyon Dam, which regulates the Colorado river in northern Arizona (USA), release waves that impact communities up to 400 km downriver (Wiele & Smith, 1996).

Alteration of flow regimes can dramatically affect floodplain habitats and, in particular, gravel bars along rivers. Gravel bars are defined as un-vegetated or poorly vegetated areas, formed by sand and gravel deposits along the channel (Sadler *et al.*, 2004). Bars are areas of elevated sediment (e.g. gravel bars) in rivers deposited by flow and lie between the edges of flood plains and the typical base-flow of a given river, thus being exposed to water level fluctuations within channels (Smith, 1974; Ward *et al.*, 1999; Bates *et al.*, 2007). Gravel bars are, therefore, inhabited by a mix of species that are adapted to expansion-contraction cycles associated with natural flow regimes, including spiders, ants and beetles (Robinson et al., 2002; Paetzold *et al.*, 2005; Tockner *et al.*, 2006; Langhans & Tockner, 2014). Likewise, streambed fauna from rivers that may experience natural expansion-contraction periods (e.g. intermittent rivers) are also adapted to this natural fluctuations. For instance, some aquatic invertebrates have larvae that can survive in sediments with low moisture content, known as the active invertebrate seedbank (Larned *et al.*, 2007; Stubbington *et al.*, 2009). Other aquatic gravel bed invertebrates undergo biological transformations to survive dry conditions. For example, some chironomid larvae form cocoons, copepods encysts, and cladocerans produce ephippia (Danks, 2000). Together with macroinvertebrate eggs, which can also resist long periods of desiccation, suspended life stages constitute the so-called dormant invertebrate seedbank, whereby they may become reanimated during a flooding or rewetting event. Invertebrate seedbanks thus comprise a variety of aquatic life stages that can persist in bed sediments during dry periods in non-permanently wet habitats (Tronstad *et al.*, 2005; Stubbington & Datry, 2013). As such, inundation of gravel bars during expansion periods (i.e. floods or flow pulses) can be an ecological “hot moment” for the dormant seedbank community that triggers hatching of desiccation-resistant eggs and transformations of other life stages to become active (Tronstad et al., 2005). In general, macroinvertebrate seedbanks (active and dormant) can be considered a source of colonists following re-hydration of temporary waters (Boulton & Lloyd, 1992; Tronstad et al., 2005).

In many rivers, gravel bars harbor an abundant and diverse assemblage of terrestrial arthropods, not only on the surface but also in deeper sediments (e.g., up to 1.1 m depth) (Framenau *et al.*, 2002; Paetzold et al., 2005; Langhans & Tockner, 2014), that are negatively influenced by changes in flow and morphology (Paetzold *et al.*, 2008). In contrast, relatively little is known about the role of gravel bars regarding active/dormant seedbanks of aquatic invertebrates and how they are affected by, regulated flows in particular (Datry *et al.*, 2012). In this study, we examined the spatio-temporal presence of active/dormant seedbanks in gravel bars along rivers experiencing a gradient in flow regulation. We expected hydrological regimes to be an important determinant in the density, taxa richness and assemblage composition of gravel-bar seedbanks in the different systems. We also expected more dense assemblages in lower areas of gravel bars near the main channel relative to areas higher and farther from the main channel due to differences in inundation frequency and duration. For example, lower areas near main channels should be inundated more frequently and at greater duration than areas higher and farther away from the main channel.

Methods

Study sites

Seedbank samples were collected from six sites within five floodplains in Switzerland: Maggia, Sandey, Sarine, Sense and Thur (Figure 1 and table 1). At all sites, seedbank samples were collected over two years in spring and summer (Thur and Sandey 2014-2015; Maggia, Sense and Sarine 2015-2016).

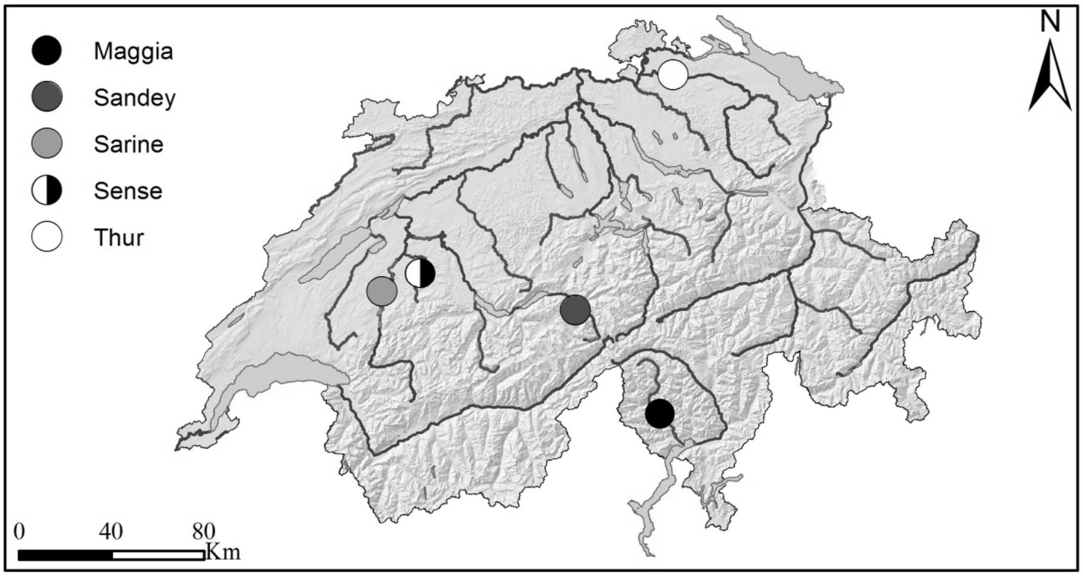

Figure 1: Map of Switzerland with main rivers showing the location of the floodplains (sampling sites) included in the study.

Maggia

The Maggia River (7th order, 220 m a.s.l.) flows through an 8 km long floodplain in southern Switzerland. Characterized by a braided channel and numerous disconnected ponds, the Maggia Floodplain represents a near-natural and heterogeneous ecosystem. However, most of the flow is diverted for hydropower production, hence the flow regime is residual with some punctuated high flows during large rain events. Seedbank samples were collected from the middle section of the floodplain near the town of Giumaglio, Switzerland.

Sandey

The Sandey Floodplain (850 m a.s.l.) is 3.4 km long and up to 600 m wide and located in central Switzerland. It contains a diversity of floodplain habitats, including the main channel (Urbach River), secondary channels, islands and floodplain forest (Doering et al., 2012). The flow regime of the Urbach River (4th order) is glacial-nival, which is characterized by high discharge during the summer when glacial ice melts. However, about 30% of the Urbach River discharge is impounded by a hydroelectric dam, for power production, since 1950. Although reduced in magnitude for hydroelectric power, the flow regime is nearly natural due to numerous spring inputs below the dam. Additionally, the Urbach River is influenced by numerous levees constructed since 1950 for flood control. The study site for the Sandey Floodplain was located in the middle reach of the floodplain.

Sarine

The Sarine River (7th order, 560 m a.s.l) is located in western Switzerland with the main river channel upstream at Rossens dam. Below the dam, the river flow is residual for 12 km before hydropeaking inputs from the Hauterive hydropower station are added. Two different study sections were located on the Sarine, one in the residual flow section (Sarine R) and one in the hydropeaking section (Sarine H). Discharge peaks in the hydropeaking section range from 3,5 to 70 m^3/s, whereas discharge in the residual section is 3,5 m^3/s.

Table 1. General characteristics of the six study systems (m a.s.l = meters above sea level).

Site	**Altitude (m a.s.l.)**	**Average discharge (m^3/s)**	**Flow regime**
Maggia	220	18	Residual
Sandey	850	2	Natural
Sarine H	565	30.8	Hydropeaking
Sarine R	575	3.6	Residual
Sense	655	4	Natural
Thur	370	47	Natural

Sense

The Sense River (6th order, 655 m a.s.l.) is located in central Switzerland. It has a morphology characteristic of a braided river with multiple secondary channels and has a natural flow regime.

Thur

The Thur River (7th order) is a peri-alpine river and the largest undammed river in Switzerland, allowing for a natural flow regime. However, the river has been channelized for 100s of years by lateral protections, especially in the lower segment, reducing the floodplain surface area. Beginning in 2000, different sections of lateral protection were removed, allowing gravel bars to develop in the widened sections. The study site for the Thur Floodplain was located in a formerly-channelized section in the lower river (370 m a.s.l.) in northeastern Switzerland, 12 km upstream of the Thur River confluence with the Rhine River.

Sediment sampling and rewetting

At each site, 2-5 samples of dry sediment (1.5 L each) were collected from the surface of gravel bars (5 cm depth) using a shovel, excluding stones larger than 5 cm (b-axis). Two types of gravel bars were sampled: non-vegetated and vegetated gravel bars (present only in Maggia and Sarine). Samples were collected from three different habitats within each gravel bar: high bar (ca. 1 m higher than base-flow water level), low bar (ca. 10 cm higher than base-flow water level) and dry secondary channels (present only in Thur and Sandey). A total of 203 samples were collected during the study. Samples were transferred into 25x14x14 cm containers (volume = 5 L), covered with a lid and transported to the laboratory. In the laboratory, containers were filled with 3 L non-chlorinated water, shaken, and water decanted through a 63 µm sieve. This process was repeated 3 times to reduce the number of potential predators in the container (Larned et al., 2007) and to determine the active seedbank community. Invertebrates retained on the sieve were stored in 70% alcohol for later processing. Then, 2-L non-chlorinated water were added to each container, installed with air stones, covered by a 1-mm mesh lid and incubated for 14 days. For incubation, containers were placed in an environmental chamber at a 12:12 h light/dark cycle and temperature set according to season (10 °C for spring and 15 °C for summer). At day 14, containers were sampled as above before the incubation period. Invertebrates retained by the sieve (hatched dormant seedbank) were preserved in 70% alcohol until processed. Due to the small size and early stage of many larvae, invertebrates were identified to family level (Oligochaeta to subclass).

Data analysis

All statistical analyses were carried out using R statistical computing software (R Development Core Team, 2015). To compare responses of macroinvertebrate seedbanks to environmental variables, the results were grouped by the different experimental factors: study river (Maggia, Sandey, Sarine, Sense and Thur), hydrological regime (hydropeaking, natural and residual), season (spring, summer), type of gravel bar (non-vegetated, vegetated), and height (secondary dry channel, high bar, low bar). A presence/absence matrix for active and dormant seedbanks was created. Relationships between invertebrates present among the factor levels was assessed using a generalized linear model with a negative binomial error distribution (Zuur *et al.*, 2009) Individuals and number of taxa per sample were converted to volume of sediment units as individuals per liter sediment (individuals/L; density) and number of taxa per liter sediment (taxa/L; taxa richness).

The influence of river, hydrological regime, season, type of gravel bar, and height on density and taxa richness of active and dormant seedbanks were explored using generalized linear mixed (glmm) models (Zuur et al., 2009). Due to the type of data (count) and that many samples contained few or no individuals, a negative binomial distribution was used in the models. Density or taxa richness of active and dormant seedbanks were included in the model as the response variable. Explanatory variables included; hydrological regime (nested in river), season, type of gravel bar and height. Replicate and study site were included as random effects, however replicate variation did not vary significantly among sites so was excluded from the models. A backward model selection analysis, starting with the full model, was performed using Akaike Information Criterion (AIC) to validate model reductions (Zuur et al., 2009).

Assemblage composition of active and dormant seedbanks each were evaluated using non-metric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix calculated from $\log_{10}(x+1)$ transformed invertebrate densities. To check for significant differences in assemblage composition among groups, a permutational ANOVA (PERMANOVA) analysis was performed. A similarity percentage analysis (SIMPER) was used to identify taxa responsible for differences and to calculate the percentage dissimilarity among groups.

Results

Presence of active and passive seedbanks in gravel bars

Active seedbanks were found in 49% (100 samples) and dormant seedbanks in 43% (88 samples) of the collected samples. The presence of active seedbanks was significantly different among sites, hydrological regime, season and gravel bar height (Figure 2, table 2). The presence of active seedbanks was similar in the Maggia, Sandey, Sarine R and Thur rivers (50, 46, 50, and 57% of the samples in each), whereas no active seedbanks were found in the Sense River samples. Active seed banks ranged from 46% to 92% across sites (mean

59%, SD 19%). Hydrological regime sampling ranged from 46% to 92% in active seed bank presence (mean 63% SD 25%), with hydropeaking regime showing clearly higher active seed bank presence (92 %) compared to natural and residual regimes (~50%). Active seed banks were predominantly found during spring sampling (64%) compared to summer sampling (42.5%). Differences in gravel bar height among samples resulted in active seed bank presences of 41% to 63% (mean 53% SD 11%), with secondary dry channel having higher presence of seedbanks compared to low and high gravel bars. The presence of dormant seedbanks ranged from 7.% to 59% across sites (mean 38%, SD 18%). Again, Sense River showed the lowest seedbank presence (7%). Presence of dormant animals was similar across hydrological regimes (42, 44 and 43% in hydropeaking, natural and residual regimes respectively). Greater presence of dormant seedbank was found in spring (61%) compared to summer sampling (34%). Similar presence of dormant seedbank was found across gravel bar height (37, 40 and 49% in secondary dry channel, high and low bars respectively) (Figure 2).

Table 2. Results of glm on the effects of river, hydrological regime, season, type of gravel bar and height on the presence of active and passive seedbanks. See text for definition of active and passive seedbanks. p: p-values following Chi-square test; df: degrees of freedom; Resid: residuals. p-values <0.05 indicated in bold.

Variables	df	Deviance	Resid. df	Resid. Deviance	p
Active seedbank					
River	5	28.95	197	252.46	**<0.001**
Hydrological regime	2	10.631	200	270.78	**0.005**
Season	1	8.29	201	273.12	**0.004**
Type of gravel bar	1	2.57	201	278.84	0.11
Height	2	5.98	200	275.43	**0.05**
Dormant seedbank					
River	5	18.17	197	259.64	**0.003**
Hydrological regime	2	0.03	200	277.78	0.98
Season	1	13.07	201	264.74	**<0.001**
Type of gravel bar	1	2.16	201	275.65	0.14
Height	2	2.24	200	257.57	0.32

Density and taxa richness

A total of 2286 individuals (macroinvertebrates) were found, including 1312 in active seedbanks and 938 in dormant seedbanks. The maximum density of active seedbanks was 141 ind./L sediment (Thur, spring, natural regime, non-vegetated, high bar), while the maximum density of dormant seedbanks was 124 ind./L sediment (Thur, spring, natural regime, non-vegetated, low bar). The Sarine River hydropeaking section had the maximum density among rivers for active seedbank (mean + SE = 13 ± 3) and Thur River for dormant seedbanks (8 ±3 ind./L sed), whereas the Sense had the lowest (0.0 and 0.1 ind./L sed, respectively) (Figure 3). The density of active seedbanks was greatest in samples of hydropeaking regimes (13.2 ± 3.2 ind./L sed), with density decreasing 3-fold at natural sites and 10-fold at residual sites (Figure 3). Dormant seedbanks at hydropeaking sites had low densities (0.2 ind./L sed).

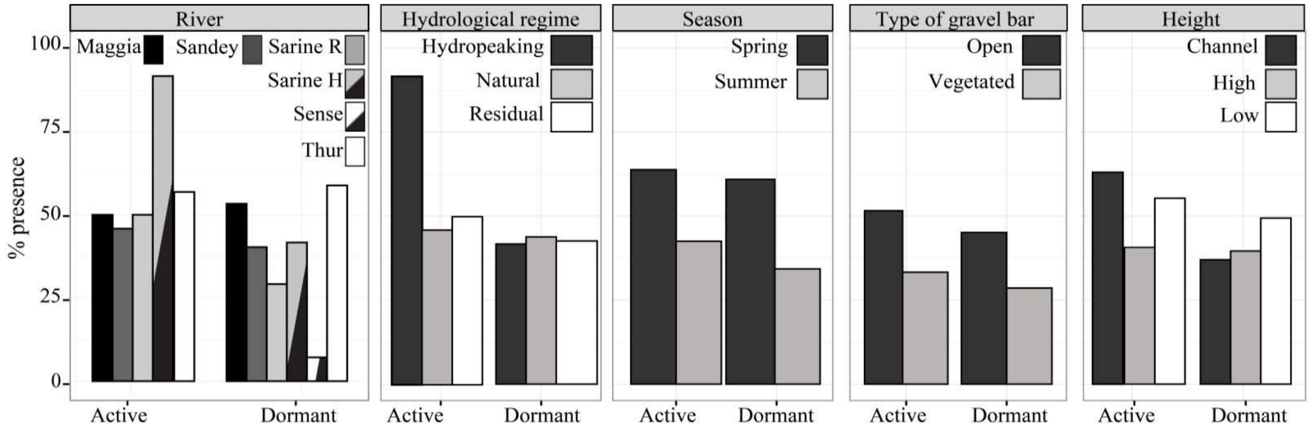

Figure 2: Percentage of active and dormant seedbank samples containing animals. Presence of active seedbank for Sense river is not shown (% = 0). Sarine R: Sarine residual; Sarine H: Sarine hydropeaking. Levels of each factor are described in the text (methods).

Overall, the densities of active and dormant seedbanks were higher in spring than in summer (Figure 3). Non-vegetated gravel bars had greater densities of active and dormant seedbanks than vegetated gravel bars. Secondary dry channels had lower densities of active and dormant seedbanks than high and low bars (Figure 3).

Some 18 different taxa were found in active seedbanks and 12 in dormant seedbanks (table 3). The highest taxa richness found in active seedbanks was 5 taxa/L sediment (Sarine, summer, hydropeaking, non-vegetated, open bar) while in dormant seedbanks we found a maximum of 3 taxa/L (Maggia, summer, residual, non-vegetated, low bar). Taxa richness of active seedbank was six time higher in samples of hydropeaking regimes (3.0 ± 0.4 taxa/L sed) compared to natural and residual regimes samples. There were no differences among seasons, type of gravel bar and heights in taxa richness (Figure 3).

Table 3: Number of individuals of aquatic macroinvertebrate collected at day 0 (active seedbank) and day 14 (dormant seedbank).

Group	Familiy	Active	Dormant
Amphipoda	Gammaridae	49	0
Coleoptera	Dytiscidae	26	1
	Elmidae	22	25
Diptera	Ceratopogonidae	11	3
	Chironomidae	140	231
	Empididae	3	3
	Limoniidae/Pedicidae	25	20
	Rhagionidae	6	2
	Stratiomyidae	1	0
	Tabanidae	1	2
	Tipulidae	24	1
Ephemeroptera	Baetidae	1	0
	Heptageniidae	4	0
Isopoda	Asellidae	2	0
Oligochaeta		984	648
Plecoptera	Leuctridae	1	0
	Perlidae	0	1
Trichoptera	Hydropsychidae	2	0
	Limnephilidae	10	1
TOTAL		1312	938

The glmm testing the effects of multiple factors on density and taxa richness s of active and dormant seedbank showed that the random factor river had more importance explaining density than taxa richness (explained variance in density models was 0.36 and 0.31, but 0.08 and 0.09 in taxa richness models; active and dormant seedbanks, respectively). Taxa richness in active seedbanks differed significantly among hydrological regimes ($P < 0.01$, d.f. = 2) and season ($P < 0.01$, d.f. = 1). Likewise active seedbank invertebrate densities also differed significantly between hydrological regimes (P = 0.03, d.f. = 2) and season (P < 0.01, d.f. = 1). Dormant seed bank taxa richness differed significantly among seasons (P <0.01, d.f. = 1) and sample height (P = 0.02, d.f. =2). Whereas dormant seed bank density differed significantly among seasons (P < 0.01, d.f. = 1) and marginally differed among regimes (P = 0.06, d.f. = 2) (table 4).

Assemblage composition and dissimilarity

In general, active and dormant seedbank assemblages were dominated by Oligochaeta, Chironomidae (Diptera), Elmidae (Coleoptera) and Limonidae/Pedicidae (Diptera). Seven families representing 18 taxa were found in active seedbanks; including Gammaridae (Amphipoda), Stratiomyidae (Diptera), Baetidae (Ephemeroptera), Heptagenidae (Ephemeroptera), Asellidae (Isopoda), Leuctridae (Plecoptera) and Hydropsychidae (Trichoptera). Perlidae (Plecoptera) were found exclusively in dormant seedbanks (Table 3).

Figure 3 : Effects of river, hydrological regime, season, type of gravel bar and height on the number of individuals (density) and taxa richness of active and dormant seedbanks. All values are means ± SE Sarine R: Sarine residual; Sarine H: Sarine hydropeaking. Levels of each factor are described in the text (methods).

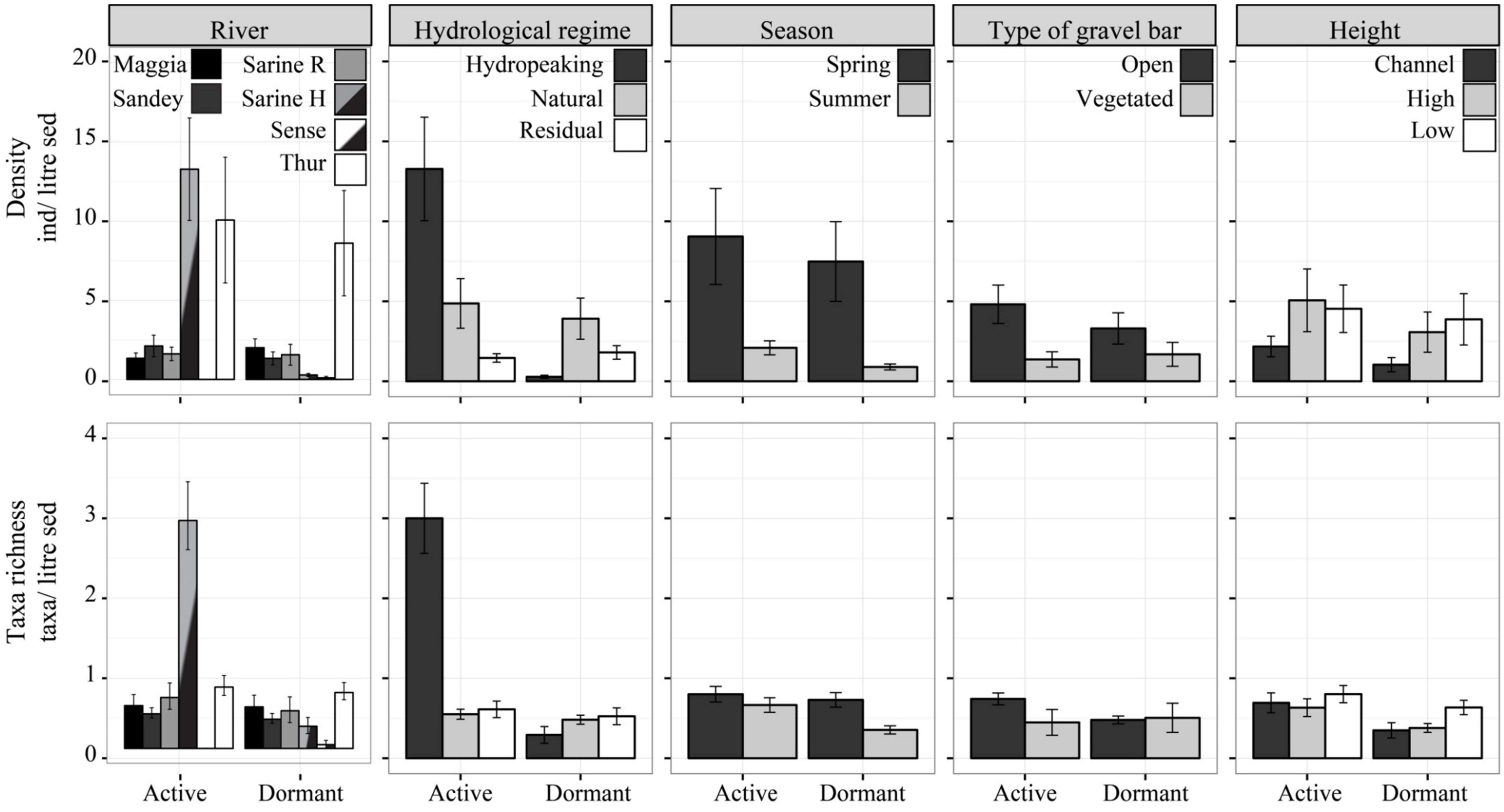

Table 4: Results of the generalized linear mixed models (GLMM) for the effects of river, hydrological regimes, season, type of ravel bar and height on the abundance and taxa richness of active and dormant seedbanks, df: degrees of freedom; sum sq: sum of square; mean sq: mean of square; p: p-values following Chi square tests, Std. Dev: standard deviation.

Density active

Fixed	df	sum sq	mean sq	p
Regime	2	7.285	3.64	0.03
Season	1	48.515	48.51	<0.001
Random	variance	std.dev		
River	0.366	0.605		

Density dormant

Fixed	df	sum sq	mean sq	p
Regime	2	3.39	1.7	0.06
Season	1	56.7	56.669	<0.001
Random	variance	std.dev		
River	0.3163	0.5624		

Taxa richness active

Fixed	df	sum sq	mean sq	p
Regime	2	21.39	10.69	0.004
Season	1	17.46	17.46	<0.001
Random	variance	std.dev		
River	0.08235	0.287		

Taxa richness dormant

Fixed	df	sum sq	mean sq	p
Season	1	19.93	16.93	<0.001
Height	2	7.75	3.87	0.024
Random	variance	std.dev		
River	0.092	0.3037		

Assemblage composition of active seedbanks differed among rivers (PERMANOVA, F = 1.85, P < 0.01) (Figure 4a). The Maggia River and Sandey River had similar active seedbank assemblages (38% dissimilarity), whereas the Thur River had a different assemblage (e.g. 73% dissimilarity with the Sandey). The Sarine River active seedbank assemblage was located on the left side of the NMDS plot (NMDS stress = 0.12), having greater variation in assemblage composition and 70% dissimilarity with the Sandey River active seedbank assemblage. The natural flow regime assemblage was located on the central right side of the

NMDS plot, while residual and hydropeaking assemblages differed and were on the bottom left side of the plot (F = 1.85, P = 0.03) (Figure 4c). Natural and residual active seedbank assemblages had a dissimilarity of 72%, while natural and hydropeaking assemblages had a 73% dissimilarity. Residual active seedbank assemblages showed much more variation than the other hydrological regimes. The NMDS also revealed differences (dissimilarity = 39%) in spring and summer active seedbank assemblages (F = 2.51, P = 0.02) (Figure 4e).

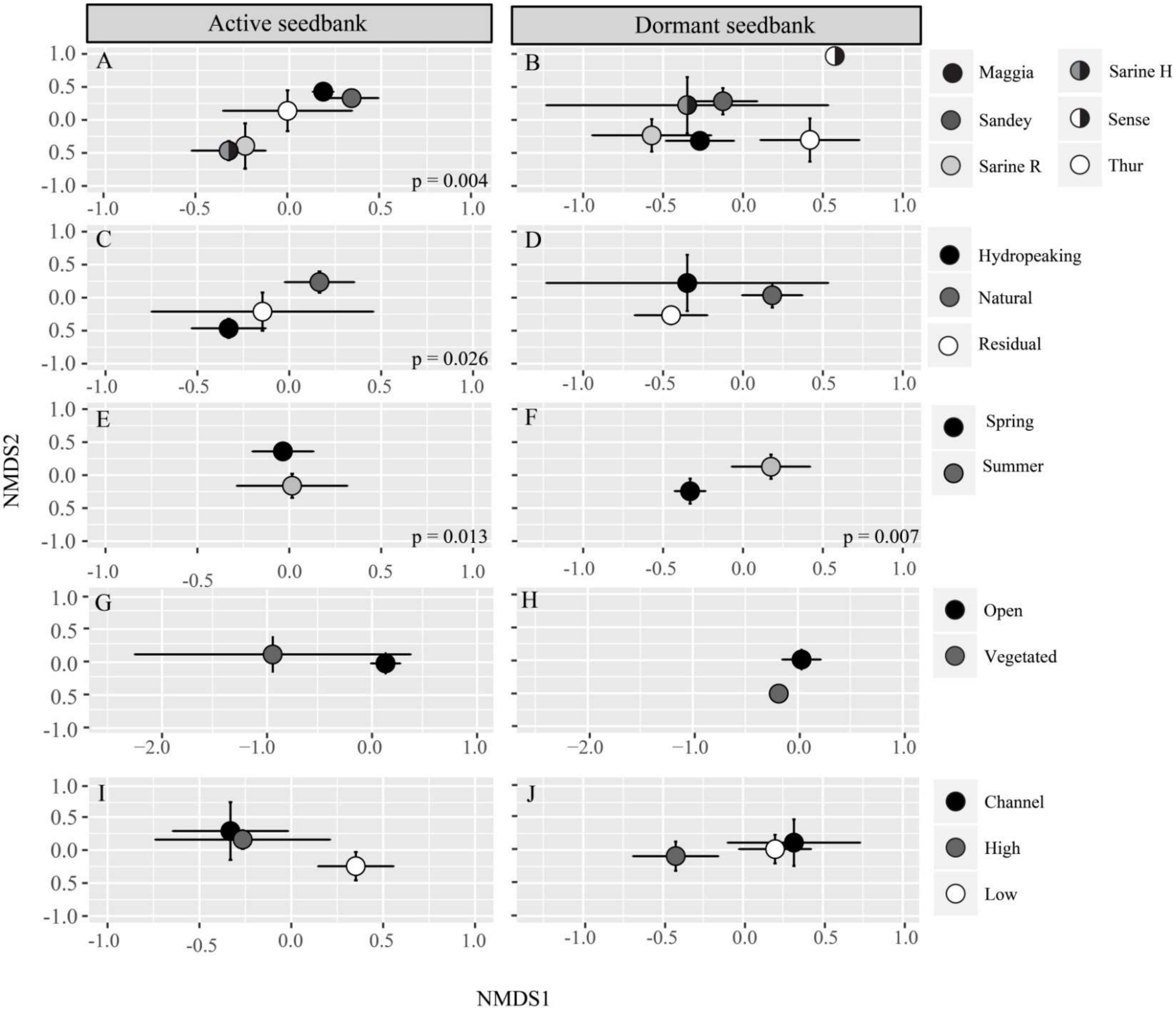

Figure 4: Non-metrical multidimensional scaling (NMDS) ordination of the aquatic macroinvertebrate assemblages. Symbols show mean ± SE of group scores. A and B show NDMS by river; C and D by hydrological regime; E and F by season, G and H by height of gravel bar; and I and J by type of gravel bar. Note that panels G and H have a different NMDS1 scale. P values are shown when PERMANOVA test indicated significant differences in community composition. Sarine R: Sarine residual; Sarine H: Sarine hydropeaking.

Active seedbank assemblages of non-vegetated and vegetated gravel bars had a non-significant dissimilarity of 39% (F =1.06, P = 0.35). Secondary channel and high bar assemblages clustered together in the NDMS plot with a dissimilarity of 70% (Figure 4i), while low bar assemblages were situated on the right side of the plot and had higher dissimilarity values with secondary channel (75%) and high bar (71%) assemblages.

Dormant seedbank assemblages of the Maggia, Sandey and Sarine rivers were similar (mean dissimilarity = 61%), while the Thur River was on the right side of NMDS (stress= 0.09) plot with a higher mean dissimilarity (75% on average). The Sense dormant seedbank assemblage was located in the upper-right corner of the plot, although differences with other rivers were not significant (PERMANOVA, F = 1.2, P = 0.19. The hydrological regime groups clustered in the center of the NMDS plot and did not significantly differ (F = 1.48, P = 0.14). Spring and summer dormant seedbanks were significantly different (F = 3.42, P = 0.007), having a dissimilarity of 72% (Figure 4f). No differences were found between non-vegetated and vegetated dormant seedbank assemblages (F = 0.5, P = 0.89). Lastly, dormant seedbank assemblages of secondary channels and low bars clustered together, while high bar assemblages were situated on the left side of the plot, showing non-significant differences (F = 0.5, P = 0.9).

Discussion

Here we examined the active and dormant macroinvertebrate seedbanks of floodplain gravel bars of regulated rivers differing in hydrological regimes. Importantly, we found active and dormant seedbanks in the gravel bars at all rivers, although seedbank presence varied spatio-temporally and with hydrological regime. Further, gravel bar seedbank assemblages also differed among rivers, suggesting local conditions likely influence seedbank dynamics. For instance, the Thur River seedbanks differed significantly from seedbanks of the Sandey and Sense rivers, although these rivers had near natural flow regimes. In this case, the Thur River was channelized and the gravel bars were recently re-established through restoration measures (Schirmer, 2014), the Sandey Floodplain and main channel are influenced by constructed levees (Doering et al., 2012), while the Sense site was a braided floodplain with inherent channel changes during high flows. The Sarine River sections (hydropeaking vs residual flows) also differed in seedbank densities dynamics, but showing a similar assemblage compositions, further attesting to the importance of local site conditions on macroinvertebrate seedbanks development. Similar results were found by Paetzold et al. (2008) where local site conditions were most important in determining terrestrial arthropod assemblages. Hydrological regime was a key factor influencing the density, taxa richness and assemblage composition of gravel-bar seedbanks, active seedbanks in particular. In rivers with a natural flow regime, aquatic macroinvertebrates inhabiting streams have adapted to the flow pulses allowing them to evolve life history strategies for gravel bar habitats (Lytle *et al.*, 2008). Bruno *et al.* (2013) showed that hydropeaking waves increased the drift of invertebrates, especially Chironomidae. In rivers with hydropeaking regimes, gravel bars are flooded more frequently, daily in many situations, depositing drift organisms once flows decrease. The increased frequency of high flows keeps gravel bar sediments moist, allowing some active taxa to tolerate the lack of water for a few days (Stanley *et al.*, 1994; Robinson & Buser, 2007). Such conditions also may explain the lack of a dormant seedbank since macroinvertebrates with suspended animation strategies are likely not adapted to the altered hydrology regime (Danks, 2000; Tronstad et al., 2005). The fact that hydropeaking increase deposition of fine sediment in gravel bar (Sear, 1995) may limit the use of gravel bars by dormant aquatic insects due clogged situation of interstitial spaces. Lastly, gravel bars in rivers with residual flows had lower densities than those with natural flows. This is likely due to the lack of hydrological lateral connectivity between the main channel and adjacent gravel bars(reduced flow pulses), decreasing the possibility of aquatic macroinvertebrates to reach gravel bar sediments at predictable periods (Ward & Stanford, 1995).

Gravel bar seedbanks (active and dormant) had higher densities in spring than summer. High flows are typical in spring in rivers with natural flow regimes but also systems under regulated flows as storage capacities of reservoirs become exceeded. These high flows allow access by aquatic macroinvertebrates to inundated gravel bars, whether through active immigration or passively due to drift. Likewise, once the animals get established in a gravel bar, and the humidity decreases, several species need to form desiccation resistant (suspended animation) stages to deal with the new dry conditions. The increased dispersal rate during spring flooding events may explain the higher rates of dormant seedbank densities in spring than in summer, when the possibilities to colonize gravel bars because of water level raise are lower. Some of the dormant stages found in spring can be as well part of the dormant stages formed during the previous fall/winter seasons, when gravel bars go dry due to the lack of high flow events. Extreme summer conditions may also explain the low numbers of active and passive seedbank. Exposed gravel bars can reach temperatures higher than 37-42°C (Tonolla *et al.*, 2010), inducing a decrease in species survival due to temperature and arid intolerances (Andersen, 1986).

Although presence of active seedbanks was greater in secondary channels and low bars compared to high bars, density of invertebrates was lowest in secondary channel than in the other heights. These results can be explained by the greater probability of the lower habitats (low gravel bar and secondary channel) to become inundated at lower high flows in which high bar habitats remain dry. However, the low density suggest that the conditions in secondary channels might not be adequate to survive as active or dormant seedbank, maybe due to the higher presence of predators (e.g. spiders, carabid beetles) in such terrestrial aquatic ecotones (Hering & Plachter, 1997; Paetzold et al., 2005).

We found a variety of different taxa in gravel bar seedbanks, as both active and dormant life cycle stages. Chironomidae and Oligochaeta represented over 80% of seedbank macroinvertebrates, representing 93% of dormant assemblages in particular. Similar results were found by Datry et al. (2012) and Stubbington *et al.* (2016), where most invertebrates found after rewetting dry sediments were Chironomidae and Oligochaeta. These groups are known to form cocoons and cysts to resist long periods under dry conditions (Boulton, 1989; Montalto & Marchese, 2005; Tronstad et al., 2005). Additionally, Castella *et al.* (1984) reported that macroinvertebrates can present distinctive communities as a consequence of morphological and hydrological conditions of the channels, which may explain the differences among hydrological regimes and habitats.

Ecological and management implications

Because most terrestrial arthropods inhabiting gravel bars feed on aquatic macroinvertebrates (Paetzold et al., 2005; Paetzold *et al.*, 2006), alterations in the densities and composition of active and dormant seedbanks in gravel bars due to flow regime modifications likely generate bottom up changes in food webs. Changes in flood cycles not only can cause food web changes in rivers but also can dramatically affect basic life-history traits of invertebrates. Species diversity dynamics are closely linked with disturbance frequency and the ability of the species to resist disturbance or rapidly recolonize newly disturbed environments. Therefore, assessment of disturbance on biodiversity dynamics is paramount to developing biomonitoring and resource management strategies (Folke *et al.*, 2004). Kennedy *et al.* (2016) showed that water fluctuations produced by hydropeaking negatively affected macroinvertebrate abundance by exposing egg masses to desiccation and reducing immigration. Likewise, the lack of flow pulses in rivers with residual flows causes channel homogenization as well as a loss in hydrological connectivity between rivers and adjacent floodplains (Ward & Stanford, 1995; Poff et al., 1997). Changes in flow regime and homogenization further impact biodiversity across the river drainage, whereby reduced river connectivity and habitat heterogeneity negatively impacts macroinvertebrate biodiversity (Finn *et al.*, 2011; Seymour *et al.*, 2016). Therefore, hydrological alteration should be consider a major issue affecting not only flow but many components of river ecosystems, such us biodiversity, food webs and organic matter/nutrients dynamics. Managing programs should predict site specific impacts and include mitigation measures based on the current research and experiences (Bruder *et al.*, 2016).

In summary gravel bars should be considered as key habitat not only for terrestrial animals but also for aquatic animals, both active and dormant, playing a special role for resilient of river ecosystems as well as to maintain food web structure. This study adds a new perspective for gravel bars in conservation, restoration and management, demonstrating that gravel bars should be taken into account as well when assessing biodiversity and in river management.

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Chapter 3

Title: Ecological assessment of a sediment by-pass tunnel on a receiving stream in Switzerland

Short title: Ecological assessment of a sediment by-pass tunnel

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Abstract

Reservoir siltation is a major problem worldwide, decreasing reservoir storage capacity, trapping entrained sediment, and altering the natural sediment regime. Sediment By-pass Tunnels (SBT) are used to connect reservoirs with downstream receiving waters during high flows to reduce sediment accumulation in the reservoir. When operating, large volumes of sediment-laden waters are released into the receiving river for short periods of time (hours). The aim of this study was to assess the impact of SBT events on the downstream riverine ecosystem. We measured physico-chemistry, sediment respiration, periphyton biomass and chlorophyll-a, and macroinvertebrate assemblages along a 5 km stretch of river during the first two years of SBT operation. During the study, 5 major SBT events occurred. Few changes were found in physico-chemistry, and mainly due to the input of tributaries entering the system. Results showed a clear reduction in sediment respiration, an indicator of ecosystem metabolism, especially after large SBT events. Periphyton levels and macroinvertebrate density/richness also decreased after SBT events. A non-metric dimensional scaling (NMDS) distinguished both temporal and spatial shifts in macroinvertebrate assemblages after SBT events, being related to downstream distance and SBT event magnitude. Based on these results, the use of SBT events should be incorporated in the adaptive management of downstream receiving waters towards mitigating regulated flows (e.g., as e-flows) and sediment deficits (e.g., sediment replenishment), thereby simulating more natural flow/sediment regimes in impounded rivers.

Keywords: sediment replenishment, environmental impact, floods, reservoir, sediment respiration, macroinvertebrates.

Introduction

The number of large dams are increasing worldwide due to growing demands for water supplies and energy, thus being one of the greatest man-made modifications of natural flow/sediment regimes in rivers (Nilsson *et al.*, 2005). Besides the 50,000 large dams (>15 meters in height) existing in the world, 3700 new dams are planned for the near future (Nilsson et al., 2005; Zarfl *et al.*, 2014). These large dams retain about 99% of upstream sediment delivery in reservoirs (Williams & Wolman, 1984) and decrease reservoir storage capacity by ca. 570 km^3 annually (Williams & Wolman, 1984; Sumi *et al.*, 2004). Besides the well-documented ecological and morphological effects on downstream waters (Ward & Stanford, 1979; Brandt, 2000; Graf, 2006), sediment accumulation in reservoirs also causes technical problems in reservoir operations (Kondolf *et al.*, 2014; Wang & Kondolf, 2014). To overcome technical problems caused by siltation, dam operators have used different techniques, such as flushing or sluicing of reservoirs, to maintain reservoir capacity while reducing sediment deficits in rivers below dams (Kondolf *et al.*, 2014). However, these techniques have been shown to impact the ecological properties of receiving rivers.

Numerous studies have documented sediment flushing-flow impacts on river morphology (Brandt, 2000) and the negative consequences of sediment deposition on riverine fish and invertebrates (Rabení *et al.*, 2005; Crosa *et al.*, 2010). Nevertheless, some studies have shown that when proper sediment management is adopted, a balance between technical and ecological demands can be reached while ecosystem degradation can be minimized (Espa *et al.*, 2015). An alternative technology in hydrologically and topographically-suitable impounded rivers are Sediment By-pass Tunnels (SBTs), which are used to connect reservoirs with downstream receiving waters (Sumi *et al.*, 2004). SBTs typically are operated during high flow events, when flows and suspended sediment from upstream enter reservoirs (Auel *et al.*, 2010). In combination with prior reservoir lowering, high flow events can mobilize and transport large volumes of accumulated sediments through the SBT. In some countries, such as Switzerland and Japan, SBTs are fairly common with 12 tunnels currently operating in Switzerland and more planned for construction (Kondolf et al., 2014). Unfortunately, SBTs are being increasingly used despite a lack of knowledge on the ecological consequences to downstream river/floodplain ecosystems. We are aware of only one study that assessed the ecological impact of SBT operations (Sumi *et al.*, 2012), but they did not examine the longitudinal or temporal effects of SBT inputs. Further, no studies to date have investigated SBT events on ecosystem functioning.

Flow regulation from dams has strongly modified the natural flow/sediment regimes of rivers and associated floodplains, thereby influencing water quality, physical habitat and biotic interactions among others (Poff *et al.*, 1997; Wohl *et al.*, 2015). In turn, these changes have lead to ecosystem degradation via river-bed erosion/colmation, habitat loss and homogenization, and organic matter accumulation (Williams & Wolman, 1984; Brandt, 2000). During the last decades, management programs focusing on flow regimes have been successfully implemented (Robinson, 2012; Olden *et al.*, 2014), whereas other similar programs have shown deficiencies by neglecting sediment dynamics (Bhowmik & Demissie, 1989; Yang *et al.*, 2011). SBTs appear to be a potential management option that could integrate more natural flow and sediment regimes in rivers below dams while still reducing siltation in reservoirs. As with environmental flows, the magnitude, frequency and duration of SBT events must be considered in respect to sediment delivery loads if SBTs are to be used in an optimally ecological manner to improve sediment regimes in managed rivers. Being a rather new management strategy, there is essentially nothing known on the ecological effects of SBT operations on receiving waters.

The primary goal of this study was to investigate the ecological impacts of SBT events in a Swiss river during the first years of operation in order to gain a better understanding of SBT use in flow/sediment regime management. We hypothesized a reduction in ecosystem properties such us organic matter processing, primary production and macroinvertebrate community composition due to the high scouring power of SBT events, with flow magnitude/duration and sediment amount as key factors influencing ecosystem response variables. Further, we expected that tributaries will have an important role in recolonization by macroinvertebrates and organic matter inputs in the system following such events. We tested our hypothesis by sampling different ecosystem properties along a longitudinal gradient below the SBT. Specifically, hyporheic sediment respiration was used as an indicator of organic matter processing, periphyton biomass as an indicator of primary production and macroinvertebrate assemblages as an indicator of biodiversity response to SBT events.

Study site description

The study was conducted in a lower section of the Albula River, Canton Grisons, in southeast Switzerland (Figure 1). The Albula is ca. 40-km long and drains a 950 km^2 catchment with an average elevation of 2300 m a.s.l. Headwaters flow from the Bergün mountains before converging as the Albula river, which then flows into the Vorderrhein river, a tributary of the Rhein river. The Albula is a 6th order river with a mean discharge of 15 m^3/s. Natural flow peaks occur in spring/summer due to snowmelt and precipitation; the HQ100 is >130 m^3/s. The Albula, together with the Julia River, is impounded at the Solis reservoir, built in 1986 and located just downstream of the town of Tiefencastel. The Albula river represents 95% of the natural inflow while Julia only 5%. Below the dam, the river flows through a narrow canyon with an average basal-width of about 25 m. Residual flow in the river below the dam is around 1 m^3/s. Three main tributaries (Rain Digl Lai, Grossbach and Prodavosbach) join the Albula in the canyon stretch, providing additional flow and being potential sources of sediment (Fig. 1).

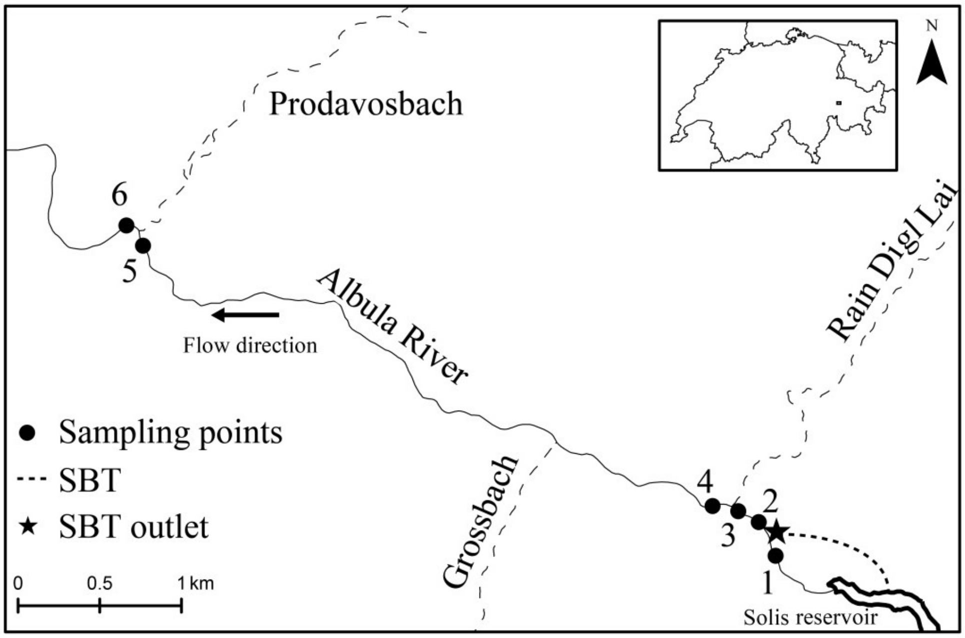

Figure 1: Map of the study stretch below Solis reservoir showing the study sites. SBT = sediment bypass tunnel.

A Sediment By-pass Tunnel (SBT) was built at Solis in 2012 to reduce siltation of the reservoir. The tunnel is 973-m long, 4.5 x 4.7-m in size, has a 1.9% slope and flow capacity of 170 m^3/s, and connects the middle part of the reservoir with the downstream receiving river at ca. 300 m below the dam. The tunnel is operated during high flow events when large volumes of sediment-laden water enter the upper reservoir (Auel et al., 2010). The 5-km study section was located downstream of Solis dam. Six sampling sites were situated along the stretch to account for longitudinal distance effects and potential flow/sediment inputs from two major tributaries. Site 1 was ca. 50 m upstream of the SBT outlet and used as a control site unaffected by SBT events. Site 2 was ca. 200 m downstream of the SBT outlet. Sites 3 and 4 (400 and 500 m downstream) were situated above and below the first tributary (Rain Digl Lai), whereas Sites 5 and 6 (4.9 and 5.0 km downstream) were above and below the lower tributary (Prodavosbach) (Figure.1). The third major tributary (Grossbach, ca. 1.5 km downstream) was inaccessible and thus not included in this study. As a normal dam operation, spillwater and bottom outlet releases occur throughout the year, affecting all study sites.

Methods

Sediment by-pass tunnel operation and sampling campaigns

The study took place during 2014 and 2015 and included 5 separate SBT events that differed in their physical characteristics (Table 1). For instance, SBT events showed differences in maximum discharge through the tunnel, reaching a maximum discharge of 179 m^3/s during August 2014 operations. The maximum total discharge also fluctuated among events, from more than 270 m^3/s in August 2014 to only 62 m^3/s in June 2015. The difference between maximum SBT discharge and the maximum total discharge was caused by simultaneous flushing releases during SBT operations (Figure 2). The total sediment released through the tunnel depended on the elevation of the lake during each operation (unpublished data, Hagmann, M.). Flushing releases also were used to flush fine sediments deposited on the river bed after each SBT event (Figure. 2).

Table 1: Sediment bypass tunnel events in 2014-2015. Maximum discharge through the bypass tunnel (Max SBT Q, m^3/s), maximum discharge during an event in the canyon including spillwater and bottom outlet release from the dam (Max tot Q, m^3/s), accumulated sediment bypass tunnel discharge during an event duration (Accum. SBT.Q, m^3), event duration (hours), and sediment transported when the tunnel was operating (Sediment, m^3).

Event	Max SBT Q (m^3/s)	Max tot Q (m^3/s)	Accum. SBT Q (m^3)	Event duration (h)	Sediment (m^3)
23/05/2014	87.2	115.3	2,763,764	10.5	9,973
29/06/2014	113.9	173.4	1,708,560	5.75	12,228
13/08/2014	179	273.7	7,407,582	14.5	31,762
15/05/2015	107.6	107.6	2,432,669	11.25	96,775
09/06/2015	62	62	1,117,974	8.5	51

Sampling campaigns were conducted five times each year in late spring, summer and early autumn, when the possibility of having a high flow event was greatest (high flow events are weather related and thus unpredictable). Sampling dates were adjusted each year to account for sampling after a particular SBT event, although a known pre-event sampling was performed in May of each year (Figure 2). In 2014, three major SBT events occurred. After the first SBT event in late May, sampling was conducted just after flow returned to residual levels. Two major SBT events then occurred the following two months, but sampling was postponed until after the last event in August due to flushing releases maintaining high flows in the canyon. Two further sampling campaigns were conducted in September and November 2014 to examine recovery following these major SBT events. The first SBT event in 2015 also occurred in late May with a post event sample collected soon after (Figure 2). Another SBT event occurred in June 2015 followed by flushing releases over a number of days. Sampling campaigns took place once flows returned to residual levels in July, September and October 2015.

Flow regime and physico-chemistry of study sites

Inflow and discharge data were obtained by the company (EWZ) operating the dam. On each sampling date, a 0.5-litre water sample was collected at each site for chemical analysis in the laboratory. Water samples were filtered (cellulose nitrate filter 0.45 µm, Sartorius Stedim Biotech) and analyzed for dissolved organic carbon (DOC), total organic carbon (TOC), nitrate-N (NO_3-N), phosphorus (PO_4-P) and total phosphorus (TP) using methods described in detail in Tockner *et al.* (1997). Electrical conductivity (E.C. at 20°C) and temperature were measured in the field using a portable conductivity meter (WTW, Germany).

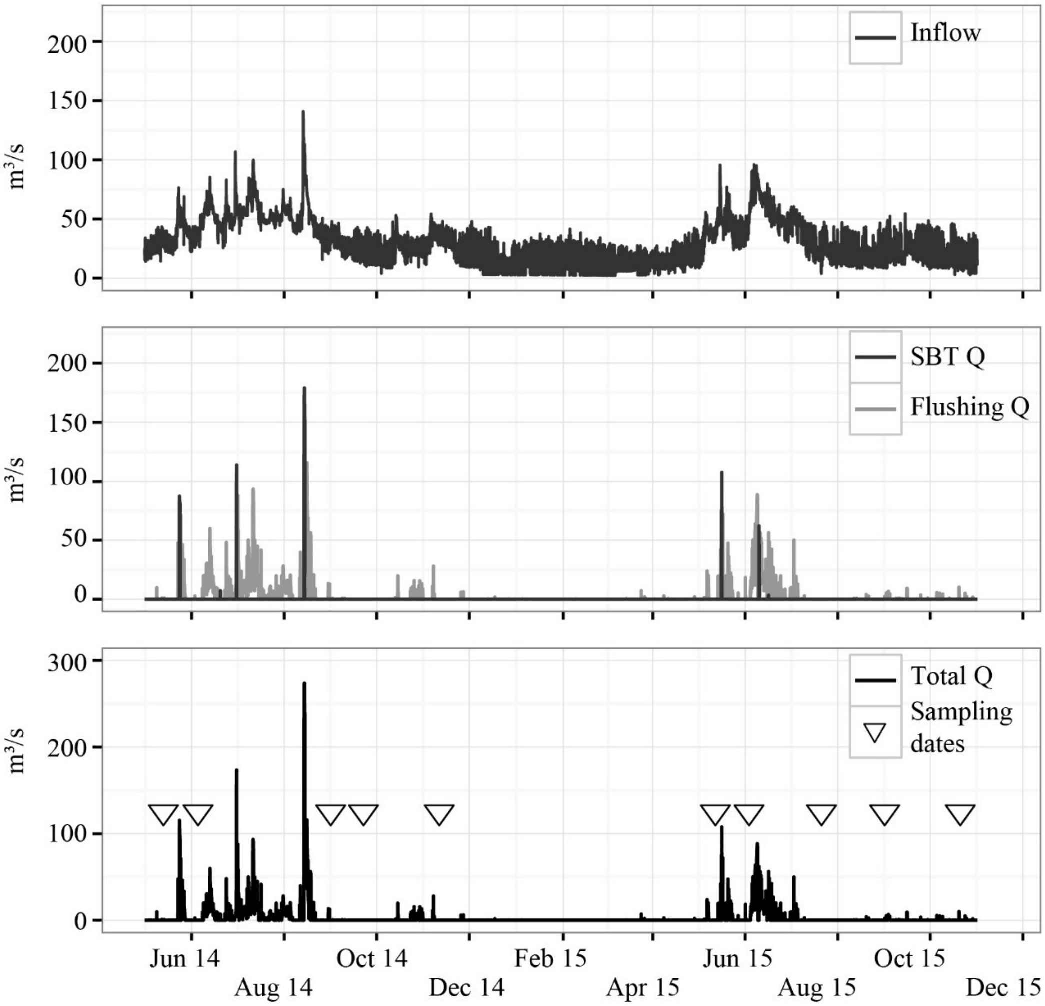

Figure 2: Inflow of Solis reservoir and discharge of the Albula River in 2014-2015 below Solis reservoir. Upper panel shows inflow of the reservoir, middle panel shows discharge from the Sediment Bypass Tunnel (SBT) and Spillwater + Bottom Outlet (Flushing Q). Lower pannel shows total discharge (Total Q) through the canyon and sampling dates (triangles).

Sediment respiration, benthic organic matter and sediment size distribution

Hyporheic sediment respiration (SR, n = 3 per site and date) was measured as change over time in dissolved oxygen concentration. Plexiglas® tubes (5.2 cm diameter, 32 cm long) were used to incubate hyporheic sediments (Uehlinger *et al.*, 2002). The top 10-15 cm of the streambed were removed first to avoid respiratory effects of epilithic periphyton. Sediment was sieved to eliminate particles >8 mm and standardize samples among sites (Doering *et al.*, 2011). Each tube was half-filled with sediments and the remaining portion filled with stream water, closed using rubber stoppers, and then buried into the streambed for 3 to 4 hours for incubation. Oxygen concentration and temperature were measured before and after incubation using a portable oxygen meter (Hach HQ40d connected to a LD10101 oxygen probe). After incubation, the contents of each tube were stored at -20°C for later analysis of organic matter. Based on the consumption of O_2 in the tube (r; g O_2 m^{-3} h^{-1}), respiration per kg of sediment was calculated (R, mg O_2/ kg h^{-1}) as follows:

$$R = r\ Vw / Gw$$

where Vw was the water volume in the tube (m^3) and Gw the weight of dry sediment (kg). R was then normalized using the Arrhenius equation at a reference temperature of 20°C to account for seasonal variation in water temperature:

$$R_{20°C} = R_T / 1.072^{\,T\text{-}T20°C}$$

where $R_{20°C}$ is respiration rate at 20°C and T is water temperature in the tube at the end of the incubation as described in Naegeli & Uehlinger (1997). In the laboratory, coarse organic matter (CPOM, >2 mm) was separated from sediments using a 2-mm sieve. CPOM samples were dried at 60°C for 48 h, weighed, combusted at 450° for 4 h and reweighed. Sediments, together with organic particles <2 mm and strongly attached organic matter, were dried at 60°C for 48 h, combusted at 450°C for 4 h and reweighed to determine fine particulate organic matter (FPOM). CPOM and FPOM were expressed as g of ash-free dry mass (AFMD)/kg sediment. Combusted sediments were sieved to separate grain size fractions >8 mm, 8-4 mm, 4-2 mm, 2-1 mm, 0-1 mm, 63 µm, and < 63 µm, and the median grain size (d_{50}) was calculated using Gradistat v8 (Blott & Pye, 2001).

Periphyton and macroinvertebrates

Five cobbles were randomly collected from each site and date, stored in plastic bags and kept at -20°C until analyzed. Periphyton was removed from the surface of each cobble using a metal brush and rinsed with deionized water. Two subsamples of the suspension were filtered through Whatman GF/F filters. One filter was dried at 60°C for 24h, weighed, combusted at 450°C for 4 h and reweighed for determination of ash-free dry mass. The other filter was used for chlorophyll-*a* analysis. Chlorophyll-a was extracted with hot ethanol and analysed by HPLC (Meyns *et al.*, 1994). The surface area of each cobble was calculated by wrapping the stone with aluminium foil and using a weight-to-area relationship (Bergey & Getty, 2006).

Three benthic samples were collected from each site/date using a Hess sampler (250-um mesh, 0.04 m^2 area) and preserved in the field with 70% ethanol. Concurrently, samples from tributaries were collected in 2015 to use as a reference. In the laboratory, macroinvertebrates were handpicked using a stereomicroscope (10x magnification), identified to family level (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Crustacea) or order level (Oligochaeta) and counted. Macroinvertebrate density and taxa richness were calculated for each sample.

Data analysis

The coefficient of variation (CV) was used to examine the temporal variation of physico-chemical characteristics among sites. Physico-chemistry measures were analyzed comparing all data among sites using principal component analysis (PCA) on log-transformed data. Normal data ellipses (main stream versus tributary) were generated with the standard probability of 0.69.

Rates of measured ecosystem properties (SR, periphyton biomass and chl-a, and macroinvertebrates density and taxa richness) at each site were compared to rates at Site 1 at residual flow (May 2014 and May 2015, respectively) to calculate the percentage rate of change after events. A two Way ANOVA on log(x+1) transformed data followed by post hoc Tukey's test was used to compare rates at affected sites (2-6) with non-affected Site 1. A stepwise multiple regression on log(x+1) transformed data was used to determine what predictive factors (distance to tunnel outlet, Max SBT Q, accumulated SBT Q, amount of sediment transported and duration of each event) influenced measured ecosystem properties. Due to collinearity, accumulated SBT Q and event duration were dropped from the model. Data from Site 1 were excluded in this analysis, since this site was not affected by SBT events. Variables were excluded in a backward direction when the Akaike Information Criterion (AIC) values of the alternative models were lower and the variables involved were significant (based on ANOVA). Relative variable importance was calculated according to the metric '*LMG"* using the package 'relaimpo' in R (Grömping, 2006).

Changes in macroinvertebrate composition were examined using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance and calculated on log (x+1) transformed densities. Two NMDS analyses were carried out, one by-site to examined longitudinal patterns, and one by-date to examined temporal patterns. Samples from sites non-affected by SBT events (Tributaries and Site 1) were excluded in the by-date analysis to avoid interference with the affected samples. Analysis of Similarity (ANOSIM) was conducted to test for among-group differences. All analyses were carried out using R software (R Development Core Team, 2015).

Results

Flow regime and physico-chemistry

Timing and magnitude of the events matched the occurrence of floods in the system (Figure**.** 2). Daily fluctuations in flow were caused by hydropeaking by an upstream dam in the Julia river and other artificial inflows from other upstream reservoirs connected by pipes. The main physico-chemical differences were found between main stream and tributaries. DOC and TOC concentrations were similar among stream sites and tributaries, although stream sites showed greater temporal variation (CV stream: DOC 36%, TOC 45%; CV tributaries: DOC 17%, TOC 22%) (Table 2). Nitrate concentrations were high in both tributaries (on average 0.57 mg N/l) and temporally stable (CV = 17% on average for both tributaries), thus causing higher values at Sites 5 and 6 (on average 0.45 mg N/l) than sites upstream (on average 0.31 mg N/l). Electrical conductivity was higher in the main river (on average 430 µS/cm) than in the tributaries (on average 376 µS/cm) and temporally constant at sites not affected by tributaries. Phosphate in tributaries showed the greatest CV (71%). The PCA revealed 2 different groups with main stream samples situated in the upper part of the plot and tributaries on the left-down side of the plot (Figure 3). The first PCA axis (PC1) explained 41.5% of the variance and was correlated with DOC and TOC, while PC2 explained 19.9% of the variance and was correlated to NO_3 and TP.

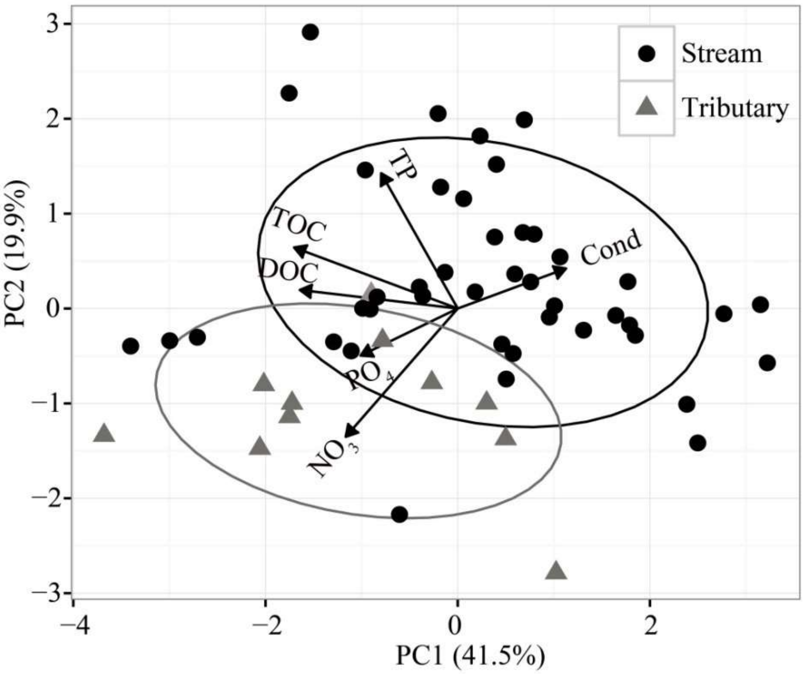

Figure 3: Scatterplot of the principal components analysis. The first two axes explained 61.4% of the variation among sites and dates. Normal data ellipses were generated with a standard probability of 0.69.

Sediment respiration, benthic organic matter and sediment size distribution

SR showed high spatial heterogeneity under residual flow conditions, ranging from 0.5 to 1 mg O_2/kg sed h^{-1}, but with no differences between Site 1 and Sites 2-6 ($p = 0.96$). All sites showed a decrease in sediment respiration after the first SBT opening in 2014 Figure. 4a). Sites downstream of the SBT showed decreases of 27% on average, while Site 1 decreased 15% due to flushing flows ($p = 0.33$). In 2014, the reduction in SR was greatest after the summer SBT events, the highest magnitude flows during this study. Sites below the SBT outlet decreased by ca. 60% of initial SR rates while Site 1 showed a significantly lower decrease of only 28% ($p = 0.048$). In September 2014, SR at Site 1 increased two-fold to 1.29 mg O_2/kg sed h^{-1}, while SR increased by only 20% at Sites 2-6 ($p<0.001$) (Figure 4a). A flushing release in October 2014 caused a decrease in SR at Sites 1-3 and an increase at Sites 5-6.

Table 2: Chemical characterization of each study site (2014-2015).

Parameter		*n*	DOC mg C/l	TOC mg C/l	NO_3 mg N/l	PO_4 µg P/l	TP µg P/l	Cond µS/cm 20°C
Site 1	mean	10	0.73	0.9	0.3	2.3	10.8	454.6
	SD		0.29	0.3	0.06	0.6	5.4	35.9
	CV		39.7	33.3	20.0	26.1	50.0	7.9
Site 2	mean	10	0.76	1.03	0.31	1.9	8.7	462.8
	SD		0.22	0.45	0.06	0.7	7.1	34.8
	CV		28.9	43.7	19.4	36.8	81.6	7.5
Site 3	mean	10	0.75	1.09	0.32	1.7	16.4	465.9
	SD		0.27	0.52	0.07	0.6	12.4	34.1
	CV		36.0	47.7	21.9	35.3	75.6	7.3
Site 4	mean	7	0.84	1.14	0.36	2.9	12.9	429.9
	SD		0.26	0.4	0.05	2.3	6.4	18.3
	CV		31.0	35.1	13.9	79.3	49.6	4.3
Site 5	mean	7	0.89	1.16	0.45	1.7	16.9	409.2
	SD		0.35	0.49	0.16	1.2	11.8	53.5
	CV		39.3	42.2	35.6	70.6	69.8	13.1
Site 6	mean	8	0.75	0.98	0.44	1.4	13.4	399.1
	SD		0.34	0.33	0.18	1.1	13.9	55.2
	CV		45.3	33.7	40.9	78.6	103.7	13.8
Tributary 1	mean	6	0.94	1.14	0.5	2.6	10.7	365.9
	SD		0.11	0.12	0.06	1.6	5.6	35.1
	CV		11.7	10.5	12.0	61.5	52.3	9.6
Tributary 2	mean	7	0.86	1.09	0.64	2.9	10.5	387.8
	SD		0.19	0.36	0.14	2.3	4.8	29
	CV		22.1	33.0	21.9	79.3	45.7	7.5

SR declined significantly at Sites 2-3 after the first SBT event in 2015 (54% and 85%, respectively), while SR increased by 9% at Site 1 (p = 0.01) (Figure 3b). A month later, SR at Site 1 increased to ca. 30% greater than rates before the first SBT event in 2015, showing significant differences with affected sites (p = 0.03). Here, SR at Sites 2-3 were 15% and 50% of initial rates, whereas SR at Site 4 decreased to 0.28 mg O_2/kg sed h^{-1}. In September 2015, SR at Site 4 almost doubled and remained the same until the end of the study. Sites 5-6 showed a similar pattern with increases in SR at the end of the study period. Stepwise regression showed that respiration was related to maximum SBT Q and sediment amount of each event ($R^2 = 0.22$), with both variables showing similar relative importance (Table 3).

FPOM levels were an order of magnitude greater than CPOM levels in hyporheic sediments (Figure. 4c-f). FPOM differed among sites, whereas CPOM varied little among sites with similar values at all sites over time; an exception was a peak value in CPOM at Site 3 in September 2015 (0.8 g AFDM/kg sed). The d50 values in sediment size increased at Sites 2-4 after the first SBT event in 2014 (Figures 4g,h), but returned to pre-event d50 values by the next sample date. Sediment size at Sites 1, 5 and 6 remained essentially the same through 2014. After the first SBT event in 2015, sediment sizes at Sites 2-3 were very sandy (0.78 and 0.25 mm, respectively), which persisted until the end of the study at Site 3. The d50 sediment size remained basically the same at the other sites throughout 2015, and d50 sediment size at Site 2 increased to pre-event values within 2 months (Figures 4g,h). FPOM amounts were related to the distance to the tunnel outlet (95% of importance) and the amount of sediment in each event (5% of importance) ($R^2 = 0.37$), while CPOM levels were related with the distance to the tunnel and to maximum discharge ($R^2 = 0.13$). The variation in d50 was explained only by sediment content ($R^2 = 0.19$) (Table 3).

Table 3: Stepwise multiple regression on ecosystem properties (response variable) against predictive physical variables. Significance level of single factors : *p <0.05, **p <0.01, ***p <0.001.

Response variable	R^2	Predictive variables	Relative importance %	p-value
Respiration	0.22	Max SBT Q	56	*
		Sediment	44	***
FPOM	0.37	Distance	95	***
		Sediment	5	*
CPOM	0.15	Distance	55	**
		Max SBT Q	44	**
Substrata d50	0.19	Sediment	100	***
Periphyton Biomass	0.43	Distance	8	*
		Max SBT Q	47	***
		Sediment	44	**
Periphyton Chlorophyll a	0.46	Max SBT Q	100	***
Macroinvertebrate Density	0.34	Max SBT Q	100	***
Macroinvertebrate Richness	0.25	Distance	10	*
		Max SBT Q	90	***

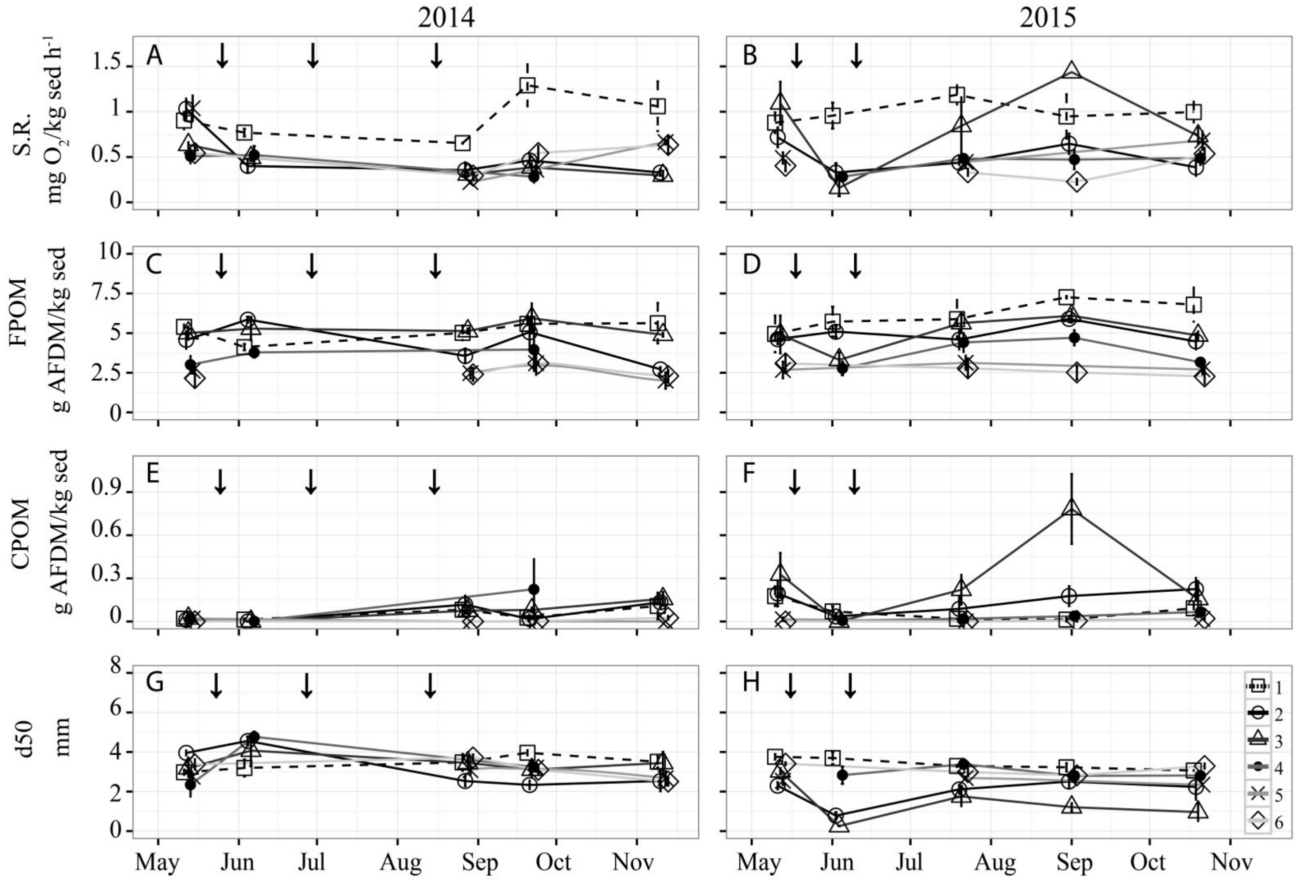

Figure 4: Temporal changes in sediment respiration (S.R) per kg sediment < 8 mm (mg O^2/kg sed h^{-1})(A, B), fine particulate organic matter (FPOM, g AFDM/kg sed)(B, C), coarse particulate organic matter (CPOM, g AFDM/kg sed)(E, F) and median grain size (d50, mm)(G, H). All values are means ± S.E. Arrows represent the date of each SBT event.

Periphyton biomass

Periphyton AFDM and chlorophyll-a showed similar response patterns over time to SBT events. Periphyton AFDM decreased at all sites following the first SBT event in 2014 to values near zero (Figures 5a,b). Site 1, only affected by flushing releases from the dam, showed the least reduction in periphyton AFDM, decreasing by 25% (from 8.6 to 6.4 g AFDM/m^2; $p < 0.001$). The reduction in periphyton AFDM was dramatic at all sites; $p = 0.99$) following the large SBT event in summer 2014 (average <1 g AFDM/m^2), followed by a rapid recovery to pre-event levels, showing differences between affected and non-affected sites ($p = 0.003$). Periphyton AFDM then showed a general decrease at all sites in October 2014, displaying significant differences between affected and non-affected sites ($p < 0.001$). After May 2015, all sites showed a reduction in periphyton biomass ($p = 1.0$). Afterwards, periphyton showed a recovery at all sites until the end of the study period regardless of the

June SBT events (all p = 1.0). Stepwise regression indicated that periphyton AFDM was related to distance to the tunnel (8% of importance), maximum discharge (47%) and sediment amount of each event (44%) ($R^2 = 0.43$) (Table 3).

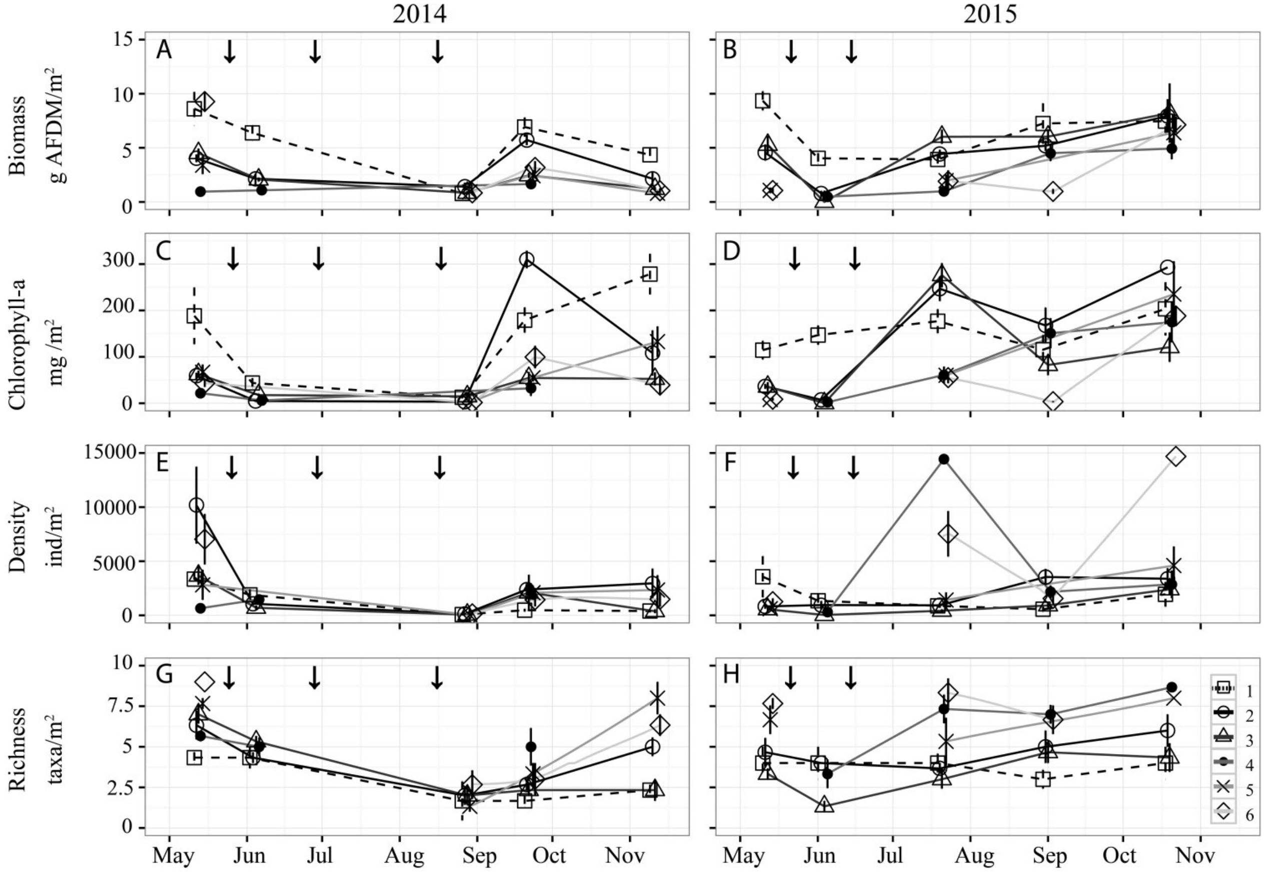

Figure 5: Temporal changes in periphyton biomass (g AFDM/m^2)(A, B) and chlorophyll-a (mg/m^2)(C, D), and macroinvertebrate density (individuals/m^2) (E, F) and richness (number of taxa/m^2)(G, H). All values are means ± S.E. Arrows represent the date of each SBT event.

Periphyton chlorophyll-a decreased at all sites after the first SBT event in 2014 showing at Site 1 a significantly lower decrease than affected sites ($p < 0.001$). Periphyton chlorophyll-a remained low at all sites throughout summer (p = 1.0) before increasing in September (Figure 5c,d). In October-November 2014, periphyton chl-a increased at Sites 1 and 5, decreased at Sites 2 and 6, and remained the same at Sites 3-4. Periphyton chl-a decreased at all sites below the SBT after the first event in 2015, showing differences between affected and non-affected sites ($p < 0.001$) (Figures 5c,d). The second SBT event in 2015 did not reduce periphyton chl-a at any site, with Sites 2-3 actually showing increases in chl-a to >250 mg/m^2. By October, periphyton biomass (AFDM, chl-a) increased to values greater than before the

SBT events of 2015 at most sites. Variation of periphyton chl-a was best explained by maximum SBT discharge ($R^2 = 0.46$) (Table 3).

Macroinvertebrates

Macroinvertebrate densities in the river ranged between 658 ind/m^2 (Site 4) to 10,000 ind/m^2 (Site 2) before the first SBT event in 2014 (Figure 5e-h). Densities at Sites 2 and 3 decreased by 89 and 81%, respectively, after the first SBT event in 2014, but increased at Site 4 by 124% (from 658 to 1475 ind/m^2). Site 1 showed a decrease of 43%, but was not significantly different than affected sites ($p = 0.99$). Densities decreased by 98% at all sites after the summer events of 2014 relative to densities in May ($p = 0.50$) . Most sites still showed low densities two months after the SBT events of 2014, except for Site 4 (Figure 5e-h). In 2015, macroinvertebrate density at Site 1 decreased after flushing flows in May and June, remaining at low numbers until the end of the study. Sites 2-6 showed a similar trend, decreasing after the May and June SBT events and then increasing to values greater than before the SBT events. Site 4 showed a peak in July and Site 6 in July and October, reaching densities up to 15,000 ind/m^2.

Macroinvertebrate taxa richness showed a similar pattern as density in 2014, decreasing on average 22 and 73%, respectively, to the sequential events (Figure 5g-h). Taxa richness increased after the SBT events of 2014 to pre-event levels, being especially evident at Sites 5-6. Taxa richness showed no severe response to SBT events in 2015, although a slight decrease was evident at Site 3 after the first SBT event. Both macroinvertebrate density and richness were related to maximum SBT discharge as well to distance to the tunnel outlet, with distance being relatively less important than maximum discharge (90%) (density, $R^2 = 0.34$ and taxa richness, $R^2 = 0.25$, respectively) (Table 3).

The effects of SBT events on macroinvertebrate assemblages differed between 2014 and 2015 (Figure 6). Macroinvertebrate composition was similar among sites in 2014 (ANOSIM, $R = 0.0$, $p = 0.70$), whereas two distinct groups were evident in 2015 (ANOSIM, $R = 0.5$, $p = 0.001$). In 2015, Sites 1-3 were grouped together as were Sites 4-6 along with the two sampled tributary assemblages. Macroinvertebrate assemblages also changed over time, showing a significant temporal shift after SBT events with a recovery to previous assemblage compositions after the SBT events (Figure s6c,d). For example, assemblages in 2014 shifted to a dominance of Oligochaeta and Chironomidae initially after the SBT events, followed by another shift to a more diverse assemblage as the system recovered (ANOSIM, $R = 0.6$, $p =$

0.001). In contrast, after the first SBT event 2015, assemblages also shifted but returned to pre-event assemblage composition within a month after the events (ANOSIM, R = 0.3, p = 0.001).

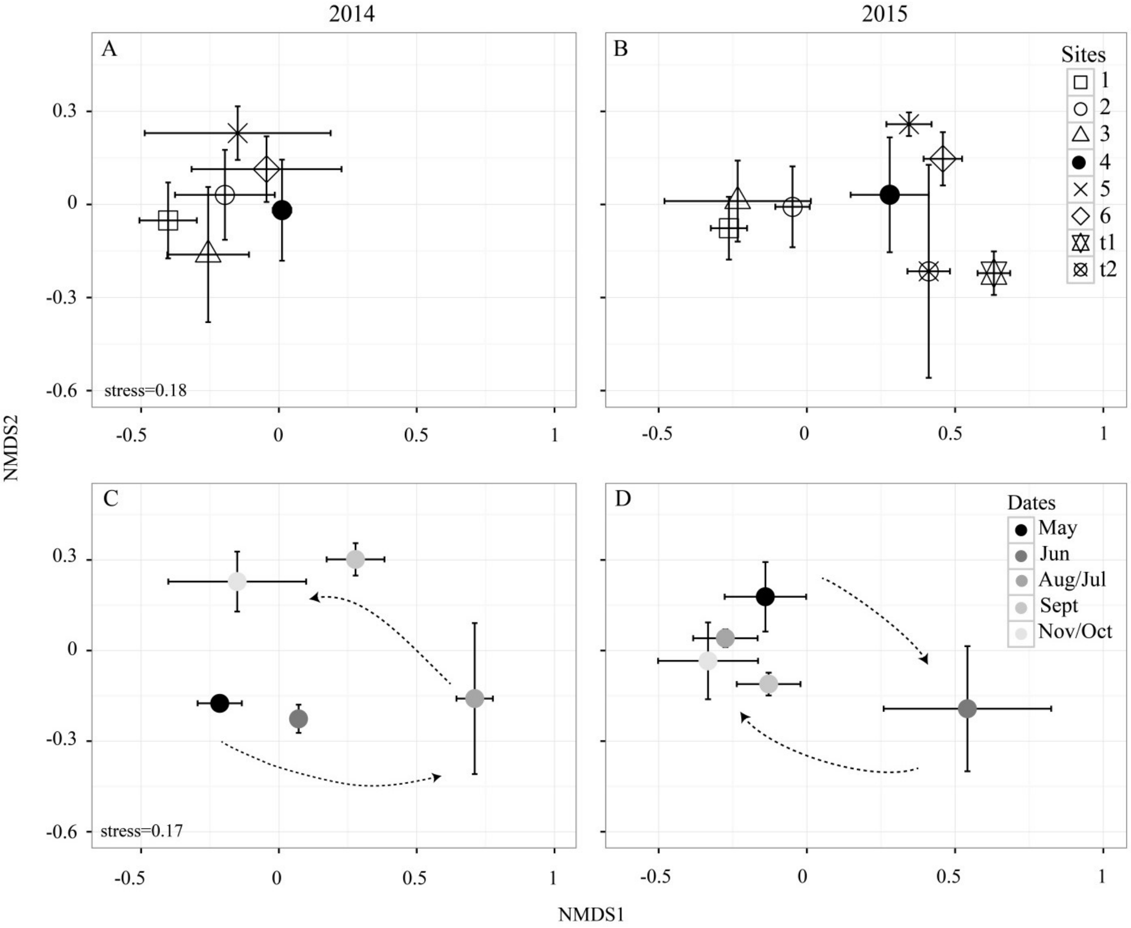

Figure 6: Non-metric multidimensional scaling (NMDS) plots based on benthic macroinvertebrate densities. Plots showing spatial variation among sites (A and B, all dates combined) and temporal variation among dates (C and D, all sites combined) by year. Legend in B applies for panel A, and legend in D applies for panel C. Dotted arrows in panel C and D were drawn by eye to better illustrate temporal changes.

Discussion

One main advantage of SBTs is that their operation characteristics (timing, frequency, magnitude, duration) can simulate natural flow in dam-regulated rivers since they are implemented only during natural high flow events. This is essential in river management since flow pluses are important drivers of biotic and abiotic interactions, organism life histories and ecosystem functioning (Bunn & Arthington, 2002; Lytle & Poff, 2004). SBTs can re-activate the longitudinal dimension of sediment regimes as well, providing sediments to downstream systems impacted by the dam. Therefore, simulating the characteristics of the natural flow/sediment regime is essential if we expect a near natural ecosystem response to floods (Wohl *et al*. 2015). Our results clearly show that specific ecosystem properties respond quite differently to SBT events in relation to flow/sediment related parameters.

SBT events had little influence on physico-chemistry along the study reach, although we observed a tributary influence on water chemistry that clearly reflected the relative flow contribution from tributaries. As shown in other environmental flow studies (Robinson & Uehlinger, 2008), a major change in the chemical make-up of receiving waters from flow releases is not expected as no changes were made to alter the water chemistry upstream. Some short-term changes may occur during the flow event depending on where water is released from the dam (e.g. hypolimnetic versus hyperlimnetic releases), but these were not recorded in our study.

More than 150,000 m^3 of sediment passed through the tunnel into the residual section during the study. It is likely that most of the sediment was transported downstream of the study stretch due to the narrow configuration of the canyon that enhanced flow competence. However, we observed sediment accumulations in wider parts of the canyon in the study section, which can induce the formation of new habitats. Only the large events influenced hyporheic respiration, suggesting small sediment-laden events lacked the competence to mobilize deeper layers of the stream bed (Uehlinger *et al*., 2002), as seen in Site 1 affected by flushing operations. Further, SBT alterations on hyporheic respiration were unrelated to distance from the SBT outlet, showing similar impacts at all sites below the SBT. However, changes in sediment organic matter were associated with distance from the SBT outlet, possibly indicating deposition of organic matter in areas near the outlet. Our hypothesis of tributaries providing organic matter to the river could not be confirmed.

All SBT events reduced periphyton levels and macroinvertebrate densities in the top layer of the stream bed, likely caused by the scouring effects of high flows. This result was expected as similar responses have been observed in other studies of flood (natural and e-flows) effects on rivers (Robinson *et al*., 2004; McMullen & Lytle, 2012; Espa et al., 2015). Biotic response patterns were associated with event magnitude, with larger events having greater impacts and recovery to pre-event communities being faster after smaller events (Robinson, 2012). Tributaries in the section, acting as a source of invertebrates, appeared to enhance the recovery of macroinvertebrate assemblages following SBT events (Robinson *et al*., 2003).

As shown in this study, SBT events can modify key components of ecosystem structure and function. An extreme magnitude or wrong frequency of events could highly modify organic matter decomposition processes, and primary or secondary production in the system, thus having severe ecosystem consequences (Jones *et al.*, 2012; Aristi *et al.*, 2014; Ponsatí *et al.*, 2015). However, the near-natural characteristics of events avoided a permanent ecosystem shift. At the same time, SBT operations increase the flow/sediment variability that often is lost in flow-regulated rivers (Naiman *et al.*, 2008; Petts, 2009). This result suggests the potential of SBTs in balancing technical and ecosystem demands, and thereby improving the sediment regime in rivers downstream of storage reservoirs suffering siltation (after Wohl *et al.*, 2015). In order to reduce the risk of permanent ecological impacts in the long-term management of such riverine ecosystems, the possibility of defining thresholds for SBT flow events (e.g., maximum discharge, sediment concentration) should be considered, as has been implemented in other rivers in terms of sediment management (Crosa *et al.*, 2010).

In conclusion, we found that SBTs, if ecologically implemented, can improve the longitudinal connectivity of sediments of rivers impounded by dams. Indeed, SBT events can be used as environmental flows to simulate more natural flow/sediment regimes of receiving waters. For instance, the physical effects caused by SBT events are likely comparable to natural floods of similar discharge and suspended sediment levels. Determination of SBT event thresholds for each system are recommended to reduce ecological risk from extreme magnitude events that are analogous to a catastrophic flood disturbance (Konrad *et al.*, 2011; Olden et al., 2014). Knowledge regarding the ecological impacts of SBT events is still poor and currently based on other e-flow studies. Consequently, further studies are needed to better understand ecological response patterns and assist learning in the adaptive management of flow-regulated rivers.

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Chapter 4

Title: Comparison of flow-sediment interactions in two rivers with contrasting flow management programs

Short title: Flow-sediment interactions

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Abstract

Severely modified flow and sediment regimes occur in most managed rivers globally. The coupling between flow and sediment regimes, which occurs at multiple temporal and scales, thus has been altered as well. Environmental flows (E-Flows) have been used to mitigate the ecological effects resulting from altered flow regimes below dams. However, little is known how E-flows interact with sediment transport and distribution below dams and the subsequent effects on ecosystem properties. In this study, we examined the influence of experimental high flows on abiotic/biotic properties of benthic sediments in two rivers with different flow management strategies (environmental high flows versus sediment bypass releases from the respective reservoirs). We found that sediment input as well as flow magnitude determined the response of biotic (sediment respiration, periphyton, macroinvertebrates) and abiotic sediment properties (stream-bed and hyporheic sediment size) in each river. In the river experiencing environmental flows with minimal entrained sediment, lateral inputs of sediment from side-slope scree fields and tributaries mostly overrode the effects of E-flows on sediment-property responses. In the river experiencing large magnitude flow and sediment inputs from the reservoir via a sediment bypass tunnel (SBT), specific SBT-event magnitudes drove sediment-property responses. This study highlights the importance of understanding system-specific flow-sediment interactions in the implementation of flow management programs in rivers for ecological mitigation.

Keywords: E-flows, macroinvertebrates, sediment respiration, river function, periphyton, flow regime, sediment regime.

Introduction

The alteration of hydrological regimes through river management is an ongoing issue worldwide (Nilsson et al., 2005; Lehner et al., 2011). Despite the human services provided by managed rivers, including industrial water-use, power generation, navigation and recreation (Gleick, 2003), the ecological degradation of river ecosystems has been acknowledged and is a major concern today (Brandt, 2000; Bunn & Arthington, 2002; Nilsson et al., 2005). Large dams and the consequent changes in flow regimes are common attributes of flow-regulated rivers (Richter et al., 1996; Poff et al., 1997; Poff et al., 2007). Current efforts to mitigate the effects of dams on downstream waters have focused on the implementation of environmental flows (E-flows) to simulate the natural flow regime of the respective river towards enhancing ecological properties in line with management objectives (Konrad et al., 2011; Olden et al., 2014). Since the first E-flow operation at Glen Canyon Dam, USA, in 1965, other flow experiments have been performed globally to evaluate alternative dam operations for ecological benefits (Olden et al., 2104; Gillespie et al., 2015). Improvements in water quality, physical habitat and biodiversity, as well as the economic value of natural resources have been shown in over 100 flow-programs across 20 countries (Cambray et al., 1997; Bate & Adams, 2000; Robinson & Uehlinger, 2008; Olden et al., 2014). High flow pulses (experimental floods) or minimum flow protocols have been the most common experiments, while fishes and macroinvertebrates have been the primary study foci and monitored parameters (Olden et al., 2014). Most studies, however, have emphasized E-flow effects at coarse temporal and spatial scales, often overlooking the importance of smaller scale dynamics in terms of response. Although some ecological responses require medium to long-term perspectives for change (i.e., most responses are not expected to occur within a single event; Robinson 2012), finer temporal and spatial scale studies are needed to assess site-specific effects of flow experiments that may influence long-term dynamics (Uehlinger et al., 2003; Robinson et al., 2004). This aspect is especially crucial when evaluating the interactions of flow with other abiotic drivers of ecosystems that occur within this time-space resolution, such us the interplay with temperature and sediment (Wohl et al., 2015).

Although the effects of sediments on river ecology are well-documented (Waters, 1995; Jones et al., 2012), the interplay of flow with sediment regimes in rivers has only recently become an emerging research priority (Wohl et al., 2015). Sediment regimes are now recognized as being important in river ecology, playing a major role in channel morphology, streambed condition, water quality, and the structure and function of biotic assemblages

(Holomuzki & Biggs, 2003; Yarnell et al., 2006; Boulton et al., 2010; Wohl et al., 2015). Similarly to E-flow, various techniques can be used to mitigate the lack of sediment dynamics due to regulated rivers. Some of the techniques emphasize the release of trapped sediments by dams, such us flushing or dredging, whereas others, such us sediment bypass tunnels (SBTs), focus on minimizing deposition in dams by routing sediment around dams (Kondolf et al., 2014). The non-linear and episodic nature of sediment regimes, with sediment processes often operating at different scales compared to flow regimes, makes it difficult to integrate flow and sediment regimes in river management programs (Melis et al., 2012). As a consequence, there is a major research gap on flow-sediment interactions regarding ecosystem processes and structure, both at finer temporal and spatial scales (Wohl et al. 2015). A better understanding of such interactions is important for defining management objectives and expectations in E-flow programs for regulated rivers.

In this study, we examined the influence of high flows on sediment properties in two flow-regulated rivers, specifically the structure and function of biotic properties of bed sediments before and after experimental flows. Both rivers are impounded by large dams but distinctly contrast in flow management protocols of downstream waters. The Spöl river has been subject to experimental flows since 2000 and sediment inputs below the dam occur naturally from adjacent scree slopes (debris fans) and various tributaries. In contrast, the Albula reservoir uses a sediment bypass tunnel that releases large volumes of sediment during the occurrence of high flows to reduce sediment filling of the reservoir (Martín et al., 2017). Study sites were situated above and below natural sediment input areas (scree slopes, tributaries) along each river system and with sediment properties measured before and after managed high flows. Our primary objective was to quantify how local sediment properties are influenced by different sediment inputs associated with managed high flows. In addition, we examined for longitudinal patterns below each dam in respect to flow-sediment interactions in relation to local sediment sources. We hypothesized that local response patterns in sediment properties would reflect the respective flow-sediment operations at each dam; i.e., the interaction of E-flow magnitude with sediment entrainment at the reservoir. Specifically, large magnitude E-flows with large amounts of entrained sediment would override any local scale sediment inputs in the rivers, whereas local-scale sediment inputs would be evident with low magnitude E-flows with minimal sediment entrainment.

Methods

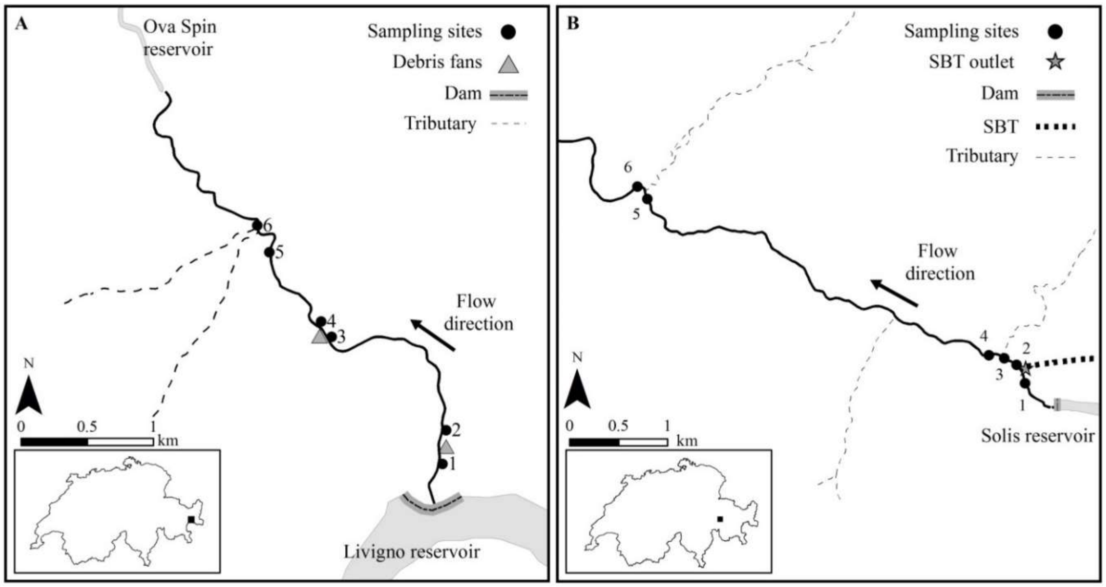
Description of study sites

Spöl: The Spöl, a 5th order river, flows through the Swiss National Park (SE Switzerland) (Figure 1). Maximum elevation of the catchment is 3302 m above sea level (a.s.l.) and the study section was at ca. 1670 m a.s.l. The river is impounded by two large dams: Punt dal Gall dam (Livigno reservoir) and Ova Spin dam (Figure 1). Punt dal Gall dam is located on the Swiss-Italian border, is 130 m high and has a storage capacity of 164 million m^3, whereas Ova Spin (ca. 5.7 km downstream of Punt dal Gall) is 73 m high with a storage capacity of 6.2 million m^3. They were built between 1960 and 1970 as part of a complex hydroelectric production scheme (Scheurer & Molinari, 2003). Prior to construction, the Spöl river had a typical glacio-nival flow regime with an average annual flow between 6.6 and 12.5 m^3/s, and annual high flows up to 140 m^3/s (Figure 2). Flow regulation between 1974 and 1999 caused residual flows below Livigno of about 0.55 m^3/s in winter and between 1 and 2.5 m^3/s during summer (Scheurer & Molinari, 2003). Due to this hydrological stability, the formation of pools upstream of lateral debris fans was enhanced (Mürle et al., 2003), dense algal mats and moss beds bloomed, an atypical invertebrate community dominated (Robinson et al., 2003), and the riverbed was clogged by fine sediments, reducing the reproductive habitat of brown trout (Ortlepp & Mürle, 2003). In summer 2000, an experimental flow program was started to restructure the streambed and improve habitat conditions in the river. During the following 16 years, residual discharge was set to about 0.5 m^3/s in winter and about 1.4 m^3/s in summer, and a varied number of floods per year (1-4 per year) with different magnitude (10-50 m^3/s) were implemented and tested, which are now part of the regulatory scheme for the river (see Robinson, 2012).

A 3.3-km section flowing through a confined valley between the two dams was used for this study. Valley side-slopes are characterised by pine (*Erico-Pinetum mugo*) vegetation (Zoller, 1995) interspersed with a number of scree slopes that enter the river as debris fans as a source of sediment. Two small tributaries that join the Spöl at about the same location ca. 3.1 km downstream of Livigno were used in this study (Figure 1). Specifically, six sampling sites (3 paired sites) were located along the study section. Sites 1 and 2 were situated upstream and downstream of a large debris fan ca. 200 m below Livigno reservoir. Sites 3 and 4 were situated above and below a large debris fan ca. 2.1 km downstream of Livigno, while sites 5 and 6 were located above and below the confluence of the two tributaries ca. 3.1 km downstream of the dam) (Figure 1). Here, the study took place in 2015 and incorporated experimental floods implemented on July 3 and September 28 (Figure 2a). Discharge was measured at a gauging station 500 m downstream of the dam by the Swiss Federal Office of Hydrology and Geology.

Albula: The 6th order Albula river flows through the Canton of Grisons (SE Switzerland) for 30 km before being impounded at Solis reservoir (65-m high with 1.5 million m^3 storage capacity). Average discharge of the river upstream of the dam was 15 m^3/s, whereas residual flow below the dam was ca. 1.0 m^3/s. Due to high sediment deposition in the reservoir, a Sediment Bypass Tunnel (SBT) was built in 2012 to reduce sediment inputs in the reservoir (Auel *et al.*, 2010). The SBT connects the middle part of the reservoir with downstream receiving waters, being operated during most high flow events. During operation, large volumes of sediment-laden water are released, reaching more than 160 m^3/s. As a normal dam operation, water is released from spillwater and a bottom outlet throughout the year (Figure 2b). A 5-km section downstream of the dam was used in the study, also flowing through a confined narrow canyon as the Spöl system. Three main tributaries join the Albula in this section (Figure 1) and potentially add sediment and modify flows in the river. Six sampling sites (3 paired sites) were situated along the study section. Sites 1 and 2 were located directly above and below the SBT outlet. Sites 3 and 4 were located above and below the first tributary ca. 450 m downstream of the SBT outlet, while sites 5 and 6 were above and below the lower tributary ca. 5-km downstream of the SBT outlet. Site 4 was excluded from the analysis because it was non-accessible for most of the study. Here, the study focused on two multiple operations of the tunnel, one in summer 2014 and one in summer 2015 (Figure 2b). Discharge in the section was monitored by the hydropower company operating the dam (EWZ).

Figure 1: Map of study systems, showing reservoirs, main river, sampling sites, and tributary and sediment inputs. A: Spöl River, B: Albula River. SBT = sediment bypass tunnel.



Field measurements before and after high flow events

The same measures were collected at all sites in both systems before and after respective high flow events. The median sediment size of the stream-bed (St-d50, cm) was calculated using the Wolman method (Wolman, 1954), measuring the b-axis of 50 stones randomly collected at each site. As a functional indicator of benthic sediments, sediment respiration (SR) was measured as changes in O_2 concentration over time using Plexiglas chambers ($n = 3$) (Uehlinger *et al.*, 2003). The uppermost sediment layer was removed to avoid the effects of respiration by autotrophs (Doering *et al.*, 2011) and hyporheic sediment was collected then with a shovel. Collected sediments were sieved before incubation to exclude particles >8 mm. Chambers were half-filled with sediment and then filled with water from the site before being sealed with a rubber stopper. Chambers were buried at the sampling site for 3-4 hours for incubation. The dissolved oxygen concentration and temperature in each chamber were measured before and after incubation (Hach HQ40d connected to a LD0101 oxygen probe). Based on the consumption of O_2 in the chamber and the sediment weight, sediment respiration (mg O_2 kg^{-1} sed h^{-1}) was calculated and normalized at a reference temperature (20°C) to account for seasonal variation (Naegeli & Uehlinger, 1997). The contents of each chamber were stored in plastic bags and kept frozen until processed. In the laboratory, the respective contents were dried at 60°C, weighed, burned at 450°C for 4 h and reweighed to determine the particulate organic matter content (POM) as ash-free dry mass (mg AFDM/kg sed). The median grain size distribution was measured from the burned sediments. Sediments were sieved at grain size fractions (>8 mm, 8–4 mm, 4–2 mm, 2–1 mm, 1–63 µm and <63 µm) and the median grain size (d50, mm) calculated using Gradistat v8 (Blott & Pye, 2001).

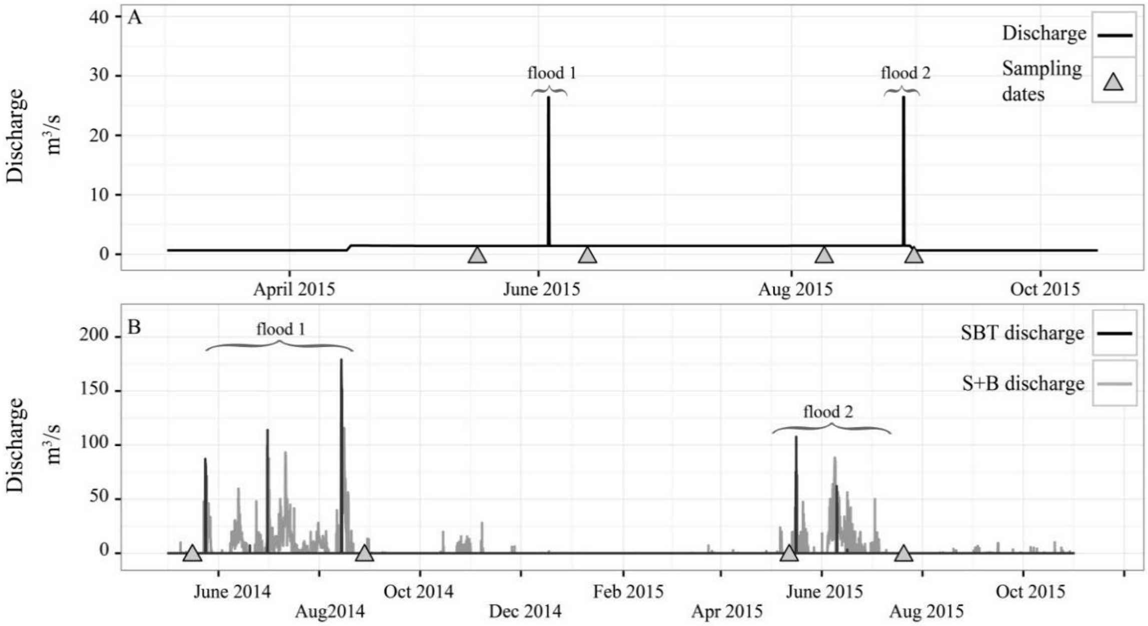


Figure 2: Discharge in the Spöl (A) and Albula (B) during the study period, and showing the sampling dates (triangles) at each river. Note the scale differences in the axes between panels A and B. S+B = spillwater and bottom outlet release.

Benthic periphyton and macroinvertebrates were collected as biotic structural indicators of sediment properties. To determine periphyton biomass, five stones were randomly collected at each site on each date and kept frozen until processed in the laboratory. In the laboratory, periphyton was removed by scrubbing each rock with a brush and rinsing with deionized water. The suspension was filtered through Whatman GF/F filters. Periphyton biomass as ash-free dry mass (g AFDM/m^2) was determined by drying at 60°C, weighing the filter, combusting the filter at 450°C for 4 h, and then reweighing the filter. The difference in weights was used as an estimate of AFDM per unit area of stone. Stone area was determined using a weight to area relationship by wrapping the stones with aluminium foil (Bergey & Getty, 2006). Three benthic macroinvertebrate samples were collected at each site on each date using a Hess sampler (250-um mesh, 0.04 m^2 area) and preserved in 70% ethanol until processing. Macroinvertebrates were hand-picked from each sample, identified to family or subclass level (Oligochaeta) and counted for estimates of density (individuals/m^2).

Data analysis

Due to differences in both management programs in terms of flow magnitude and frequency, a direct comparison between rivers using absolute values of high flow effects was not possible. Therefore, the relative change in biotic and abiotic properties caused by each flood at each site was used to allow for a general comparison between systems and among sites. To define the site-specific influence of each high flow event, the percentage in decrease/increase of each variable (relative change of the mean) was calculated using the following equation, with X being the mean of the different indicators used to describe different sediment properties at each site.

$$\left(\frac{Xafter - Xbefore}{Xbefore}\right).100$$

A two-tailed paired t-test was used to compare the effects of each flood at each site for all variables except for St-d50 due to lack of replicates. Although Site 1 in Albula was not affected by the SBT, the relative changes are also shown to illustrate the difference between SBT operations and dam release (spillwater) operations. To have a better understanding of the influence of high flows on sediments at the reach scale, the coefficient of variation (CV) of each variable was calculated for each date and averaged for each site. Site 1 in the Albula was excluded in the CV calculation.

Results

Indicator responses at the Spöl

Experimental floods caused changes in substrate size in stream-bed (St-d50) and hyporheic (H-d50) sediments (Figure 3a-b). Average St-d50 in Spöl was 5.8 cm before flood 1. After flood 1, there was an increase in stream-bed sediment size at sites 1, 2, 4 and 6 (19, 27, 40 and 6%, respectively), whereas sites 3 and 5 showed a decrease in size, increasing average size of sediment to 6.3 cm. Flood 2, in contrast, produced a slight decrease in St-d50 at all sites (10% on average, max. = 15%, min. = 1%) except at site 6, where it increased by 59%. Hyporheic d50 before flood 1 was 3.01 mm on average. At sites 1 to 4, sediment H-d50 remained the same after flood 1, with not significant changes ($p > 0.05$) ranging from a decrease of 3% to an increase of 6%. However, there was a large increase in hyporheic sediment size of 76% at site 5 ($p=0.04$) and 94% at site 6 (no p available).

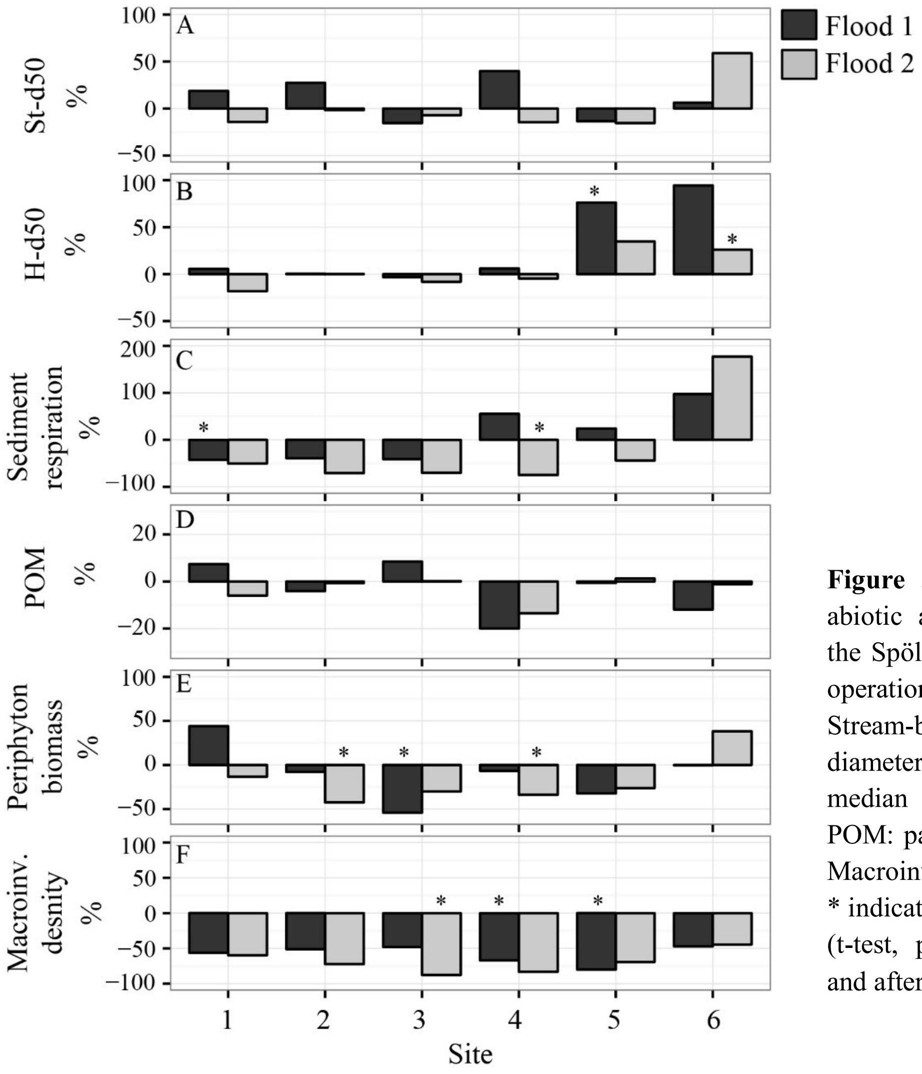


Figure 3: Relative change in abiotic and biotic indicators in the Spöl River caused by e-flow operations in 2015. St-d50: Stream-bed median sediment diameter, H-d50: hyporheic median sediment diameter; POM: particulate organic matter, Macroinv: macroinvertebrates. * indicates significant differences (t-test, p=0.05) between before and after each flood at each site.

After flood 2, sites 1 to 4 showed a general decrease in H-d50, being maximum at site 1 (decrease of 18%, p = 0.28) and minimum at site 2 (no change). At sites 5 and 6 there was again an increase in d50 of 35% and 26% respectively, being only significant at site 6 (p = 0.03). Details of absolute values are given in supplement table S1.

Sediment respiration ranged from 0.89 to 0.23 mg O^2 kg^{-1} sed h^{-1} before flood 1. Sediment respiration decreased by 40% at sites 1-3 after flood 1, although being significant only at site 1 (p = 0.01), whereas it increased at sites 4, 5 and 6 by 55, 24 and 97%, respectively (all p > 0.05). After flood 2, sediment respiration decreased at all sites (62% on average, from 0.54 to 0.23 mg O^2 kg^{-1} sed h^{-1}, max. = 75% at site 4 (p = 0.03), min. = 44% at site 5 (p = 0.06)) except site 6, where it increased by 177% (p = 0.12) (Figure 3c). POM absolute values ranged from 3.39 to 2.15 mg AFDM/kg sed being the relative change minor, ranging from a decrease of 20% to an increase of 7.4%. Changes in POM produced by flood 1 were greater than changes caused by flood 2 at all sites, although the differences between before and after flood were not significant ($p > 0.05$). After flood 1, sites located above a sediment input showed a positive or no change in POM, whereas sites located downstream of input areas showed a decrease in POM. In flood 2, this spatial pattern was not found (Figure 3d). More details of SR and POM absolute values are shown in supplement table S1.

Before flood 1, periphyton biomass ranged from 3.03 to 0.79 g AFDM/m^2. After flood 1, periphyton biomass increased at site 1 (44%), decreased at sites 2, 3, 4 and 5 (8, 54, 7, and 32%, respectively, although being significant only at site 3 ($p = 0.02$) and showed no change at site 6. Flood 2 resulted in biomass decreases at sites 1, 2, 3, 4, and 5 (13, 42, 30, 34, and 25%, respectively), being significant at sites 2 and 4 ($p < 0.01$ in both cases) and an increase of 38% at site 6 (Figure 3e). Benthic macroinvertebrates decreased in density at all sites (average = 58%, max. = 80% at site 5, min. = 48% at site 3, being significant at sites 4 and 5 ($p < 0.01$ for both) after flood 1, decreasing density from 8223 ind/m^2 to 3040 ind/m^2. Flood 2 caused a similar response (from 6844 to 1656 ind/m^2), with an average decrease of 70% in macroinvertebrate densities, being the only significant change at site 3 (90%) ($p = 0.03$).

Indicator responses at the Albula

Albula St-d50 was 4.8 cm on average before flood 2. Flood 2 resulted in a decrease in St-d50 at sites 1, 2 and 3 (34, 24 and 84%, respectively) and an increase at sites 5 and 6 (32 and 13%, respectively) (Figure 4a). Hyporheic d50 increased from 3.1 mm to 3.2 mm after flood 1. Locally, flood 1 caused a significant decrease of 36% ($p = 0.01$) in hyporheic sediment size (H-d50) at site 2, but an increase, although statistically not significant ($p > 0.05$) at sites 1, 3, 5 and 6 (10% on average). After flood 2, sediment H-d50 decreased on average from 2.8 to 2.5 mm. H-d50 decreased at sites 2 and 3 (8 and 43%, respectively), increased at site 5 (5%) and decreased by 12% at site 6 (Figure 4a). Here, site 1 decreased only 2%. Both high flows caused a decrease in sediment respiration at all sites affected by the SBT (Figure 4c). Absolute values decreased from 0.75 to 0.30 mg O^2 kg^{-1} sed h^{-1}. The average decrease in sediment respiration after flood 1 was 55% (max. = 78% at site 5, min. = 47% at site 6), being significant at sites 2, 3, 5 and 6 ($p = 0.01$, <0.01, 0.03 and 0.02, respectively). In contrast, flood 2 caused a decrease of 25% on average at all sites affected by SBT (max. = 39% at site 2, min. = 10% at site 5). Sediment respiration at site 1, upstream the SBT, decreased after flood 1 (33%) and increased after flood 2 (38%). Sediment POM decreased by 20% at site 2 and increased by 12% at site 6, with no clear pattern between floods or sites. More details of SR and POM absolute values are shown in supplement table S1.

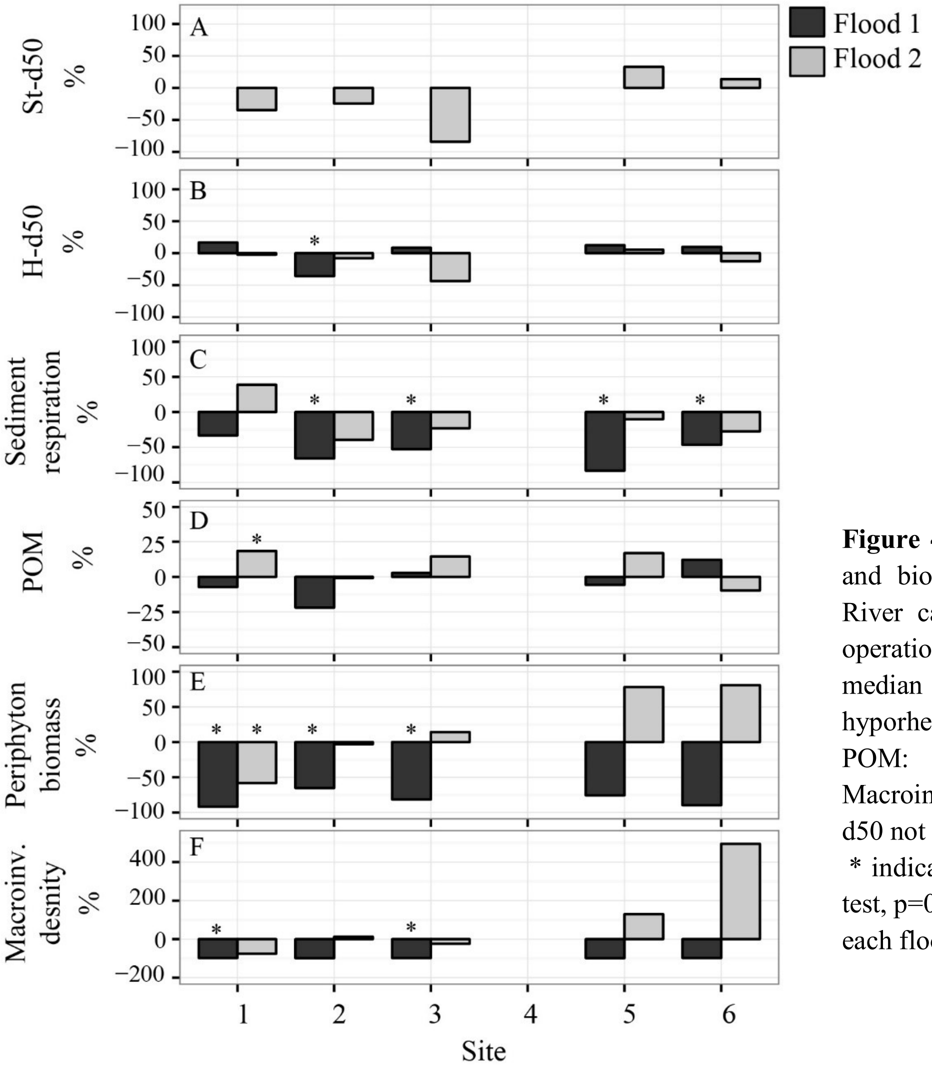


Figure 4: Relative change in abiotic and biotic indicators in the Albula River caused by two SBT multiple operations. St-d50: Stream-bed median sediment diameter, H-d50: hyporheic median sediment diameter; POM: particulate organic matter, Macroinv: macroinvertebrates. St-d50 not available for flood 1. * indicates significant differences (t-test, p=0.05) between before and after each flood at each site.

Periphyton biomass was 4.43 g AFDM/m^2 on average before flood 1, decreasing at all sites after flood 1 (average = 80%, max. = 90% at site 6, min. = 72% at site 2). It also decreased at Site 1 by 92%. The periphyton decrease was significant at sites 1, 2 and 3 ($p < 0.01$ in all cases). In contrast, periphyton biomass increased at most sites affected by SBT after flood 2, from 3.0 to 3.6 g AFDM/m^2 on average. Site 2 showed a slight decrease in biomass of 3%, whereas at sites 3, 5 and 6, biomass increased by 14, 78 and 81%, respectively. Site 1, however, showed a significant decrease in biomass (58%, $p < 0.01$). Macroinvertebrate density decreased (~100%) at all sites after flood 1, being significant at sites 1 and 3 ($p = 0.03$ for both sites). After flood 2, in contrast, densities decreased at site 1

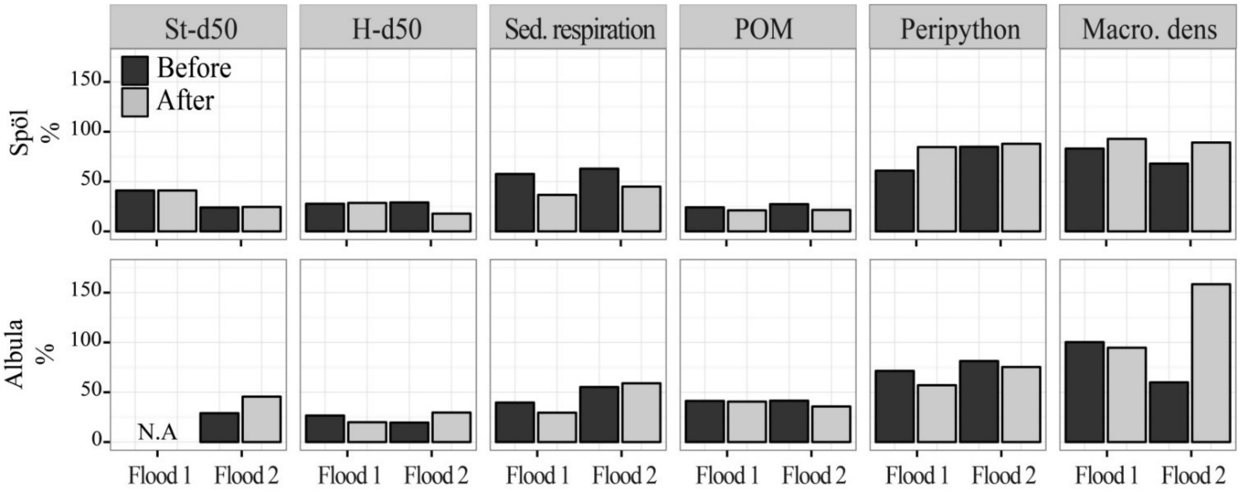
(75%), increased at site 2 (12%), decreased at site 3 (24%), and increased at sites 5 and 6 (129 and 500%, respectively) (Figure 4f).

Spatial variability of ecosystem indicators

The coefficient of variation (CV) of biotic and abiotic indicators showed differences among rivers and sites (Figure 5). In the Spöl, stream-bed St-d50 CV was similar before and after floods, although it changed between seasons (41% after flood 1, 24% before flood 2). Hyporheic-d50 CV was similar before and after flood 1, and slightly decreased after flood 2. Sediment respiration CV decreased after both floods (36% after flood 1, 28% after flood 2), although values varied between floods. Similarly, the POM CV also decreased after both floods (12 and 21%, respectively). The periphyton biomass CV moderately increased after flood 1, while no effect was seen after flood 2. Macroinvertebrate density CV at the Spöl increased after each flood, although there was a substantial decrease in density CV after the flood number 1 and the sampling before flood 2.

In the Albula, St-d50 CV was greater after flood 2 (30% before, 45% after), whereas Hd50 CV slightly decreased after flood 1 and increased after flood 2. Sediment respiration CV showed a decrease (30%) after flood 1 and an increase after flood 2 (59%). As in the Spöl, respiration CV was high until the occurrence of the second flood. POM CV slightly decreased after flood 2. Periphyton CV decreased after flood 1 and flood 2, whereas the macroinvertebrate density CV slightly decreased after flood 1, decreased again before flood 2, and greatly increased after flood 2.

Figure 5: Coefficient of variation of system indicators for samples collected before and after each operation. St-d50: Stream-bed median sediment diameter, H-d50: hyporheic median sediment diameter; Sed. Respiration: sediment respiration, POM: particulate organic matter, Macro. Dens: macroinvertebrate density. St-d50 not available before and after flood 1.



Discussion

The main goal of this study was to examine sediment properties above and below sediment input areas following high flow events in two regulated rivers. The Spöl experiences high flow events with minimal upstream sediment entrainment, whereas the Albula experiences high flows that include substantial sediment amounts (i.e., inputs from a sediment bypass tunnel at the reservoir). The magnitude of the high flows also differed between the rivers, being relatively greater in the Albula. A secondary goal was to determine any longitudinal patterns in sediment properties following the high flow events in both rivers. We found variable responses in ecosystem indicators between rivers and between flow events within and along each river.

In the Spöl, hypolimnetic high flows with minimal sediment are released from the dam at predetermined times and with a predefined magnitude and duration. Sediment inputs in the residual stretch are derived mostly from large scree slopes situated along the river and various tributaries entering the system. Historically (last 5+ years), the magnitude of experimental floods in the Spöl have been ~30 m^3/s to incorporate results from ecosystem monitoring, although these flows are lower than natural flood peaks (~40 m^3/s) before river management (Robinson, 2012). The two floods in the current study were of similar magnitude and duration (ca. 8 hours each with peak flows of ca. 3 hours), although one occurred in late spring and the other in autumn. This seasonality may have influenced the observed results as discussed below.

Despite the observed resistance of the hyporheic zone to flow disturbance (Matthaei et al., 1999; Uehlinger, 2000), experimental floods in the Spöl were of sufficient magnitude to disturb and mobilize the structure of the stream-bed and hyporheos, reducing hyporheic respiration and benthic flora and fauna. This decrease in ecosystem properties is often observed following large floods (Fisher et al., 1982; Uehlinger & Naegeli, 1998; Uehlinger et al., 2003). The reduction of macroinvertebrates, algae, and hyporheic heterotrophs (respiration) reveal the efficiency of experimental-floods for simulating the effects of a natural flood in terms of stream-bed disturbance.

Although both floods in the Spöl included in our study were similar in magnitude and duration, their ecological effects differed, suggesting some other factors interacted with flow in observed responses. The different effects of floods on hyporheic H-d50, sediment respiration and periphyton appeared related to the distance from the dam (a longitudinal effect). Sediment respiration and H-d50 increased after floods at lower sites in the river ca. 3-km downstream of the dam. The lack of substantial sediments in the water released at the dam may have intensified the “hungry waters” effect (Williams & Wolman, 1984; Kondolf, 1997), with the floods having a higher eroding and transport capacity in the stretch near the dam until the carrying capacity associated with discharge is attained downstream (Lane, 1955; Brandt, 2000). In contrast, POM differed between sites located above and below sediment input areas in the Spöl. The decrease in organic matter (POM) at sites below scree slopes and tributaries might be related to the type of sediment delivered by scree slopes and tributaries; here being mainly dolomitic and calcareous sediments (Mürle et al., 2003). This sediment input may contain some organic matter, but most likely it would be transported and deposited further downstream, thus leaving sediment with low amounts of organic matter. Debris fans below the scree slopes are controlled by a complex interaction of topology, geology, vegetation and weather conditions (Baroni et al., 2007; Procter et al., 2012). This complexity is reflected in high temporal variability in the amount and size of sediment at fan bottoms, thus influencing local sediment distributions in the receiving stream, as shown by the heterogeneous changes after floods in streambed St-d50 at the different sites. Another factor that may drive the response to floods is the cumulative effects of disturbance in the system. The last experimental flood in the Spöl before this study occurred on the 23 September 2014.

Therefore, the system had no flow disturbance for 9 months until flood 1 in June 2015. On the contrary, between flood 1 and 2 there was only 1.5 months. Considering that the frequency of disturbance can determine changes in ecosystem processes and in organisms (Resh et al., 1988; Townsend et al., 1997), the response of indicators to flood 2 might be related to the cumulative flood effects.

In the Albula, high flows comprised several high peaks of different magnitude, including releases of sediment-laden water through the SBT and reservoir spill water with minimal sediment (Martín et al., 2017). Here, the results of indicator response variables suggested that the flood effects were primarily driven by flow magnitude. After flood number 1, with various magnitude flow/sediment events, hyporheic respiration, periphyton biomass and macroinvertebrate density all decreased along the entire 5-km study stretch. Most likely, the canyon morphology of Albula river promoted the transport of water and sediment downstream, inducing streambed mobilization. Further, this large magnitude SBT operation likely reduced or minimized any tributary influence on sediment properties. The role of tributaries may be important when SBT events are of lesser magnitude, as tributaries can act as a source macroinvertebrates as well as sediments to receiving waters (Robinson et al., 2003). In contrast, the impact on biotic indicators was lower after flood 2, suggesting a gradual pattern related to the distance to the dam. Similar results were observed in the Ebro River (Spain) after flushing operations (i.e., release of sediment-laden waters), where the effectiveness of removing macrophytes from the stream-bed was reduced with distance downstream (Batalla & Vericat, 2009). Despite the evident movement and scouring of sediments during high flows, the structure of stream-bed and hyporheos sediments showed a highly patchy response, with some areas showing an increase in sediment size and others a decrease, probably due to channel morphology or large substrate (boulders or tree logs) present in the streambed (Matthaei et al., 1999; Robinson et al., 2004).

The change in spatial variability (measured as CVs) in biotic indicators due to floods was noticeable in both rivers. After floods, respiration CV decreased in both systems due to the general impact of high flows, which reduce respiration at all sites, decreasing spatial variability. As an exception, after flood 2, the Albula did not show any change in CV, likely due to the low effect of the operation at most of the sites. Periphyton in the Spöl showed great spatial variability, increasing after floods, whereas periphyton CV decreased after each flood in the Albula. Similarly, macroinvertebrate CV was higher after both floods in the Spöl and after flood 2 in the Albula, which was lesser in magnitude. This fact suggests that floods, especially those of high magnitude, have the capacity to homogenise the entire system, lateral inputs of sediment being inducers of heterogeneity as they create a discontinuity in the longitudinal disturbance effects of a flood. These hotspots may offer a refugia from floods and a source of recolonists after disturbance (Palmer et al.,1996, Lake 2000).

Management perspectives

The interactions between flow and sediments are complex, with different flow management scenarios potentially resulting in quite different responses in ecosystem properties. As shown in our study, the responses in sediment properties, and the consequent ecosystem changes, may greatly depend on the particular river system, and may differ from natural floods (Batalla & Vericat, 2009). Understanding these system-specific responses in terms of flow management are crucial towards clear goal design and evaluation of implemented programs (Kondolf et al., 2014; Wohl et al., 2015). For example, in the Spöl, although being in a deficit situation of sediment input due to the dam, sediment supplied by tributaries and lateral scree slopes seem to be ecologically sufficient to meet management goals and should be taken into account when evaluating and adapting system-specific objectives. Olive & Olley (1997) described a similar situation in an Australian river, where sediment input from tributaries was substantial in relation to flows released at the dam. In these cases, simulation of natural flows would be a primary factor towards sustaining ecosystem integrity. However, in rivers where the input of sediment by natural sources is lacking or insufficient, other techniques need to be considered to guarantee an optimal flow/sediment interaction. In the Colorado system, two main tributaries that supply sediment to Colorado River only provide about 10% of the pre-dam sediment supply (Wright et al., 2005), generating unstable conditions resulting in sandbar erosion (Melis et al., 2012). Similarly, in the Albula, where the main sediment input is from upstream and contributions and lateral inputs are lacking, sediment input by the SBT seem to be an efficient technique to maintain ecologically-optimal flow/sediment regimes, as long as the magnitudes of high flows and sediment are near natural values (Martín et al., 2016, submitted). Therefore, a specific evaluation of each system and the possible interactions between sediment and flow should be considered under river management to better maintain the integrity in ecosystem function and structure.

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Supporting information

Table S1. Summary of ecological indicator results in the Spol and Albula by site and date, and the percentage (%) relative change. St-d50: Stream-bed median sediment diameter, H-d50: hyporheic median sediment diameter; SR: sediment respiration; POM: particulate organic matter; Peri: Periphyton; Macro: macroinvertebrates. n.a: not available

		SPOL								ALBULA							
St-d50		Flood1				Flood2				Flood1				Flood2			
cm		before	after		%	before	after		%	before	after		%	before	after		%
Site 1		7.4	8.7		18.7	6.7	5.7		-14.2	n.a	n.a		n.a	7.1	4.7		-34.7
Site 2		2.9	3.7		27.4	3.8	3.8		-1.6	n.a	n.a		n.a	5.8	4.4		-24.6
Site 3		9.2	7.8		-15.5	5.2	4.8		-7.1	n.a	n.a		n.a	8.3	1.3		-84.1
Site 4		6.51	9.1		39.9	5.7	4.9		-14.6	n.a	n.a		n.a	0.0	6.3		n.a
Site 5		4.1	3.5		-13.4	3.8	3.2		-15.5	n.a	n.a		n.a	4.7	6.3		32.9
Site 6		4.5	4.8		6.3	4	6.4		58.9	n.a	n.a		n.a	5.0	5.7		13.7
H-d50		Flood1				Flood2				Flood1				Flood2			
mm		before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%
Site 1	mean	3.35	3.54	0.72	5.7	4.21	3.45	0.28	-18.1	2.98	3.48	0.31	16.8	3.76	3.30	0.09	-12.3
	sd	1.07	0.47			0.71	0.19			0.23	0.73			0.23	0.09		
Site 2	mean	2.92	2.94	0.98	0.4	2.70	2.70	0.99	0.1	3.95	2.53	0.01	-36.0	2.30	2.11	0.57	-8.1
	sd	0.36	0.24			0.35	0.28			0.21	0.43			0.31	0.39		
Site 3	mean	2.79	2.71	0.84	-3.2	2.72	2.50	0.58	-8.1	3.18	3.45	0.19	8.6	3.02	1.75	0.10	-42.0
	sd	0.39	0.32			0.62	0.30			0.79	0.58			0.27	0.85		
Site 4	mean	3.97	4.22	0.64	6.1	3.91	3.73	0.77	-4.6	2.35	n.a	n.a	n.a	n.a	3.38	n.a	n.a
	sd	0.39	0.49			0.81	0.21			1.04	n.a			n.a	0.12		
Site 5	mean	2.13	3.76	0.04	76.2	2.63	3.55	0.23	34.9	2.75	3.08	0.11	12.1	2.55	2.68	0.44	5.4
	sd	0.20	0.46			0.55	0.50			0.21	0.34			0.36	0.12		
Site 6	mean	2.87	5.59	n.a	94.4	2.55	3.21	0.03	26.1	3.37	3.72	0.18	10.3	3.41	2.98	0.23	-12.5
	sd	1.03	0.03			0.43	0.35			0.45	0.26			0.12	0.33		

		SPOL								ALBULA							
SR		Flood1				Flood2				Flood1				Flood2			
mg O_2 kg^{-1} sed h^{-1}		before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%
Site 1	mean	0.89	0.51	0.01	-42.7	0.82	0.41	0.29	-50.3	0.90	0.60	0.13	-33.3	0.88	1.19	0.09	35.2
	sd	0.06	0.05			0.13	0.02			0.17	0.01			0.20	0.18		
Site 2	mean	0.80	0.49	0.20	-39.4	0.59	0.17	0.13	-70.9	1.03	0.36	0.01	-65.0	0.72	0.44	0.11	-38.9
	sd	0.24	0.07			0.27	0.02			0.19	0.15			0.19	0.04		
Site 3	mean	0.61	0.36	0.27	-41.2	0.68	0.20	0.13	-70.2	0.64	0.31	< 0.01	-51.6	1.09	0.84	0.69	-22.9
	sd	0.23	0.17			0.32	0.04			0.05	0.03			0.41	0.55		
Site 4	mean	0.40	0.62	0.47	55.3	0.77	0.19	0.03	-74.9	0.51	n.a	n.a	n.a	n.a	0.48	n.a	n.a
	sd	0.27	0.29			0.18	0.05			0.13	n.a			n.a	0.06		
Site 5	mean	0.27	0.33	0.38	24.0	0.29	0.16	0.06	-44.3	1.04	0.22	0.03	-78.8	0.49	0.45	0.70	-8.2
	sd	0.01	0.10			0.11	0.10			0.24	0.02			0.11	0.12		
Site 6	mean	0.23	0.46	n.a	97.3	0.09	0.25	0.12	177.1	0.54	0.30	0.02	-44.4	0.40	0.33	0.17	-17.5
	sd	0.02	0.04			0.1	0.05			0.11	0.06			0.1	0.07		

POM		Flood1				Flood2				Flood1				Flood2			
mg AFDM/kg sed		before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%
Site 1	mean	3.16	3.39	0.61	7.3	3.23	3.03	0.86	-6.2	5.40	5.01	0.41	-7.2	4.95	5.88	0.01	18.8
	sd	0.55	0.34			1.00	0.78			0.25	0.80			2.01	2.10		
Site 2	mean	2.86	2.74	0.64	-4.2	3.07	3.05	0.97	-0.7	4.57	3.56	0.08	-22.1	4.62	4.59	0.94	-0.6
	sd	0.33	0.56			0.78	0.15			0.96	0.80			0.54	1.07		
Site 3	mean	3.13	3.39	0.19	8.3	2.99	2.99	0.99	0.0	5.00	5.13	0.68	2.6	4.91	5.63	0.47	14.7
	sd	0.67	0.61			0.59	0.53			0.71	0.28			2.06	1.09		
Site 4	mean	3.14	2.51	0.43	-20.1	2.62	2.27	0.59	-13.4	3.01	n.a	n.a	n.a	n.a	4.41	n.a	n.a
	sd	1.14	0.06			0.81	0.32			0.95	n.a			n.a	1.03		
Site 5	mean	2.85	2.83	0.97	-0.7	2.42	2.46	0.94	1.7	2.62	2.48	0.47	-5.3	2.68	3.13	0.68	16.8
	sd	0.63	0.68			0.52	0.38			0.31	0.58			0.90	0.78		
Site 6	mean	2.87	2.53	n.a	-11.8	2.18	2.15	0.87	-1.4	2.15	2.40	0.34	11.6	3.09	2.78	0.76	-10.0
	sd	1.42	0.62			0.41	0.21			0.91	0.71			0.94	1.07		

		SPOL								ALBULA							
Peri. Bio		Flood1				Flood2				Flood1				Flood2			
g AFDM/m2		before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%
Site 1	mean	3.03	4.36	0.06	43.9	2.19	1.89	0.45	-13.7	8.61	0.78	< 0.01	-90.9	9.34	3.93	< 0.01	-57.9
	sd	1.82	1.66			1.62	1.13			3.48	0.10			1.97	0.84		
Site 2	mean	2.21	2.04	n.a	-7.7	1.31	0.76	< 0.01	-42.0	4.03	1.42	< 0.01	-64.8	4.56	4.43	0.88	-2.9
	sd	1.03	2.23			0.45	0.36			0.80	0.81			1.67	0.88		
Site 3	mean	2.58	1.18	0.02	-54.3	1.03	0.72	0.18	-30.1	4.51	0.84	< 0.01	-81.4	5.28	6.02	0.60	14.0
	sd	0.87	0.48			0.77	0.41			0.94	0.37			1.80	1.46		
Site 4	mean	2.29	2.14	0.79	-6.6	0.83	0.55	< 0.01	-33.7	0.95	n.a	n.a	n.a	n.a	0.98	n.a	n.a
	sd	1.16	0.33			0.27	0.27			0.69	n.a			n.a	0.21		
Site 5	mean	1.44	0.96	n.a	-33.3	0.60	0.44	0.36	-26.7	3.39	0.83	0.05	-75.5	1.10	1.97	0.06	79.1
	sd	0.70	0.55			0.21	0.22			1.83	0.35			0.58	1.25		
Site 6	mean	0.79	0.79	0.99	0.0	0.48	0.66	0.08	37.5	9.28	0.95	n.a	-89.8	1.06	1.91	n.a	80.2
	sd	0.49	0.36			0.26	0.15			2.02	0.43			0.48	2		

Macro density		Flood1				Flood2				Flood1				Flood2			
ind/m2		before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%	before	after	t-test p	%
Site 1	mean	17341.7	7558.3	0.11	-56.4	7375.00	2966.67	0.06	-59.8	3350.0	75.0	0.04	-97.8	3566.7	875.0	0.29	-75.5
	sd	5953.1	1275.1			4314.15	2344.19			1239.2	109.0			3292.6	222.2		
Site 2	mean	2550.0	1241.7	0.47	-51.3	8250.00	2291.67	0.18	-72.2	10183.3	125.0	0.10	-98.8	825.0	925.0	0.84	12.1
	sd	1862.0	1204.5			3746.58	1327.91			6162.5	132.3			368.3	392.9		
Site 3	mean	3150.0	1633.3	0.09	-48.1	11791.67	1433.33	0.03	-87.8	3666.7	66.7	0.04	-98.2	558.3	425.0	0.77	-23.9
	sd	909.3	562.5			2843.45	1091.54			1454.6	38.2			470.6	238.5		
Site 4	mean	12725.0	4191.7	< 0.01	-67.1	7783.33	1316.67	0.09	-83.1	658.3	n.a	n.a	n.a	n.a	14425.0	n.a	n.a
	sd	2565.8	3028.6			3939.41	664.42			237.6	n.a			n.a	12004.4		
Site 5	mean	10816.7	2158.3	0.01	-80.0	5325.00	1633.33	0.19	-69.3	2816.7	41.7	0.18	-98.5	616.7	1416.7	0.33	129.7
	sd	2957.0	1530.8			2149.56	1239.29			2409.1	14.4			142.2	1218.9		
Site 6	mean	2758.3	1458.3	0.48	-47.1	541.67	300.00	0.36	-44.6	7033.3	141.7	0.09	-98.0	1266.7	7533.3	0.12	494.7
	sd	2139.9	650.2			152.75	229.13			4041.5	87.8			528.2	3645.2		

Synopsis and outlook

Synopsis

Flow and sediment interactions are complex, occurring across different spatial and temporal scales. This complexity is even more pronounced in regulated rivers, where flow and sediment regimes are highly modified, thus the interactions become more obscure. As a consequence, this interaction is one of the main challenges that rivers managers must handle nowadays when developing programs to fulfil ecological and societal requirements (Konrad *et al.*, 2011; Kondolf *et al.*, 2014; Wohl *et al.*, 2015).

This thesis investigated the influence of flow and sediment dynamics on ecosystem structure and function, focusing on Swiss managed rivers. The results presented here (Box 1), although reflecting the intricacy of flow-sediment interactions (FSR), revealed specific influences on certain processes and organisms, which may be useful for future consideration in research, management and restoration (Box 2).

Ecosystem structure and function, and the underpinning organisms, have been the primary research foci in the last decades in terms of their importance for ecosystem service provisions (Frainer *et al.*, 2014; Truchy *et al.*, 2015). Therefore, defining how they are affected by anthropogenic actions, as well as how FSR alterations can be mitigated, is a challenge towards preserving ecosystem services. In general, the specific processes and organisms studied in this thesis are linked to flow and sediment dynamics, thus significant changes in the components of FSR will alter relevant properties of ecosystems. For instance, a decrease in flood frequency can disrupt natural organic matter cycling, linked to temperature, flow and organic matter inputs (Petersen & Cummins, 1974; Tank *et al.*, 2010), which intensifies the degree of carbon processing and has general metabolic consequences (Aristi *et al.*, 2014). Similarly, river channelization alters organic matter processing by decreasing morphological diversity and reducing retention of allochthonous organic matter (Lepori *et al.*, 2005; Lorenz *et al.*, 2012). A primary result of this thesis was that the use of river restoration and experimental floods (i.e., chapters 1, 3, 4) are efficient tools to restore flow and morphological interactions, thereby recovering the role of disturbance in ecosystems as a main driver of organic matter processing, habitat heterogeneity, and macroinvertebrate composition.

Box 1: Summary of the main results of the thesis

*Chapter 1***:** Integrating ecosystem functional and structural variability into river restoration

- Lateral protection removal induces greater temporal variability in functional and structural indicators.
- Different ecosystem properties are affected differently by flow and sediment regimes; periphyton and macroinvertebrate density are mainly driven by flow, whereas sediment respiration and macroinvertebrate taxa richness are affected by flow-morphology interactions.
- Intra-annual flow variability is a key driver of flow-sediment interactions because it triggers morphological changes at the habitat scale.

*Chapter 2***:** Macroinvertebrate seedbanks of gravel bars in flow regulated rivers

- Gravel bars harbor both active and passive macroinvertebrate seedbanks.
- Density and taxa richness of seedbanks are driven by flow regulation and seasonality, although site-specific conditions are also important because they can influence historical assemblages.
- Hydropeaking and residual flow schemes greatly modify active and passive seedbank densities because they modify daily and seasonal water level fluctuations.

Chapter 3: Ecological assessment of a SBT on a receiving stream in Switzerland

- SBT operations have a negative influence on receiving waters, with maximum discharge and amount of sediment released being the main drivers of impacts.
- Despite the sudden and general decrease of sediment respiration, periphyton and macroinvertebrate density and richness, the system recovers relatively rapidly, suggesting that effects are similar to natural floods.
- Tributaries entering the system have a positive influence on the recovery of macroinvertebrate assemblages.

Chapter 4: Comparison of sediment-flow interactions in two rivers with contrasting flow management programs

- Sediment attributes of the streambed, and associated biotic properties, are determined by flow magnitude and sediment input.
- Lateral inputs of sediment generate morphological heterogeneity by interacting locally with flow, for relatively medium floods in particular.
- Large volume of sediment laden waters by SBT create an homogenization of the river decreasing most ecosystem indicators, the effects being mainly driven by magnitude and not by local conditions.

As seen in this thesis, flow and sediment dynamics not only affect streambeds but also adjacent areas, gravel bars and floodplains, which are home to a large number of species (Robinson *et al.*, 2002; Tockner *et al.*, 2006) and provide a number of ecosystem services, such as nutrient retention and removal (Naiman & Décamps, 1997; Ward *et al.*, 2002;

Shrestha *et al.*, 2012). My results showed that gravel bars are an important habitat for macroinvertebrate seedbanks and assemblage properties are affected by changes in flow regime (chapter 2). Although not tested in my study, flow alteration also has indirect consequences on macroinvertebrate seedbanks by modifying gravel bar morphology, for example by inducing gravel bar fixation by plants due to the lack of disturbance(i.e. residual flow) (Mürle *et al.*, 2003). Therefore, the interaction of flow and sediment is again crucial for understanding and managing river ecosystem dynamics.

Box 2: Implications for management practices

Chapter 1:Spatial temporal variability in river restoration

- Lateral protection removal re-activates flow-sediment interactions (i.e., morphological changes), which improve the natural heterogeneity of ecological processes and organisms.
- It is crucial to define restoration/management goals (i.e., specific ecosystem functions or organisms) in order to predict the influence of flow-sediment interactions.
- It is decisive to account for different temporal and spatial resolutions (i.e., intra and inter-annual flow, and habitat to reach scale) when monitoring/evaluating a restoration or management program.

Chapter 2: Macroinvertebrate seedbanks in gravel bars

- Gravel bars should be included in conservation/restoration plans, as they play an important role in river-riparian food web dynamics and macroinvertebrate community persistence.
- Hydropeaking and residual flow schemes must assess the impact of their activities on gravel bars, and, if necessary, implement mitigation actions to reduce impacts.

Chapter 3: Impacts of sediment bypass tunnels (SBT)

- SBT operations improve connectivity of water and sediment of dammed rivers, thus they can be incorporated in the adaptive management of flow-sediment regimes.
- Magnitude, timing and frequency of operations should match the natural characteristics of natural floods in each system to avoid negative ecological consequences.

Chapter 4: Flow-sediment interactions in flow management programs

- The interaction between flow and sediment must be included in river management, as they can influence the impact of floods on river processes and organisms.
- The presence of natural inputs, lateral sediments and flow, can maintain heterogeneity in the system.

Outlook

During this thesis, some new questions have arisen, which would require future consideration:

i) The influence of flow-sediment interactions on ecosystem structure and function is heterogeneous, differently and mutually affecting each specific process and organism. This fact, together with the increasing number of stressors in riverine landscapes (Tockner *et al.*, 2010), brings to light the need of additional studies for a more detailed assessment of how ecosystem processes are affected by the interaction of multiple stressors, including flow-sediment regime alterations, and how ecosystem service provisions are altered.

ii) Thus far, flow regime and its variability have been well described across different regions and climates (Poff *et al.*, 1997; Poff *et al.*, 2006). Similarly, some studies have described some of the main components of river sediment, such as the total outputs of main rivers (Holeman, 1968; Meade, 1996) or sediment transport (Scott *et al.*, 2010). However, and due to the lack of long-term data and the complexity of input, output, transport and storage along the river continuum (Vannote *et al.*, 1980), a suitable characterization of sediment regime variability is still needed. Some preliminary work is presented in Yarnell *et al.* (2015), where examples of interrelated flow and sediment processes are described, although more precise research is needed to expand the spatial scope of interactions to different geographic and climatic contexts. A complete classification of flow-sediment interactions in different types of rivers would be, therefore, a crucial tool for guiding managers towards the desired integration of sediment regimes into river management.

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