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Research article

Drawdown flushing of a hydroelectric reservoir on the Rhône River: Impacts on the fish community and implications for the sediment management

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ABSTRACT

Sediment flushings of hydropower reservoirs are commonly performed to maintain water resource uses and ecosystem services, but may have strong impacts on fish communities. Despite the worldwide scope of this issue, very few studies report quantitative *in situ* evaluations of these impacts. In June 2012, the drawdown flushing of the Verbois reservoir (Rhône River) was performed and subsequent impacts on the fish community were assessed, both inside the reservoir (fish densities by hydroacoustic surveys) and downstream (short-term movement and survival of radio tracked adult fish). Results showed that after the flushing fish acoustic density decreased by 57% in the reservoir, and no recolonization process was observed over the following 16 months. Downstream of the dam, the global apparent survival of fish to the flushing was estimated at 74%, but differed between species. The nine-year delay from the previous flushing and thus the amount of sediments to remove were too stressful for the low-resilience fish community of the Rhône River. Alternative flushing schedules are discussed to reduce these impacts.

1. Introduction

River fragmentation and regulation by damming are among the most severe human impacts on freshwater ecosystems worldwide (Dynesius and Nilsson, 1994). About 47% of world's large rivers (>1000 $m^3.s^{-1}$) are impacted by a cumulative upstream reservoir capacity which exceeds 2% of their annual flow (Lehner et al., 2011). Within these reservoirs, sediment trapping is one of the major issues managers have to face, with strong socio-economic and environmental outcomes (Owens et al., 2005). They have to maintain sedimentation at an acceptable level, and a common technical measure consists in releasing deposited sediment downstream (Kondolf et al., 2014).

Current hydropower development and the increasing number of dams raise severe questions about subsequent ecological impacts, especially concerning sediment flushing from reservoirs (Zarfl et al., 2015). Drawdown flushing involves eroding the deposited sediments and ensuring their transportation by flow through low-level gates of the dam (Kondolf et al., 2014). This requires the complete emptying of the reservoir to allow the resuspension of fine sediments and moving bedloads by increased flow erosivity, and finally a flow augmentation to flush away the sediment load. Suspended sediment concentrations (SSC) below dams can widely vary (Buermann et al., 1995; Brandt, 1999). When performed on a regular basis and synchronized with high flows, such an operation can be minimally harmful to the ecological functioning, with low mortalities and an ability to develop resilience in the downstream populations (Gutzmer et al., 2002; Owens et al., 2005). Conversely, when performed during base flow, the sediment load is generally excessive and causes substantial ecological impacts (Kondolf, 1995).

Many publications address the impacts of SSC on aquatic ecosystems, including fish (review by Kemp et al., 2011). Impacts on fish are various and may be direct, such as behavioural responses, metabolic changes, physiological and histological damages, or indirect through habitat modification. Impacts largely depend on the species and life stage through specific biological and ecological functional traits (Schwartz et al., 2011), but many other factors can interplay such as water temperature, the origin, composition and physical structure of sediment particles, presence of shelter, or the duration and intensity of the disturbance (Kemp et al., 2011).

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Because of these many sources of variation, predicting or empirically evaluating *in situ* biological responses to SSC is challenging. Newcombe and MacDonald (1991) combined the duration of exposure and concentration of the suspended sediment load to define a stress index, used as a proxy for the severity of the disturbance, while impacts on fish were categorized as behavioral, sub-lethal, or lethal. Accounting for taxonomy, fish size, life history and sediment particle size, Newcombe and Jensen (1996) showed that the 'severity of ill' effects (SEV) on fish depended on the concentration and duration of the disturbance. Salmonids are acknowledged to be more sensitive to SSC than other species such as cyprinids, and young fish are more sensitive than adults (Newcombe and Jensen, 1996; Crosa et al., 2010). Overall, most results come from laboratory experiments, and may not be realistic in nature. Also, investigations mainly focus on salmonid species due to their conservation or fisheries interest, while knowledge is much scarcer for other families. Despite the concern that management authorities, fishermen and environmentalists express about sediment flushings, their effects on fish communities in the field have as yet been poorly documented, especially inside reservoirs.

The aim of this paper is to evaluate the short and medium-term (*i.e.* up to 16 months) impacts on the fish community of a drawdown flushing of a hydropower reservoir, both upstream and downstream of the dam. Using an original combination of radio tracking and hydroacoustic approaches, we assessed the spatial-temporal changes in overall density of the fish community in the reservoir, and the behaviour and survival of the main common species of this river reach. We compared observed impacts to predicted ones using the SEV model (Newcombe and Jensen, 1996), and calculated expected impacts for past sediment flushings on the same reservoir. Results are discussed in the light of operational sediment management issues for hydropower reservoirs.

2. Methods

2.1. Study area

The study area was located on the Rhône River, 98,500 km^2 basin area, 812 km long, flow 1720 m^3.s^{-1} at its delta (Olivier et al., 2009), and focused on a 24 km long section from the outlet of Lake Geneva to the France-Switzerland border (Fig. 1). Three run-of-the-river hydropower dams have been erected along this section. The Seujet dam, which is at the outlet of Lake Geneva, regulates the lake level and the flow in the downstream Rhône River (annual mean flow = 251 m^3.s^{-1}). Approximately 15 km downstream, the Verbois dam is a 34 m high dam devoted to hydropower production. Its reservoir is 11.4 km in length, 13 Mm^3 storage capacity, and it has a mean width (±s.d.) of 116.2 m (±35.8 m) and a mean depth of 11.4 (±3.0 m) (Olivier et al., 2009). The Chancy-Pougny dam is located 7 km downstream of Verbois. It is 10.7 m high and its reservoir is 3.7 km long. At the time of the study, only the Seujet and Verbois dams were equipped with fish bypasses. Excluding reservoirs, lotic reaches are between 3 and 6 m in depth, depending on river bed morphology and flow regulation, and up to 114 m wide. The flow regime in this section of the Rhône River combines the water released from Lake Geneva through the Seujet dam and the water coming from the Arve River (mean flow = 79 m^3.s^{-1}; Fig. 1). This important tributary, characterized by a very high suspended sediment load, drains the Mont Blanc alpine massif and annually carries about 500,000 tons of flysch and molasse particles into the Rhône River (Bravard and Clémens, 2008), most of which are deposited in the Verbois reservoir. Two smaller tributaries (Allondon and Laire) flow into the Rhône River along the study area (Fig. 1). In these two rivers, pools were dug in gravel deposits at their mouths (65-m length and 1.5-m depth) prior to the flushing to provide fish refuge areas. The fish community in the study area is composed of 18 species, among which chub (*Squalius cephalus*), barbel (*Barbus barbus*), roach (*Rutilus rutilus*), European perch (*Perca fluviatilis*), and brown trout (*Salmo trutta)* are the most abundant (GREN, 2009). Little information is available about the composition and structure of the fish community in the reservoir, but limnophilic species such as tench (*Tinca tinca*), bream (*Abramis brama*), carp (*Cyprinus carpio*) or northern pike (*Esox lucius*) are present.

2.2. Verbois reservoir management and drawdown flushing operation

The Verbois reservoir was managed by means of triennial drawdown flushings from 1969 to 2003. Because of significant environmental impacts (e.g. water quality, fish behaviour and mortality, bird nesting perturbation: Roux, 1984; Hofmann et al., 2001; ECOTEC, 2003; GREN, 2003) and growing societal discontent, the next flushing was postponed to look for alternative, less harmful options, and was finally scheduled from 9 to 22 June 2012, with an estimated volume of 5.6 Mm^3 of trapped sediment (SIG and SFMCP, 2013a).

The flushing consisted of a three-step process. First, the reservoir was completely emptied from 9 to 12 June 2012, during which sediments were mainly swept away (Fig. 2). Second, from 11 to 15 June 2012, successive flow flushes were created by releasing water from the Seujet dam to remove more cohesive sediment benches. Third, the reservoir was refilled on 21 and 22 June 2012. Note that the water level remained low between 15 and 21 June (Fig. 2) because of heavy maintenance work. An estimated volume of 2.69 Mm^3 of deposited sediment was evacuated during this flushing (from bathymetric data, SIG and SFMCP, 2013a), the release lasting from 10 June at 03:50 to 21 June 2016 at 18:00. At the same time, a coordinated flushing operation was carried out at Chancy-Pougny dam. Reservoir water level was lowered from 9 to 10 June 2012, and maintained empty until 15 June 2012 to take advantage of flow flushes for eroding sediment in the Chancy-Pougny reservoir. Then, the Chancy-Pougny reservoir refilling was planned on 15 June 2012 as the expected sediment release beyond was negligible (SIG and SFMCP, 2013a).

2.3. Hydroacoustic data collection

Hydroacoustic surveys were performed on the Verbois reservoir using a zigzag sampling design on 33 consecutive transects, from one bank to the other, cruising at a speed of approximately 8 km.h^{-1} (Guillard and Vergès, 2007). The trajectory was determined before the study to obtain representative data according to Aglen (1983). The degree of coverage, defined as the ratio of the total length (km) of all transects over the square root of the reservoir area (km^2), equalled 8. A Simrad EK60 echosounder (SIMRAD, Oslo, Norway), 70 kHz, using a 256 ms pulse length (Godlewska et al., 2011) and pinging at 5 pings per second, was used to acquire data. The circular split-beam transducer, 11.16° × 11.46° at −3 dB, was fixed on the right side of a small aluminum boat, 0.30 m below the water surface and emitted vertically (Samedy et al., 2013). The transducer was linked to a computer with the Simrad ER60 software, connected to a GPS to record boat positions.

Two pre-flushing and nine post-flushing nocturnal hydroacoustic surveys were performed from May 2012 to October 2013 to determine the fish density evolution in the reservoir (Fig. 3). Acoustic data were analysed using Sonar 5-Pro software (v. 6.0.1; Balk and Lindem, 2011). Detection thresholds were set at −50 dB for individual targets, or 'Single Echo Detection' (*SED*), and at −56 dB for echo-integration in accordance with recommendations of standards (CEN, 2009; Parker-Stetter et al., 2009). These

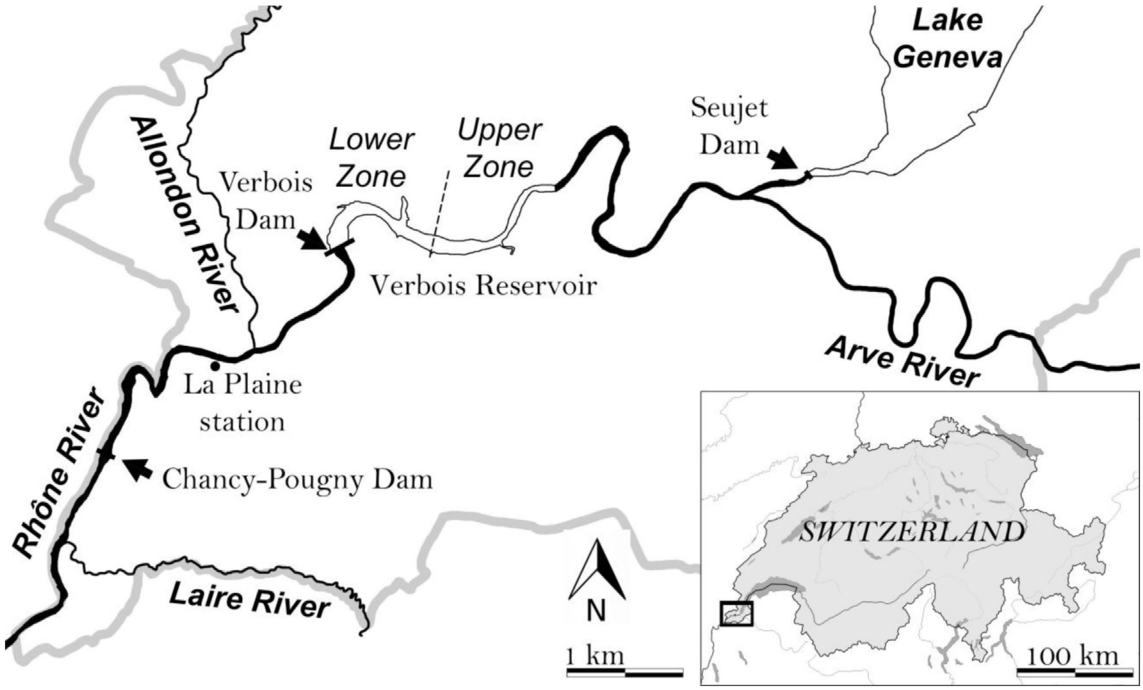

Fig. 1. Map of the study area. The acoustic sampling area (Verbois reservoir) is in white. Grey lines represent the French-Swiss border.

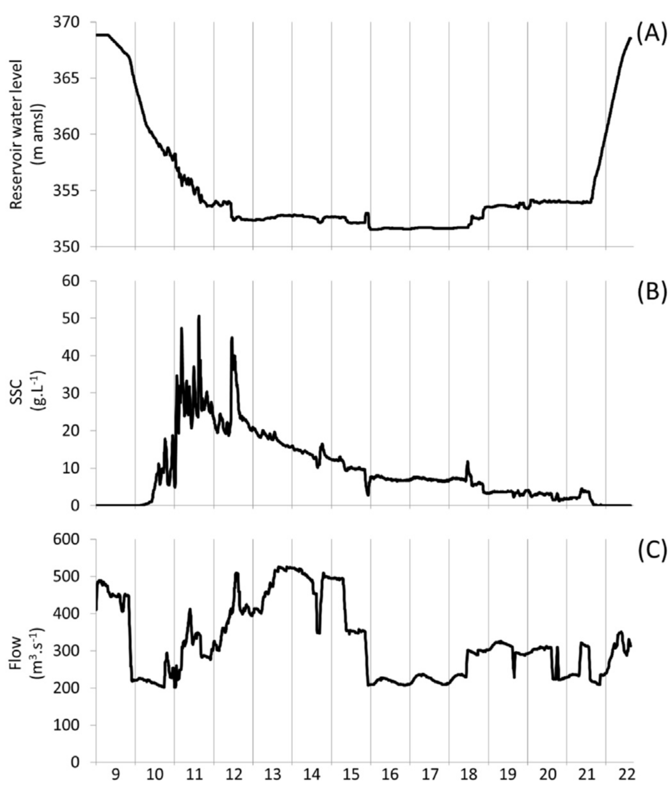

Fig. 2. Water level in the Verbois reservoir (A: m above mean sea level, measured at the Verbois dam), evolution of suspended sediment concentration SSC (B: $g.L^{-1}$, measured at La Plaine station), and Rhône River flow (C: $m^3.s^{-1}$, measured at the Verbois dam) during the flushing (from 9 to 22 June 2012; data: Services Industriels de Genève).

thresholds were chosen to limit the detected fish to a size of approximately 50 mm using Love's (1971) equation (Simmonds and MacLennan, 2005) and to avoid coarse suspended particles. A bottom 0.5-m layer was delimited to avoid including bottom detection in analyses and was accurately checked. All files were also checked for undesired non-fish echoes such as bubbles, macrophytes, debris, and buoys, which were deleted from the echograms (Emmrich et al., 2012). The upper 2-m layer of water was not included in analyses due to the blind area close to the sounder (Simmonds and MacLennan, 2005).

Due to its hydro-morphological configuration (depth, water velocity, available habitats for fish), the reservoir area was divided in two zones (Fig. 1). The 'lower zone', with 15 transects, covers the deepest part of the reservoir and is characterized by low velocities. The 'upper zone', covered by 18 transects, has shallower depths, velocities up to 0.5 $m.s^{-1}$ and provides reed macrohabitats along the banks.

Acoustic density values were expressed in S_A ($m^2.ha^{-1}$; MacLennan et al., 2002) as a proxy for fish density (Boswell et al., 2010) for each transect (sampling unit), and data were not transformed into biomass (Emmrich et al., 2012; Yule et al., 2013). To test whether the flushing modified fish density within the reservoir, the evolution of acoustic density values (S_A) was compared across surveys (both at the whole reservoir scale and detailed per zone) using the Kruskal-Wallis rank sum test to detect differences among surveys (nonparametric tests: data did not meet the hypotheses of normality and variance homogeneity even after data transformation). Consecutive pairs of surveys were compared with the Wilcoxon rank sum test to identify where differences occurred (with significance level corrected for multiple comparisons by the Bonferroni method 'α_i'). Acoustic body length classes were also analysed using Target Strength (*TS*, in dB; MacLennan et al., 2002) from *SED*. A transect was considered as the basic statistical unit when the number of *SED* was >30 targets, otherwise, consecutive transects were pooled. For each statistical unit, a mean *TS* calculated in the linear domain was estimated. Mean *TS* were compared

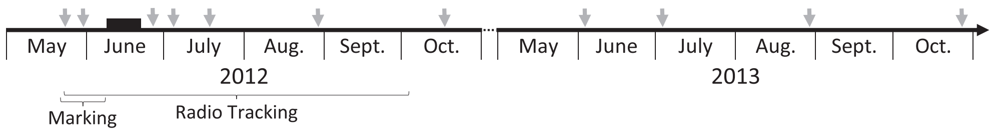

Fig. 3. Study schedule. The black area represents the flushing period. Grey arrows above time scale show time of hydroacoustic surveys. Brackets below the time scale represents the periods of marking operation and radio tracking sessions.

between surveys, for both the whole reservoir and by zone, using the Kruskal-Wallis and Wilcoxon rank sum tests to detect differences (with significance level corrected for multiple comparisons by the Bonferroni method 'α_i'). All analyses were performed with the R statistical software (version 2.15.1; R Development Core Team, 2008).

2.4. Radio tracking data collection

Radio tracking monitoring was approved by "*Direction Générale Nature et Paysage*" of Canton Geneva (Switzerland) to estimate individual fish movements and survival. Forty-nine adult fish were caught between 22 May and 7 June 2012 (Fig. 3), during three consecutive purges of the fish by-pass of the Verbois dam, the most effective way to catch targeted fish in this river. Fish were caught using dipnets as the water slowly receded after the feed-water valve had been closed. Two cyprinids (barbel, N = 23; chub, N = 16) and one salmonid (brown trout, N = 10), representative of the local Rhône River rheophilic fish fauna (GREN, 2009), were sampled. Fish were anesthetized in a solution of tricaïne MS-222 (100 mg.L^{-1}), weighed (mean individual weight ± s.d.: barbel = 846.5 ± 509.2 g, chub = 847.8 ± 392.3 g, trout = 600.7 ± 350.4 g) and measured (mean individual length ± s.d.: barbel = 427.3 ± 90.4 mm, chub = 387.4 ± 63.7 mm, trout = 402.3 ± 57.2 mm). They were tagged with an externally mounted radio-transmitter (F1970 model, 4.8 g in air, 15 ms pulse length, 148 MHz frequency range; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) fixed through the dorsal muscles under the dorsal fin (Bridger and Booth, 2003) in agreement with the 2% tag to body weight ratio (Winter 1996). External transmitters were used as most of the tagged fish (cyprinids) were in the spawning period, and surgical implantation can increase mortality of gravid females (Winter 1996; Bridger and Booth, 2003). Tags were equipped with an activity switch that transmitted at different pulse rates depending on whether the fish displayed swimming activity or remained motionless. Fish were released on the same day after fully recovered equilibrium and spontaneous swimming activity.

Most of the tagged fish (N = 35: 13 barbels, 12 chubs and all 10 trout) were released downstream of the dam to evaluate movement and survival when sustaining SSC from flushing. However, a sub-sample of tagged fish (N = 14: 10 barbels and 4 chubs) was released upstream of the dam, at the exit of the fish by-pass, to supplement the hydroacoustic surveys by describing the movement, survival and drift of fish present in the reservoir during the flushing. No fish was released into the fish by-pass as it was closed during the flushing operation.

Fish were tracked all along the study area (Fig. 1), from Seujet dam to Swiss-French border on the Rhône River and the last 2.7-km section of Arve River at its mouth. Tracking was performed during daylight using an R2000 receiver with a three-element folding Yagi antenna (Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) and located with an evaluated accuracy of 100 m. Tracking sessions were performed from 25 May to 29 August 2012, once a week until end of June and every two weeks thereafter (Fig. 3). Tracking was intensified during the first days of the flushing, from 8 to 13 June 2012, to daily locate individuals. A late tracking was performed on 2 October 2012 to ensure a final status to motionless fish.

From individual positions of fish downstream of the Verbois dam, the mean distance to the dam was estimated per species for each tracking session. Cormack-Jolly-Seber mark-recapture models (Lebreton et al., 1992) were also fitted to estimate daily survival rates during the reservoir flushing. Both the species and the tracking session effects were tested on apparent survival rates (Φ) and capture probabilities (p) by comparing the corrected Akaike Informative Criterion (AICc, for small samples) on all nested models from the Species x Session effects interaction to the null model (constant). Daily survival rates were estimated from the best-adjusted model considering the lowest AICc ($\Delta_{AICc} > 2$; Burnham and Anderson, 2002). Models were computed using the MARK software (version 6.1; White and Burnham, 1999). At the end of the flushing, an overall apparent survival rate Φ_{SO} was estimated per species from fish still displaying swimming activity or upstream movement over all fish still tracked at the beginning of the reservoir flushing.

To determine whether tributaries could serve as refuges for fish during the flushing, two fixed detection stations (R4500 datalogger/receiver, Advanced Telemetry Systems Inc., Isanti, Minnesota, USA) were installed at the mouth of the Allondon and Laire rivers (Fig. 1). They were connected to submerged antennas (20 cm long bare coaxial cable) to detect any tagged fish entering the tributaries. A third datalogger coupled to an omnidirectional magnetic mount antenna was positioned in the downstream part of the fish by-pass of the Verbois dam to detect any fish coming close to it. The three stations were supplied with 12-V batteries and recorded fish detection from 1 June to 28 August 2012.

2.5. Estimation of 'severity of ill effect'

The Newcombe and Jensen (1996) 'severity of ill effect' (SEV) model, used as a proxy for the severity of the disturbance, enabled us to compare the predicted effects by the model with empirical estimates obtained during the present flushing, and to compare with predicted effects for previous flushings, from 1987 to 2003. The model combines the exposure duration *ED* (in hours) and the intensity of the sediment load (*SSC*; mean concentration in mg.L^{-1}) to define a stress index SEV:

$$SEV = a + b \times \ln(ED) + c \times \ln(SSC)$$

where a, b and c are regression coefficients estimated by Newcombe and Jensen (1996). Impacts on fish were categorized as behavioural, sub-lethal, or lethal according to the SEV value. The severity of ill effect was calculated by considering the whole period of sediment release due to the drawdown flushing operation. SSC were measured at La Plaine station, downstream of the Allondon river mouth, by the "*Services Industriels de Genève*" (Fig. 1). Due to its weak discharge compared to the Rhône River during the drawdown flushing (respectively 2.31 m^3.s^{-1} vs. 330.35 m^3.s^{-1}), the Allondon River did not significantly bias the SSC measures. For barbel and chub, SEV was calculated using Model 6 (adult freshwater non-salmonids), while Model 2 was used for trout (adult freshwater salmonids; Newcombe and Jensen, 1996). Effects were predicted using the Newcombe and Jensen (1996) scale of the severity of ill effects.

3. Results

3.1. Acoustic density in the reservoir

The acoustic density S_A significantly changed across the eleven surveys (K = 54.1 df = 10, P < 0.0001). Immediately before and after the flushing, the two surveys showed a significant drop of 57.0% in S_A over the whole reservoir (W = 521, P < 0.0001; Fig. 4). The acoustic density S_A dropped by 66.8% in the lower zone (W = 210, P < 0.0001), but no significant difference was detected in the upper zone (W = 80, P = 0.0047 > α_i), even though the mean S_A value decreased by 43.3% (Table 1). Out of the flushing period, no statistical difference was detected across surveys. Between the two pre-flushing surveys, S_A did not differ (W = 62, P = 0.0141 > α_i). Similarly, S_A remained low and stable all along the post-flushing period (Wilcoxon rank sum tests: P > α_i; Fig. 4). Considering all the post-flushing surveys, acoustic densities S_A in 2012 and 2013 remained significantly lower than before the flushing, both for the upper (2012: W = 690.5, P = 0.0014; 2013: W = 356, P = 0.0002) and lower zones (2012: W = 822, P < 0.0001; 2013: W = 640.5, P < 0.0001; Table 1).

In parallel, mean *TS* did not differ among pre- and post-flushing surveys over the whole reservoir (Wilcoxon rank sum tests: P > α_i).

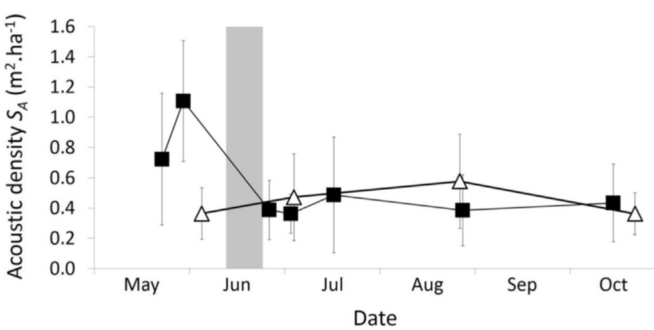

Fig. 4. Evolution of acoustic fish density S_A (m^2.ha^{-1}; mean ± s.d.) on the whole Verbois reservoir for 2012 (black squares) and 2013 surveys (white triangles). Grey rectangle represents the flushing operation (in 2012).

3.2. Fish survival and movements

Among the 49 radio tagged fish, 42 were still present in the study area by 8 June and were detected at least once thereafter: 22 barbels (out of 23 initially tagged), 15 chubs (out of 16 initially tagged) and only 5 trout (out of 10 initially tagged). Due to their low number, trout have been treated apart in the results. For cyprinids, the detection probability by mobile tracking was high throughout the study (mean capture probability *p* during flushing ± s.d.: 0.823 ± 0.029, range: 0.665 to 0.965).

3.2.1. Cyprinids movement patterns

Among the 14 cyprinids released upstream of the dam, 13 were monitored during the study, and displayed three types of movements. Three individuals remained in the upper part of the reservoir until the end of flushing and were lost after the refilling of the reservoir. Two individuals moved further upstream despite the very low reservoir level, travelling 13.4 km (chub) and 12.9 km (barbel) from their release position. Seven fish moved downstream of the dam during the first days of flushing, and they were then pooled with the group below the dam for analyses. Finally, a barbel disappeared at the beginning of the flushing and was never detected again.

Out of the 25 fish released downstream of the dam, 24 were detected at the beginning of the study. All cyprinids remained upstream from the Chancy-Pougny dam through the study, with the exception of two individuals found dead just downstream of the dam. During the flushing, a global downstream movement was observed for both species. Barbels moved downstream on average by 1041 m (mean distance to the dam ± s.d.: 1996 ± 949 m), while

Table 1
Estimates of S_A (m^2.ha^{-1}; number of transects, mean ± s.d., and coefficient of variation C_V) on the upper and lower zones of the Verbois reservoir for each hydroacoustic survey.

	Upper zone			Lower zone		
[a]Survey time	*n*	S_A (m^2.ha^{-1})	C_V	*n*	S_A (m^2.ha^{-1})	C_V
23.05.2012	8	1.05 ± 0.39	0.37	9	0.43 ± 0.21	0.48
30.05.2012	5	1.02 ± 0.37	0.37	10	1.15 ± 0.42	0.37
27.06.2012	7	0.59 ± 0.18	0.31	12	0.27 ± 0.06	0.23
04.07.2012	17	-	-	12	0.36 ± 0.13	0.36
18.07.2012	17	0.57 ± 0.38	0.67	4	0.14 ± 0.07	0.47
29.08.2012	10	0.46 ± 0.27	0.58	10	0.31 ± 0.18	0.59
17.10.2012	17	0.45 ± 0.20	0.44	14	0.42 ± 0.32	0.77
[b]05.06.2013	*1*	*0.20*	-	6	0.39 ± 0.17	0.44
04.07.2013	14	0.64 ± 0.28	0.43	12	0.28 ± 0.15	0.53
28.08.2013	9	0.73 ± 0.39	0.54	12	0.47 ± 0.19	0.40
24.10.2013	8	0.36 ± 0.13	0.41	13	0.36 ± 0.15	0.41

[a] Dotted line represents the flushing operation.

[b] S_A values for upper zone is based on a single value (n = 1), thus no statistical comparison was performed.

chubs moved downstream on average by 1451 m (mean distance to the dam ± s.d.: 3322 ± 1673 m; Fig. 5). The largest downstream movement was observed on 11 June 2012 (drifting speed: 814 ± 710 m.day^{-1} for barbels, 789 ± 873 m.day^{-1} for chubs) for both species, corresponding to the day with the highest mean SSC. Later, individuals from both species held a steady position until the end of the flushing.

3.2.2. Cyprinids use of tributaries

Cyprinids were detected inside the Allondon tributary during the reservoir flushing. Two barbels and four chubs were detected by the fixed station and were continuously recorded between 2 and 8 days inside the stream. The mobile tracking revealed that all 6 individuals stayed either inside or in the immediate vicinity of the stream all along the flushing. No Cyprinid was detected entering the Laire tributary.

3.2.3. Cyprinids survival rate

By the end of the flushing (20 June), 29 individuals of the 37 present at the launch of operation were still displaying swimming activity, representing a global apparent survival rate Φ_{SO} of 78.4%, including both species (Table 2). Among the 8 remaining fish, two remained motionless until the end of the tracking and 6 were lost during the flushing and never detected again. Per species apparent

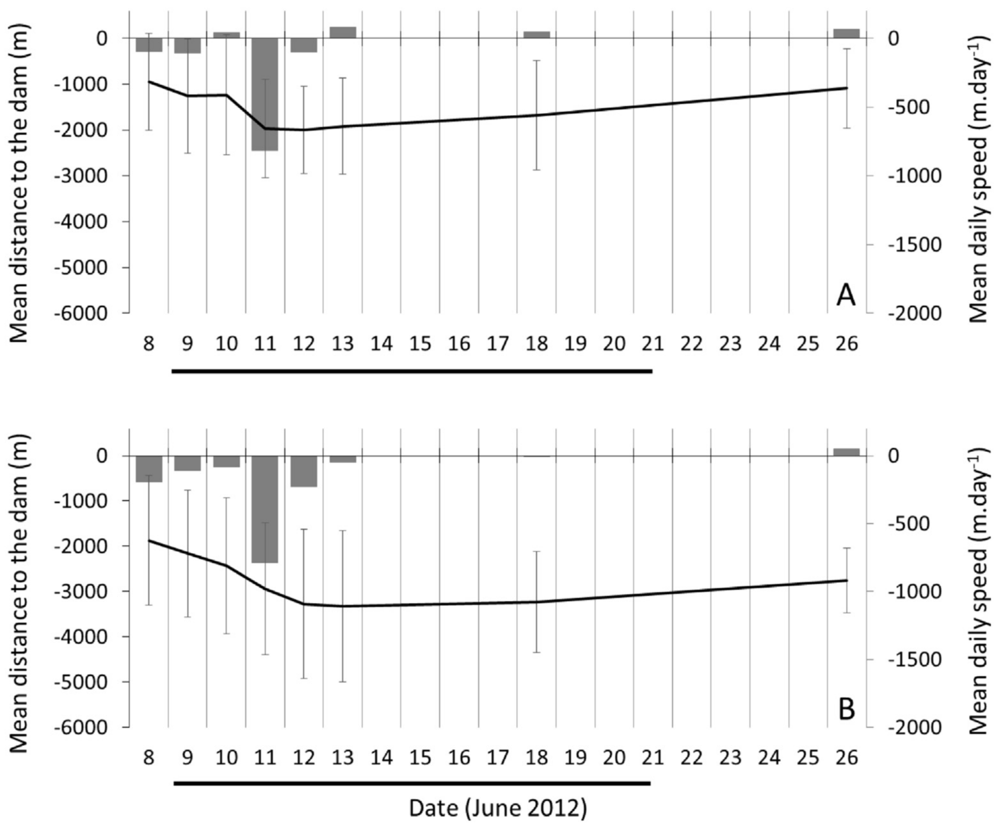

Fig. 5. Evolution of mean distance (m ± s.d.; black line) of radio tagged fish downstream of the dam and mean daily speed (m.day^{-1}; grey bars) per species (A: *Barbus barbus*; B: *Squalius cephalus*) during the flushing and shortly after (from 8 June 2012 to 26 June 2012). Flushing period is represented by horizontal line below the dates.

Table 2
Number (N) and percentage of radio tracked individuals following their status (displaying swimming activity, motionless, and lost) at the end of the reservoir flushing (June 20th) for each species and group.

	N tracked	Number of radio tracked individuals			Percentage of radio tracked individuals		
		Active	Motionless	Lost	Active	Motionless	Lost
Barbus barbus							
Downstream	13	10	2	1	76.9	15.4	7.7
Upstream	5	4	0	1	80.0	0.0	20.0
Up. to down.	4	3	0	1	75.0	0.0	25.0
TOTAL	22	17	2	3	77.3	9.1	13.6
Squalius cephalus							
Downstream	11	8	0	3	72.7	0.0	27.3
Upstream	1	1	0	0	100.0	0.0	0.0
Up. to down.	3	3	0	0	100.0	0.0	0.0
TOTAL	15	12	0	3	80.0	0.0	20.0
Salmo trutta							
Downstream	5	2	0	3	40.0	0.0	60.0
All species							
TOTAL	42	31	2	9	73.8	4.8	21.4

Table 3
Estimates of severity of ill effect (Newcombe and Jensen, 1996) for fish exposure to suspended sediment in the historical events of Verbois reservoir flushings from 1987 to 2012 (data: Services Industriels de Genève), per species family (with corresponding SEV model number from Newcombe and Jensen, 1996).

Year of reservoir flushing	Parameters		Severity of ill effect	
	Exposure (h)	Mean concentration of suspended sediment (g.L^{-1})	Salmonids Adults (model 2)	Non-salmonids Adults (model 6)
1987	81	4.37	10.1	9.6
1990	80	8.06	10.6	9.8
1993	105	6.87	10.6	9.9
1997	70	9.37	10.6	9.7
2000	78	7.16	10.5	9.7
2003	97	5.00	10.3	9.8
2012	278	11.00	11.4	10.7

survival rates Φ_{SO} were 77.3% for barbel and 80.0% for chub (Table 2). Out of the four barbels and three chubs that drifted through the dam during the first days of the flushing, all but one barbel were still displaying swimming activity on 20 June (Table 2).

Using AICc selection, only the time effect was retained for both survival and capture probabilities, without difference between species (*Φ(time).p(time)* model: $\Delta_{AICc} = 3.006$ over *Φ(null).p(time)* model). Before the flushing, the daily survival rate Φ was estimated at 1.000. A significant decrease in the daily survival rate was observed only during the first three days of the flushing (9 June: 0.992 ± 0.039, 10 June: 0.923 ± 0.060, 11 June: 0.957 ± 0.043). Thereafter, the daily survival rate returned to 1.000 and remained constant.

3.2.4. Case of trout

Out of the 10 trout released, all but two disappeared from the study area before the flushing (N = 5) or on the first days of operation (N = 3; Table 2). Among these, one individual was lastly detected by 10 June at the Laire confluence for a few hours and then disappeared. The two individuals that remained in the study area displayed swimming activity at the end of the flushing or beyond, representing an apparent survival rate Φ_{SO} of 40.0% (Table 2). The first one drifted downstream by 3341 m between 9 and 11 June and maintained its position afterwards. The second one was never detected by radio tracking but reappeared after the flushing at the fixed detection station below the Verbois dam from 6 to 31 July 2012.

3.3. Estimation of 'severity of ill effect'

During the drawdown flushing, which lasted 278 h (from 10 June 2012, 03:50 to 21 June 2012, 18:00), the mean SSC released was 11.00 g.L^{-1}. Severity of ill effect models estimated SEV values of 11.4 and 10.7 for models 2 and 6 respectively (Table 3). SEV of 11 and 12 predict lethal effects, with 20–40% and 40–60% mortality, respectively (Newcombe and MacDonald, 1991; Newcombe and Jensen, 1996).

In comparison, for the previous flushings between 1987 and 2003, the high SSC levels lasted from 70 to 105 h, with mean sediment concentrations ranging from 4.37 to 9.37 g.L^{-1}. SEV values were estimated between 10.1 and 10.6 for model 2 and between 9.6 and 9.9 for model 6 (Table 3), predicting paralethal and lethal effects, from delayed hatching, reduced fish density and growth rate, increased predation or severe habitat degradation to 0–20% mortality.

4. Discussion

Our study highlighted that a drawdown flushing has substantial impacts on the fish density inside the reservoir, mostly because of drift, and that such impacts could be long-lasting due to the low resilience of the community. Downstream, high SSC led to a decrease in the apparent survival rates of fish and induced significant downstream movements.

4.1. Methodological issues

For such a large ecosystem, no standard methodology is available to evaluate the impacts of a flushing on fish. Hydroacoustics and radio tracking are widely accepted methods to study freshwater fish populations (Murphy and Willis, 1996). Hydroacoustics are mostly performed in marine environments (Simmonds and MacLennnan, 2005), deep lakes (Taylor et al., 2005) and estuaries (Guillard et al., 2012; Samedy et al., 2013). Applying this method to a reservoir was challenging due to the hydraulic and sedimentary conditions (lotic sections upstream, high load of suspended matter, drifting inorganic and woody debris, air bubbles, etc.). We overcame this problem by meticulously checking the data, using detection thresholds in accordance to fish size, and performing night rather than day surveys, as fish leave the substratum for the water column, shoals break up, and individuals are distributed more homogeneously (Kubecka and Duncan, 1998; Drastik et al., 2009). In accordance to Aglen (1983) the degree of coverage was higher than 6, and comparable to hydroacoustic studies in similar environment (from 3.1: Emmrich et al., 2012; to 12.3: Guillard and Vergès, 2007). Furthermore, subsequent surveys did not reveal statistical differences (unpublished data), suggesting that data acquired in this study were representative. Radio tracking is a powerful method to assess fish movement (Baras, 1997; Ovidio et al., 2004), but it is strongly dependent on water depth, which may limit the probability of detection in reservoirs. In spite of this, the recapture probability and the number of monitored fish remained high throughout the study.

A BACI (Before-After-Control-Impact; Underwood, 1992) sampling design would have been more robust to unravel the impacts of sediment flushing from natural fish density variations. Unfortunately, relevant control sites are not easy to find, and we were not able to perform more temporal surveys before the flushing. We consequently used short time intervals between surveys and sampled immediately before and after the flushing for hydroacoustics, whereas radio tracking was intensified until monitoring daily movements. In the absence of any major disturbance, the fish density in the reservoir was not expected to vary drastically among seasons, except at the end of summer when the 0+ year class fish reach a size which can be sampled, as shown in a reservoir of the Rhône River (Fruget et al., 1999). Here however, we omitted targets whose size was < 50 mm, so we did not sample the 0+ year class. Therefore, the changes noticed in the fish community, as well as many field observations of numerous dead fish along the river margins downstream of the Verbois dam (unpublished data), were much more consistent with the effects of the flushing than with natural seasonal variations. Thus, despite these methodological limitations, the coupling of both methods and the sampling design used provided a body of evidence that converge all to the conclusion that the flushing impacted the fish community.

4.2. Fish density of the reservoir

The flushing severely affected the fish community within the reservoir, with a higher magnitude in the lower zone near the dam: while the overall acoustic density decreased by 57% in the whole reservoir, the drop reached 67% in the lower zone. Comparing total fish catches by net sampling before and immediately after the 1990 flushing in the Verbois reservoir, Hofmann et al. (2001) observed a similar loss in fish density, imputed to fish drifting during the emptying of the reservoir. The decrease in fish density detected in the present study was probably the result of individual drifts due to high water velocities, SSC, and reduction of habitat volume, as suggested by observations of radio tagged fish going through the dam gates during the first days of the flushing. Indeed, abrupt changes of reservoir water level occurred during the lowering phase, probably leading to very strong currents close to the dam. In the first 24 h, the reservoir water level dropped by 8.17 m, including a 6.15 m drop over an 11-hours period from 9 to 10 June 2012 (Fig. 2). Fish from the upper zone of the reservoir encountered milder and more progressive water velocities, less fluctuation in water levels and lower SSC (SIG and SFMCP, 2013a), which allowed them to remain in the main channel or to find shelter close to the substrate or banks. Indeed, the radio tracking survey showed that some individuals maintained their position in the upper zone, or even kept moving upstream. The upper zone community is likely more rheophilic than in the lower zone, with most species better able to cope with changing water velocities and depths, as noted by Richeux et al. (1994) at the queue of the Pareloup reservoir (France) during the 1993 flushing. Concerning the fish community size structure, we could have expected an under-representation of small individuals after the flushing as they are less likely to resist the strong currents and reservoir lowering. However, no change was observed on mean body length of fish (mean *TS*). This suggests that the methodological limitations and the acoustic detection thresholds, excluding from the analysis the fish < 50 mm, could imply that some variations remained undetected. Otherwise, the flushing may have indeed impacted indifferently the whole community structure.

To our knowledge, only one study considered the recolonization process of a reservoir after a flushing (Hofmann et al., 2001). Here, we showed that the resilience of the Verbois reservoir's fish community is weak, as no increase in the density was observed 16 months after the flushing. This result disagreed with Hofmann et al. (2001), who reported on the same reservoir a rapid recovery (≈3 months) of the fish community after the year 2000 flushing. The recolonizing process can originate either from upstream, from Lake Geneva and the Arve River, or from downstream of the dam through the fish pass. However, this fish pass has a poor efficiency, and only a small number of fish per year uses it (ECOTEC, 2010). The Seujet dam at the outlet of Lake Geneva probably also impeded the recolonization process. Overall, our results stress that connectivity along the river continuum, including lake-river and tributary-main channel connections, is of key importance in the recovery from a disturbance.

4.3. Fish survival and movement

For the three species, the apparent survival at the end of the flushing was 74%, but differed between species. Brown trout seemed to be the most sensitive species, but we cannot exclude the hypothesis that the lost fish either moved far downstream or remained sheltered in deep pools all through the study. One trout initially considered as lost reappeared in July below the Verbois dam, and half of the tagged trout disappeared before the onset of the flushing, thus strongly limiting the analyses and conclusions about this species. Post-tagging impacts on fish movements or migration are still poorly understood, while dedicated studies generally focused on physiological effects, tag retention rates and mortality (Jepsen et al., 2015). If lost fish effectively died after the tagging, they would have been probably detected motionless in the study area. Broell et al. (2016) observed in shortnose sturgeon *Acipenser brevirostrum* that some individuals rested on the river bottom and displayed lower tail beat frequencies (lower swimming activity). Thorstad et al. (2014) showed that adult sea (brown) trout (*Salmo trutta)* tagged with external radio transmitter may be impacted by the size of the transmitter, with a shorter upstream spawning migration distances, but did not detect any post-tagging downstream movement.

The estimated daily survival rate of cyprinids fell during the first three days of the flushing, when SSC was the highest. The magnitude of the impact depends on multiple factors, including species and life-stage, composition, particle size, concentration and duration of sediment releases, presence of pollutants or other stressors, and availability of refuges (Bash et al., 2001; Kemp et al., 2011). A better tolerance to SSC can be expected for cyprinids, but little is known for this family, and there may be substantial differences between species (Sutherland and Meyer, 2007; Gray et al., 2014). Elevated SSC are widely known to potentially induce lethal effects (e.g., Hesse and Newcomb, 1982; Roux, 1984; Garric et al., 1990), but *in situ* quantitative estimates of fish survival are rarely achieved.

Crosa et al. (2010) estimated a loss of 40–70% in brown trout densities following the flushing of an alpine reservoir where the mean SSC was < 5 g.L^{-1} (max: 70–80 g.L^{-1}). Similarly, Espa et al. (2016) reported trout density drops of 15–50% in downstream sections of the Cancano reservoir after a flushing operation. After a 6-h exposure to a SSC of 82 g.L^{-1}, Newcombe and MacDonald (1991) observed 60% mortality in rainbow trout individuals.

Under the assumption that the apparent survival estimated in the present study is representative of a 'true survival', the estimated percentages of fish still displaying swimming activity after the flushing operations were consistent with predictions of Newcombe and Jensen's (1996) models, similarly to other studies (Bergstedt and Bergersen, 1997; Crosa et al., 2010). For the present drawdown flushing, their models predicted lethal effects from 20% to 60% mortality depending on the species (non-salmonids vs. salmonids). The potential mortality estimated in the present study, but clearly observed all along the study area during the flushing (numerous dead fish downstream of the dams, unpublished data), may be due to reduced oxygen acquisition with increased SSC (Bruton, 1985). Indeed Garric et al. (1990) concluded that the worst impacts on brown trout survival were due to a synergistic effect between a high SSC and a low oxygen concentration. In our case, the oxygen concentration remained close to saturation (> 7 mg.L^{-1}) throughout the flushing (SIG and SFMCP, 2013b). However, we can infer that the SSC was so high that fish could not draw enough oxygen from the water, as particles may coat the respiratory epithelia and infiltrate between gills, impeding gas exchange and inducing hypoxia and asphyxia (Martens and Servizi, 1993; Wilber and Clarke, 2001).

Apparent survival rates provided for the present drawdown flushing represented a short-term survival. However, a delayed, longer-term mortality cannot be excluded. Physical damage to gills can indeed lower an individual's resistance to disease and parasites, due to increased metabolic costs and physiological stress (Redding et al., 1987; Sutherland and Meyer, 2007). Loss of trophic resource as the benthic invertebrate fauna (Kefford et al., 2010), reduced food uptake and growth (Sweka and Hartman, 2001; Michel et al., 2013), as well as lower tolerance to toxicants (Lloyd, 1987) may also have implications on a longer time scale.

Finally, it is worth mentioning that the transmitter weight excluded the monitoring of small individuals (yearlings and juveniles). Moreover, the sampling in the fish pass possibly selected only those individuals best capable of swimming and ascending the river. Thus, the true survival rate for the whole community could be much lower than the one presently estimated (Roux, 1984; Crosa et al., 2010).

A drifting behaviour was observed for both barbel and chub from the onset of the flushing. Both species migrate upstream at this time of year to reach suitable spawning grounds (Fredrich et al., 2003; Ovidio et al., 2007), as observed annually on the Rhône River and reported by the fish bypass monitoring (ECOTEC, 2010). Hence such downstream movements are naturally unexpected and can be directly related to the flushing. Downstream movements were nonetheless limited, as fish moved on average 1.5 km. A 4.8 km downstream displacement was observed for salmonids following a sluicing in the Wind River, Wyoming (Bergstedt and Bergersen, 1997). Increasing SSC can cause an avoidance response, with fish drifting until they find more suitable areas. Such avoidance is commonly observed in experimental designs (Robertson et al., 2007). In natural streams with sediments diffusing all across the wetted section, fish may be more prone to move downstream and toward the river banks where SSC may be slightly lower than in the main channel (A. Poirel, Electricité de France, personal communication). Observations of fish rapidly moving either into the Allondon tributary or in its immediate vicinity at the onset of the SSC increase may reveal the importance of tributaries for local populations in the face of such a disturbance. Their role as refuges has been already largely discussed (Niemi et al., 1990), and some studies empirically demonstrated their use by fish mainly during extreme flooding (Koizumi et al., 2013) or drought (Davey and Kelly, 2007). Here, the Allondon provided clear water and hydraulically quiet habitats, thus allowing a more rapid recovery of the fish from elevated SSC (Niemi et al., 1990).

4.4. Implications for sediment management

Habitat template-based theories (Southwood, 1988; Townsend and Hildrew, 1994) suggest that biological and demographic traits of species are key elements to predict their population dynamics and resilience facing such disturbances. Disturbances are associated to temporal heterogeneity and are characterized by their severity, most often their magnitude, frequency, and/or predictability (Poff and Ward, 1990). Thus, apart from the technical and operational issues managers have to cope with, the sediment management dilemma for the ecosystem health is quite simple in its formulation: is it better to perform i) small but frequent flushings, or ii) large but infrequent ones? The first strategy involves shorter duration flushing and releases lower mean and maximum SSC values. The second one is of longer duration and releases higher mean and maximum SSC values. In the present paper, the SEV model predictions (Newcombe and Jensen, 1996) for the 2012 flushing implied high rates of mortality for all species, which were confirmed by empirical estimates and direct observations of dead fish. By comparison, SEV values for previous flushings suggested that small but frequent triennial flushings would moderately mitigate the impacts on adult fish, and should therefore be preferred.

Such an approach may be too simplistic in the case of management operations that are planned recurrently, and that can alter the structure of the community over the long-term. SEV models predict a global impact for a single disturbance event, and does not account for species differential resistance and resilience. Over a long period of time, one can speculate on whether a population is less affected by frequent disturbances of low magnitude that occur several times during the lifetime of a species, or by high magnitude events encountered only exceptionally during their lifetime. This very likely will depend on specific traits such as fecundity, age at maturity, lifetime, survival rates, mobility, or demographic structure, as well as on competitive interactions with co-occurring species (Townsend and Hildrew, 1994; Syms and Jones, 2000). Roux (1984) suggested that community change due to the decline in salmonid (brown trout and European grayling *Thymallus thymallus*) abundances and proportions in the Upper-Rhône River could partly be attributed to the successive Verbois reservoir flushings because of a shorter life cycle and a higher sensitivity of salmonids to SSC than cyprinids. A better quantitative assessment of SSC on population abundances is a prerequisite for further studies, and a coupling with population dynamics models would constitute a step towards a better understanding of SSC impacts on fish. It is worth noting that despite extensive reviews about the impacts of SSC on river biota and habitats, this particular issue of the most 'ecologically friendly' sediment release practice has been poorly addressed in the literature (Espa et al., 2015).

5. Conclusion

The increasing number of dams along watercourses worldwide and their management have become a challenge for the preservation of riverine ecosystems. However, outcomes of sediment management operations on river biota are rarely *in situ* evaluated. Here, we show that a drawdown flushing of a large reservoir on the Rhône River resulted in a decline in fish densities inside the reservoir and may have induced up to 60% overall apparent mortality of adult individuals, depending on the species. The high degree of fragmentation of the river continuum appears to be an aggravating factor, which may explain the low resilience of the fish community. Finally, a clear limitation of the scientific knowledge is the scaling up of observed results across biological (from the individuals and reservoir community to the whole ecosystem), spatial (from the study area to the watershed; Montgomery and Buffington, 1998), and temporal scales (from the immediate post-flushing effects to the long-term evolution of community structure). No doubt that the way towards less harmful and more sustainable fine sediment management strategies should assess the impacts on multiple-scales.

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